

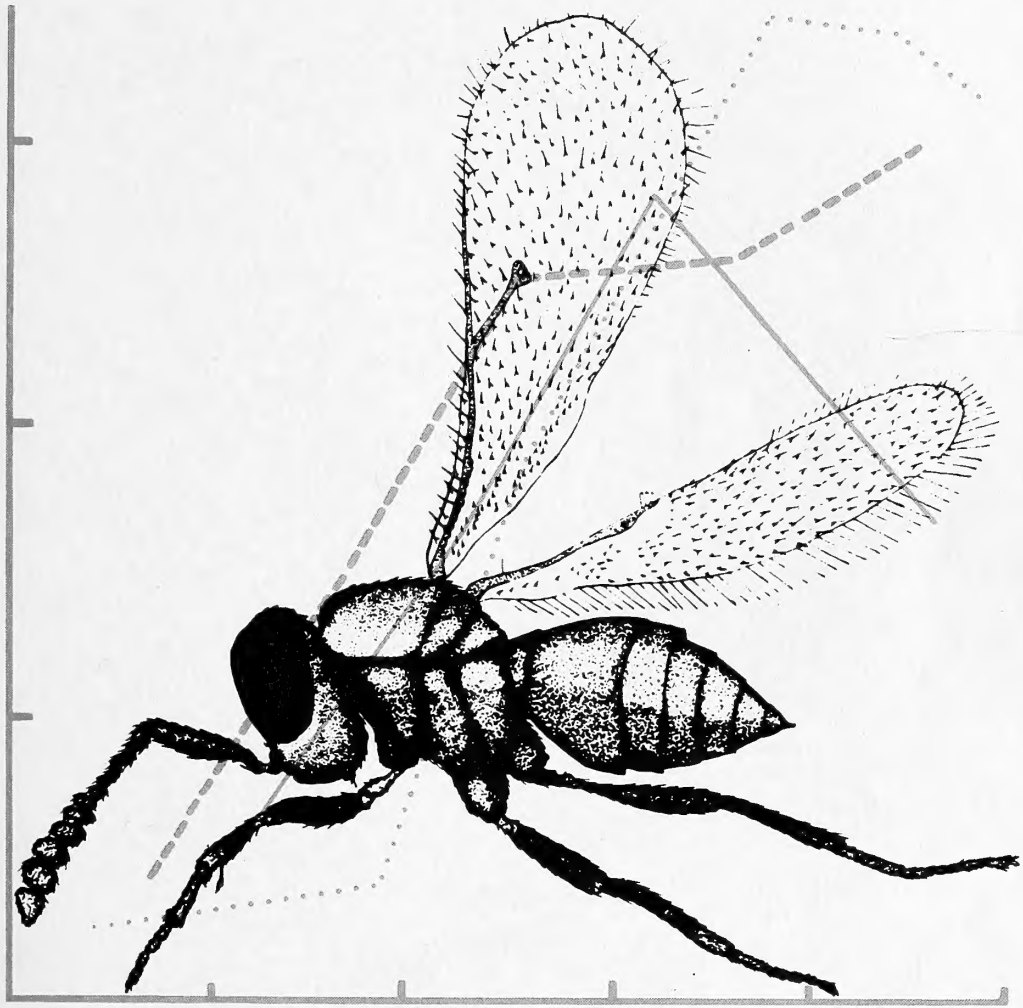
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Current Topics in Forest Entomology

Selected Papers from the XVth International Congress of Entomology
Washington, D.C., August 1976



United States Department of Agriculture
Forest Service

General Technical Report WO-8
February 1979

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W.E. Waters, Editor
(University of California, Berkeley, California)

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Certain pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife -- if they are not handled properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticide containers.

PREFACE

The papers in this volume represent a special selection of those presented in the technical sessions of the Forest Entomology Section of the XV International Congress of Entomology in Washington, D.C., August 19 to 27, 1976. These sessions, a major component of the Forest Entomology program, were organized under the eight topics by W.E. Waters, Section Chairman and Organizer, with the assistance of Harold O. Batzer, H.C. Coppel, C.J. DeMars, A.T. Drooz, W.J. Mattson, M.L. McManus, J.B. Simeone, and D.L. Wood. Six related topics comprise the subject matter of this volume. With the participants responsible for each, these are:

- I. Detection, Evaluation, and Prediction of Forest Pest Insect Populations -- C.J. DeMars, Forest Service, U.S. Department of Agriculture, Berkeley, California.
- II. Assessment and prediction of Pest Insect Impacts on Forest Uses and Values -- H.O. Batzer, Forest Service, U.S. Department of Agriculture, St. Paul, Minnesota.
- III. Concept and Practice of Integrated Pest Management in Forestry -- D.L. Wood, Department of Entomological Sciences, University of California, Berkeley, California.
- IV. Biological Control of Forest Insects -- A.T. Drooz, Forest Service, U.S. Department of Agriculture, Research Triangle Park, North Carolina.
- V. Novel Approaches to Forest Insect Control -- H.C. Coppel, Department of Entomology, University of Wisconsin, Madison, Wisconsin.
- VI. Forest Insect Ecology and Control -- M.L. McManus, Forest Service, U.S. Department of Agriculture, Hamden, Connecticut.

At the Congress, the sessions on Topics V and VI met jointly with the Biological Control Section.

The papers of a session entitled The Role of Arthropods in Forest Ecosystems were considered to be of broader interest to forest ecologists and resource managers and are to be published separately by Springer-Verlag, New York, under the editorship

of W.J. Mattson. The subject matter of another session, Insect Pests of Wood in Structures (co-sponsored with the Stored-Products and Structural Insects Section) also justified separate publication of its major papers; these will appear in the journal Organismen und Holz (Duncker und Humblot, Berlin), edited by Professor Günther Becker.

A number of papers evoking interest and discussion at the Congress unfortunately were not suitable for publication because of special use of visual materials, an audience response format, or other technical reasons.

The support of K.R. Shea, Director of Forest Insect and Disease Research, and M.E. McKnight, Staff Entomologist, Forest Service, U.S. Department of Agriculture, Washington, D.C., is gratefully acknowledged.

W.E. Waters., Editor

The statements of the contributors from outside the U.S. Department of Agriculture may not necessarily reflect the policy of the Department.

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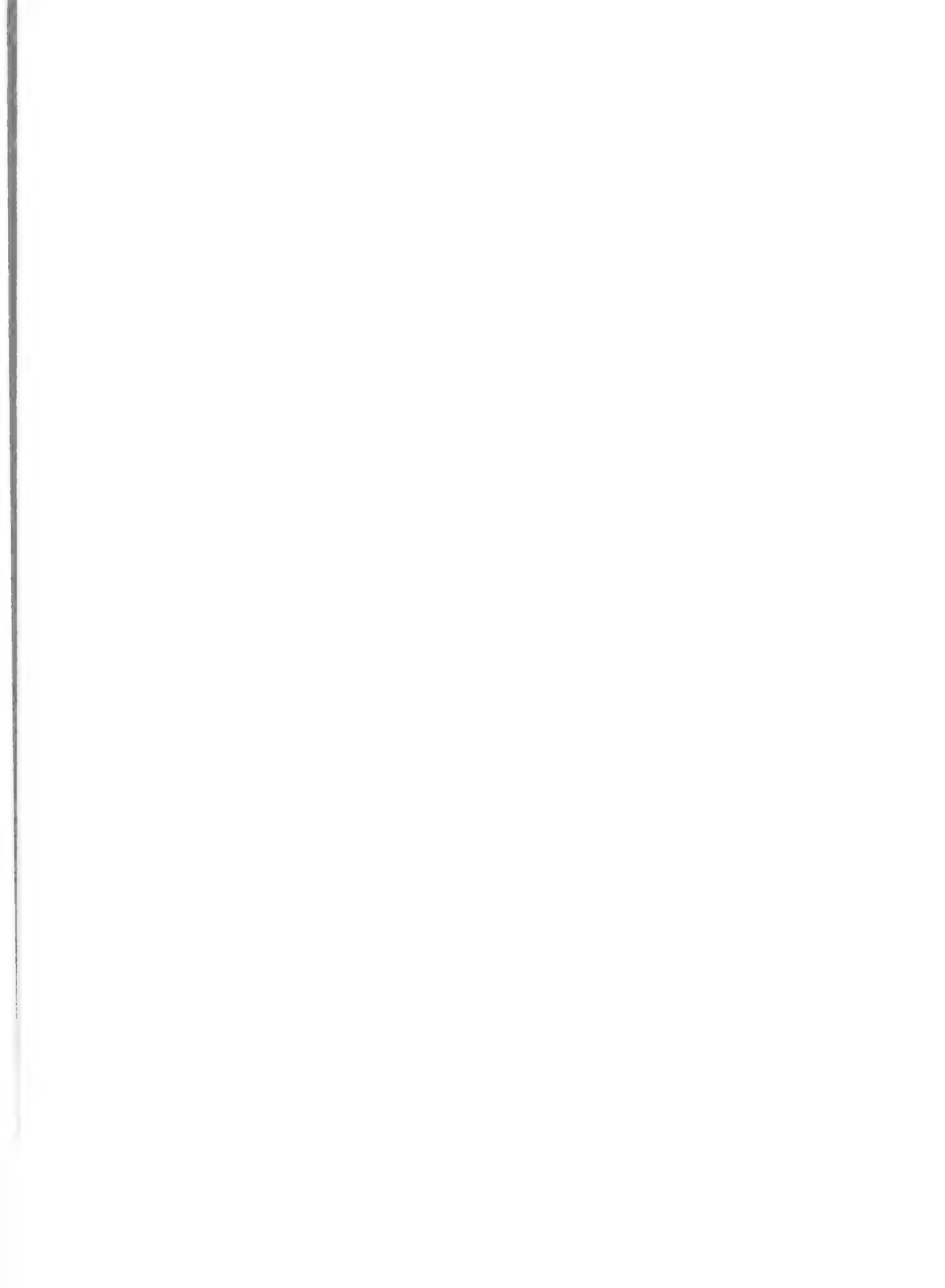
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I. DETECTION, EVALUATION, AND PREDICTION OF FOREST PEST INSECT POPULATIONS

Systematic Variable Probability Sampling for Estimating a Douglas-Fir Cone Population¹

T. Evan Nebeker and W. Scott Overton²

Introduction

In studying the dynamics of a Douglas-fir cone moth (*Barbara colfaxiana* (Kft.)) population on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Nebeker 1974), a means of estimating the total numbers of cones was required to estimate absolute population densities of the various immature stages of *B. colfaxiana* on a given area. In addition to being useful as a research tool, such a technique might also be useful in the management of seed production areas and orchards if it allowed advance planning of manpower and logistic requirements. The procedure discussed will be exemplified by results obtained during 1971 on the Buckhead Seed Production Area, Lowell Ranger District, Willamette National Forest, Oreg.

Estimation of Cone Population

A systematic sampling design with variable probability was used to estimate the total number of cones on the Buckhead Seed Production Area. This technique uses pre-

scribed probability proportional to an index variable (ppx).³

The general method was used for many years in sample surveys prior to the series of papers by Hartley and associates (c.f., Hartley and Rao 1962 and Hartley 1966) which outlined the theory. In general, the technique is very useful in many cases of practical sampling, and provides the most convenient variable probability sampling scheme with fixed sample size. Recent references in the forestry area are Stage (1971) and Overton *et al.* (1974).

The procedure requires that each tree in the universe (or sample)⁴ be characterized by an index variable that is related to the variable of interest for that unit. If a list of the index variable can be obtained cheaply, then ppx systematic sampling can be more efficient than other sampling methods. How much more efficient depends on the character of the functional relation between the index and the variable of interest. Generally, a positive correlation is an indication of gain, and a negative correlation can lead to loss in efficiency.

In the present application, the index variable was defined as the relative number of cones on a tree, with the number of cones

¹ Based in part on research conducted by the senior author in partial fulfillment of the degree Doctor of Philosophy at Oregon State University, Corvallis, Oreg. This work was supported by a National Science Foundation Training Grant, GZ-1372, in "Pest Population Ecology."

² Respectively, Department of Entomology, Mississippi State University, Mississippi State, Miss. and Department of Statistics, Oregon State University, Corvallis, Oreg.

³ The notation ppx is used to designate probability proportional to a variable, x. The notation pps sometimes used in this context is better reserved for probability proportional to (sample) sum, a technique useful in similar circumstances.

⁴ Variable probability sampling can be applied at any level in a sampling scheme. Our application to *all* trees in the universe of interest is a special case.

being the variable of interest. The index was then assigned in visual relation to the tree having approximately the greatest number of cones. Inspection was from the ground.

Each tree in each of 10 plots was given an Index I according to the criteria outlined in table 1. Trees were ranked in order of index, from the highest to the lowest in each plot, and the accumulative total T_I was calculated for all 10 plots.

Table 1.--Summary of indexing system and criteria for each index

Index (I)	Range	Criteria
1.00 .90 .80	.75-1.00	Heavy -- cones throughout the crown, dense
.70 .60 .50	.50- .74	Medium -- cones throughout the crown, sparse; or mid- and upper-crown only, dense
.40 .30	.25- .49	Light -- cones in mid- and upper-crown, sparse to dense
.20 .10 .00	.00- .24	Very light -- cones only in upper crown or scattered very sparsely

With the time available for sampling, it was decided that samples of $n = 12$ of the $N = 365$ cone bearing trees were to be selected as sample units to estimate the total number of cones on the area. To select a sample of $n = 12$, a sample interval s had to be computed:

$$s = T_I/n$$

and a random number r between 0 and s selected.

Sample selection then follows the rule: a tree t_i is in the sample if a number from the set $\{r, r+s, r+2s, \dots, r+(n-1)s\}$ is contained in the interval (T_{i-1}, T_i) ,

where

$$T_i = \sum_{j=1}^i I_j, T_0 = 0$$

If $s > \text{Max } I$, then this sample will contain exactly n trees, and the probability of inclusion in the sample will be $\pi_j = nI_j/T_I$ for each j . If some I 's are greater than s , the interval must be modified appropriately.

After the sample trees were selected, the

same procedure was again followed in selecting the whorls to be sampled. Whorls were enumerated and indexed. Four whorls per tree were selected. Within each selected whorl, one branch was selected at random, with equal probability for total cone enumeration. The sample selection can be summarized in the following steps:

- Step 1. Assign an index I to tree j in the area.
- Step 2. Arrange the indices from highest to lowest in each plot and sum indices over all trees in the area.

$$\sum_{j=1}^N I_j = T_I$$

- Step 3. Select n trees of the total N cone bearing trees systematically with probability proportional to I_j .
- Step 4. Assign an index W_i to each whorl i on a selected tree.
- Step 5. Arrange the whorl indices W_i from highest to lowest for this tree and sum the indices.

$$\sum_{i=1}^K W_i = W$$

- Step 6. Select k whorls of the total K whorls per tree systematically with probability proportional to W_i .
- Step 7. From each of the selected whorls, select one branch at random (numbering the m_i branches clockwise with the one pointing most northerly as number one) with equal probability.
- Step 8. Count all live cones y on the branch selected.

The sample unit estimations for whorl, tree, plot, and area can be summarized as follows:

- Step 1. Estimation of the number of cones on the i^{th} whorl is:

$$\hat{t}_{yi} = m_i \cdot y$$

where: m_i = number of branches in the i^{th} whorl.

Step 2. Estimation of the number of cones on the j^{th} tree is:

$$\hat{t}_{yj} = \sum_{i=1}^k \frac{\hat{t}_{yi}}{\pi_i}$$

where:

$$\pi_i = \frac{kW_i}{W}$$

The inclusion probability of the i^{th} whorl on the j^{th} tree.

Step 3. Estimation of the number of cones on the area is:

$$\hat{T}_y = \sum_{j=1}^n \frac{\hat{t}_{yj}}{\pi_j}$$

where:

$$\pi_j = \frac{nI_j}{T_I}$$

and n = number of sample trees.

Step 4. Estimation of the number of cones per plot requires identification of the conditional in-

clusion probabilities for these plots.

$$\hat{T}_{ya} = \sum_{j=1}^{n_a} \frac{\hat{t}_{yj}}{\pi_{caj}}$$

where:

$$\pi_{caj} = \frac{n_a I_j}{T_{Ia}}$$

the conditional inclusion probability of the j^{th} tree in plot a being sampled.

Considering the entire area, an estimate of the variance of \hat{T}_y is conservatively approximated (overestimated) by:

$$\hat{V}(\hat{T}_y) \doteq N \left(\frac{N-n}{n} \right) \left(\frac{1}{n-1} \left(\sum_{j=1}^n \hat{t}_{yj}^2 - \frac{(\sum \hat{t}_{yj})^2}{n} \right) \right)$$

Table 2 summarizes the estimates for each of the 12 trees sampled and then projects an estimate of the total cones on the area. As mentioned before, the precision of the estimates depends on how well correlated the index was with the actual number of cones.

Table 2.-- Area (\hat{T}_y), Plot (\hat{T}_{ya}), Tree (\hat{t}_{yj}) and the contribution (\hat{t}_{yj}/π_j) of each tree to the total (\hat{T}_y) cone estimates and indices for the Buckhead Seed Production Area, September 1971

Plot no.	No. of cone-bearing trees	Mean Index	Tree no. sampled	π_j	Index	\hat{t}_{yj}	\hat{T}_{ya}	\hat{t}_{yj}/π_j
I	36	.60	24	.07088	.85	523	34,744	7,379
			31	.02502	.30	791		31,615
II	22	.43	--	--	--	--	--	--
III	43	.45	14	.07505	.90	3209	43,877	42,758
			42	.04170	.50	615		14,748
IV	34	.44	29	.05837	.70	1355	27,597	23,214
V	57	.34	3	.06671	.80	2977	45,570	44,626
			5	.01668	.20	252		15,108
VI	61	.29	6	.03336	.40	385	16,245	11,541
VII	47	.31	36	.05837	.70	4778	49,354	81,857
			29	.00417	.05	20		4,796
VIII	19	.39	--	--	--	--	--	--
IX	11	.39	--	--	--	--	--	--
X	35	.45	8	.07505	.90	3505	90,290	46,702
			11	.02919	.35	2924		100,171

$$\hat{T}_y = 424,523$$

$$\sqrt{\hat{V}(\hat{T}_y)} = 164,567$$

$$\sum \hat{t}_{yj}/\pi_j = 424,515$$

Theoretically, if the index was absolute, there would be perfect positive linear relationship between the index and the actual number of cones, and the variance of the estimator would be zero, except for the contri-

bution of within-tree estimation error. In general, various estimates for this sort of sampling do not accurately reflect the gain in precision from the technique, and this is one area in which work needs to be done.

Table 3.-- Summary of the tree (\hat{t}_{yj}) and the whorl (\hat{t}_{yi}) cone estimates for the Buckhead Seed Production Area in September 1971

Plot no.	Tree no.	Tree index	Whorl no.	Whorl index	m_i	y	\hat{t}_{yi}	π_i	\hat{t}_{yj}
I	31	.30	15	.6	3	12	36	.32000	791
			14	.9	6	17	102	.48000	
			12	.9	5	15	75	.48000	
			10	.8	6	22	132	.42667	
			11	.8	5	19	95	.31068	
24	.85	15	.8	5	19	95	.31068	523	
		11	.9	4	19	76	.34955		
		7	.8	5	0	0	.31068		
		4	.4	4	0	0	.15534		
		15	.9	5	39	195	.29032		
III	14	.90	15	.9	5	39	195	.29032	3209
			12	.9	5	67	335	.29032	
			10	.8	7	51	357	.25807	
			7	.6	5	0	0	.19355	
			10	.7	6	9	54	.47458	
42	.50	10	.7	6	9	54	.47458	615	
		9	.4	5	16	80	.27119		
		8	.4	4	14	56	.27119		
		7	.5	6	0	0	.33898		
		17	.9	3	19	57	.39130		
IV	29	.70	17	.9	3	19	57	.39130	1355
			15	.9	5	28	140	.39130	
			14	.8	4	26	104	.34783	
			11	.5	4	30	120	.21739	
			8	.8	3	9	27	.50000	
V	5	.20	8	.8	3	9	27	.50000	252
			7	.9	4	16	64	.56250	
			6	.9	4	6	24	.56250	
			4	.7	6	3	18	.43750	
			12	.9	6	76	456	.26471	
3	.80	12	.9	6	76	456	.26471	2977	
		9	.8	5	37	185	.23529		
		6	.8	5	22	110	.23529		
		1	.2	6	0	0	.05882		
		13	.7	6	7	42	.29474		
VI	6	.40	13	.7	6	7	42	.29474	385
			11	.9	7	4	28	.37895	
			9	.9	4	16	64	.37895	
			6	.5	6	0	0	.21053	
			13	.9	4	173	692	.34952	
VII	36	.70	13	.9	4	173	692	.34952	4778
			10	.9	6	152	912	.34952	
			6	.7	6	0	0	.27185	
			4	.6	4	11	44	.23310	
			7	.5	3	2	3	.62500	
29	.05	7	.5	3	2	3	.62500	20	
		6	.5	5	1	5	.62500		
		5	.7	3	2	6	.87500		
		3	.6	3	0	0	.75000		
		18	.7	3	113	339	.22764		
X	8	.90	18	.7	3	113	339	.22764	3505
			16	.9	5	73	365	.29268	
			13	.9	9	3	27	.29268	
			7	.7	7	22	154	.22765	
			10	.9	6	22	132	.43374	
11	.35	10	.9	6	22	132	.43374	2924	
		7	.8	9	4	36	.38554		
		9	.7	4	19	96	.33735		
		6	.4	8	54	432	.19277		

It can be seen in table 3 that a number of whorls with high indices had low cone estimates and vice versa. This apparently reflects the variation in cones per branch at a given whorl. It is indicated that, to improve the estimates, the branches in each selected whorl should also be indexed and selected in the same manner as the whorls and trees.

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Trend Prediction in Forest Insects

H. Klomp¹

Introduction

In predicting the trend of forest insects, we try to forecast the future population density of an insect with some precision from observed facts and experience. The aim of the predictions is to provide a basis for deciding whether or not to control injurious insects.

The purpose of predictions for control actions follows from the object of a control strategy, maximization of the benefit/cost ratio (Conway 1973):

$$\frac{\text{cost of damage}_1 \text{ uncontrolled} - \text{cost of damage}_2 \text{ controlled}}{\text{cost of control}_3}$$

This objective function being accepted, the control worker is confronted with the problems of:

1. forecasting and evaluating damage when the population remains unchecked;
2. estimating in advance the reduction of damage under different control programs; and
3. estimating the cost of the control program adopted.

The estimation of (3) is relatively easy, because most of the costs are labor and materials. To solve the more complicated problems raised under (1) and (2), it is necessary to have an expectation of the damage caused by the insect in the future. Plant damage is related to insect density, and because trend prediction refers to trends in insect abundance, we shall consider insect density instead of damage.

The main features of trend prediction for practical purposes are:

1. formulating a prediction of the density at time t_x ($x > 0$), based on demographic data determined at time t_0 ;
2. stating the probability that the predicted density will be correct; and
3. recurrent surveying in the field of the demographic data referred to under (1).

These features will be elucidated briefly.

The formulation of a predictive function requires information on the relationship between population data at t_0 (which may refer to the density, the reproductive rate, and/or the mortality rate) and the density at time t_x . It is valuable to know how detailed this information should be in order to make a prediction that will be correct with a given probability, P . It is demonstrated later in this paper that the amount of information required is dependent on the pattern of fluctuation and on the nature of the key factor(s), which primarily contribute to population change.

The interval, $t_0 - t_x$ should be long enough to enable the control worker to calculate expenses and profits, and to make the practical preparations necessary for the control program adopted.

According to the predictive function mentioned above, economic infestation levels can be expected to occur at t_x , when the demographic data at t_0 reach critical values. For the control worker, it is important to know the probability that this expectation is correct. This probability can only be derived from historical population data, the data which are also needed to derive the predictive function. In general, the probability of a correct prediction will increase with a reduction in the interval $t_0 - t_x$, because the more variable factors have been excluded.

¹ Research Institute for Nature Management, Arnhem, Netherlands

It will be necessary for the control worker to know whether or not the demographic data reach critical values at t_0 . Therefore, a method is required to recurrently estimate the size of the population variables, which are incorporated in the predictive equation. The practical side of this aspect of trend prediction will not be considered in this paper.

Predictions Based on the Density of the Preceding Generation

In univoltine insects, the simplest relationship between the densities (N) of two successive generations can be expressed by the difference equation

$$N_{t+1} = N_t \times R_t \quad (1)$$

where R_t is the net rate of reproduction over generation t . In some species, the variations in N_{t+1} are mainly due to variations in N_t ,

because R_t is relatively constant. In such species, the overall range of fluctuation is considerably greater than the range of change between successive generations. As a result, predictions can be based on the serial correlation between successive generations.

An example of this type of fluctuation is presented by the larch bud moth (*Zeiraphera diniana* Gn.) in the Upper Engadin in Switzerland. Baltensweiler (1971) reports for 1950-1969 the highest larval density of this species roughly 50,000 times greater than the lowest density. The range in the rate of increase or decrease between successive generations varies between 6 and 14 times, with exceptional decreases of up to 100 times. The correlation between successive larval densities is presented in figure 1.

Baltensweiler (1971) also reported that there was general defoliation in the area when $\log N > 5.8$. This level can be reached only when the \log density of the previous generation ($\log N_t$) is higher than 4.7, thus establishing the critical level. Economic damage demanding large scale control action in

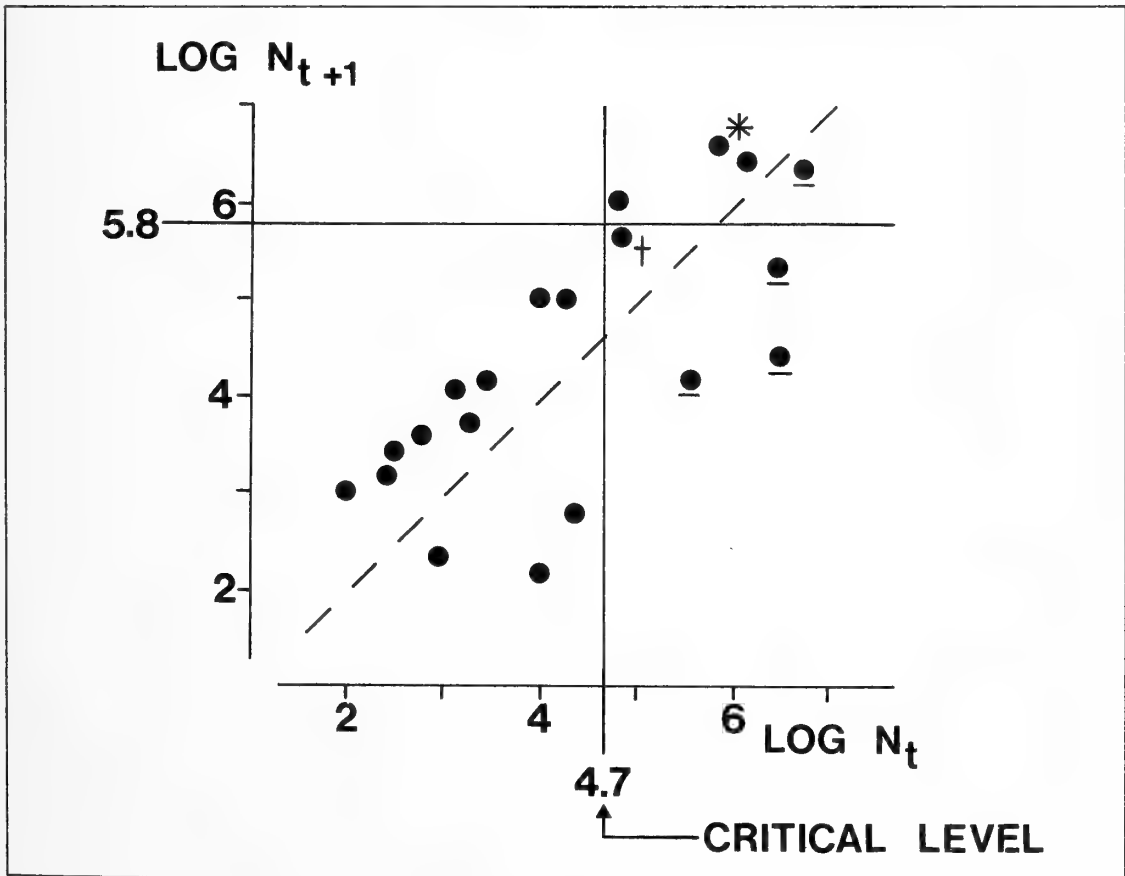


Figure 1.--Correlation between successive larval densities in a population of larch bud moth, Upper Engadin, Switzerland, 1950-69. (See text.)

generation $t+1$ is predicted when the critical level in generation t is surpassed, but the prediction will only be correct in 50 percent of the cases (fig. 1). The predictive value of a relationship of this type is low, even though it is based on a considerable body of data: *viz.* the density of larvae over a period of 20 successive years, data which is unavailable for the great majority of other harmful insects.

However, important additional information is available for the larch bud moth which can be used to improve the probability of a correct prediction. Auer (1961) and Balten-sweiler (1964) have shown that the pattern of fluctuation of this moth in the Engadin is cyclic with periodic defoliation occurring every 8-9 years. This implies that, from the prediction point of view, the descending part of the cycle can be left out of consideration. The density figures for this part of the cycle are located below the 45° line in figure 1, and those higher than the critical level are underlined. When these are discarded, predictions can be expected to be correct in 75 percent of the cases.

In general, even this is far from a firm basis for decisionmaking with respect to control actions. In this cyclic species, however, a wrong decision does not have serious consequences, because, first of all, in the ascending part of the cycle, the density of generation $t+1$ will at least be very close to the level of general defoliation, once the critical level has been surpassed in generation t (fig. 1, point marked with a dagger). Secondly, if the defoliation level is not yet reached in $t+1$, it will certainly be reached one generation later ($t+2$) (fig. 1, point marked with an asterisk), and this will be prevented by successful control in generation $t+1$.

The prevention of defoliation touches upon another important aspect of trend prediction in this species. The cyclic behavior of the population results from a time lag in the reaction of the food plant to defoliation. The quality of the larch needles is reduced for 3 to 4 years after partial or complete defoliation. This affects both the reproduction and the mortality of the population resulting in the regression phase of the cycle (Benz 1974). Therefore, preventing defoliation will disturb the cycle, and this may have far-reaching consequences for the whole system, and hence for trend prediction. It has been suggested by Van den Bos & Rabbinge (1976), based upon a simulation model of the dynamic behavior of the larch bud moth, that excluding the effects of food quality, while leaving food quantity and parasitoids as effective

mortality factors, results in population densities fluctuating at an extremely high level which would probably cause mass tree mortality after some years. This suggests that, in the field, parasitoids will be unable to stabilize host density at a low level when defoliation is prevented by chemical control. If this is so, the host will rapidly build up its numbers, and will reach defoliation levels once more. However, the number of years after which this will happen is not fixed. To monitor this would require an intensification of the field survey program, which is already rather extensive due to the asynchronous occurrence of peak densities in different parts of the species range.

In the larch bud moth, the predictability of infestation levels one generation ahead is relatively high, due to the regular cyclic behavior of the population. When there is less regular periodicity and population declines can also occur without preceding defoliation, the chance for a correct prediction is considerably lower. Using the population data of the pine looper (*Bupalus piniarius* L.) published by Schwerdtfeger (1935, 1941) and re-plotted on a logarithmic scale by Varley (1949), a graph was prepared of the serial correlation between successive pupal densities (figs. 2A and B). Varley reports that outbreaks were recorded in 1888, 1894, 1900, 1905, 1917, 1928, and 1936, but Schwerdtfeger (1941) has pointed out that the relatively low peaks of 1894 and 1905 did not reach significant infestation levels. Consequently, large scale defoliation by the larval stage does occur when the preceding log pupal density ($\log N_{t+1}$) is equal to or higher than 0.5. As shown in figure 2B, this density level is reached only when the log pupal density in the preceding generation ($\log N_t$) is equal to or higher than -0.6. However, predictions based on this critical level have a low probability of being correct, because outbreaks occurred in only 8 out of 23 years ($P=0.35$).

As was the case with the larch bud moth, the years after an outbreak (underlined in fig. 2) are immaterial to the argument. When these years and the year 1881/82 (squared in fig. 2B), which had an unknown prehistory, are discarded, the predictability of outbreaks improves substantially ($P=0.58$), but is still too low for practical use.

Predictions Based on Density and the Net Rate of Reproduction

When the range of overall fluctuation of a population is only slightly greater than the

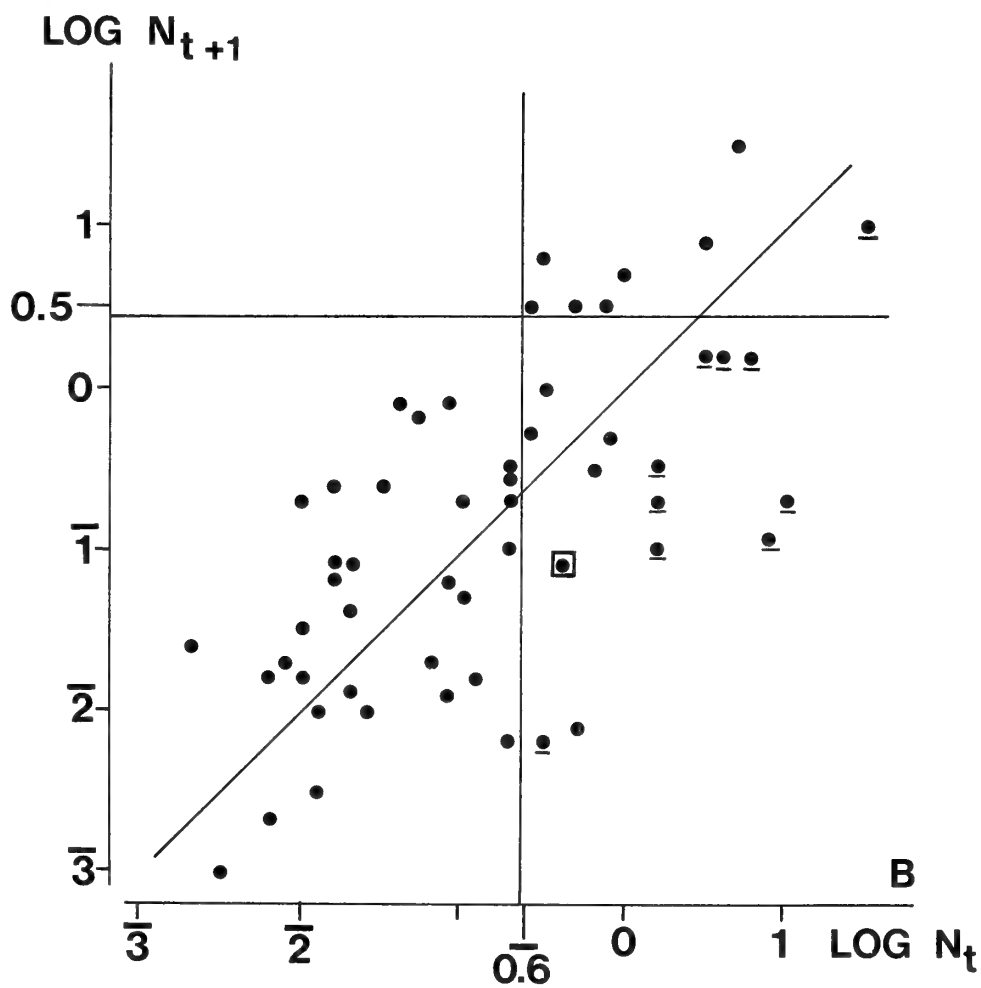
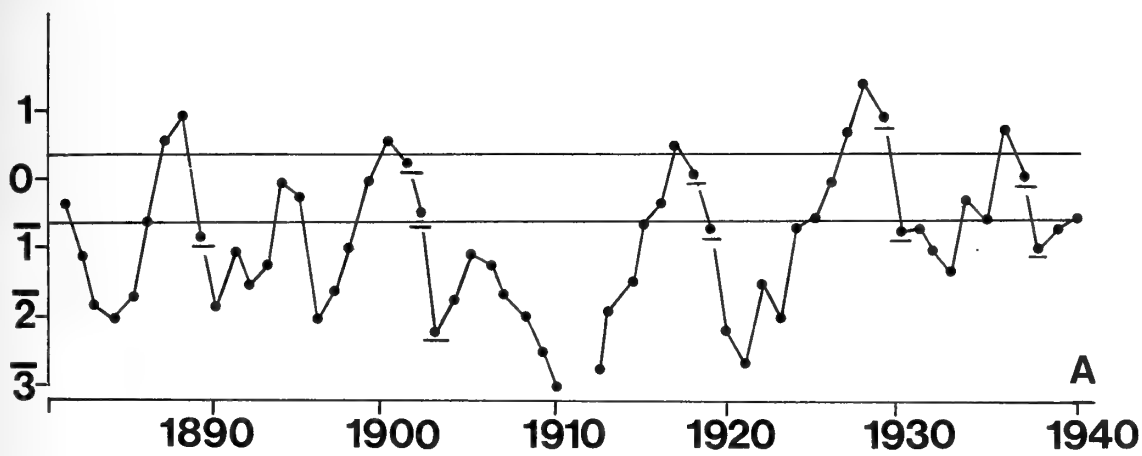


Figure 2.--Fluctuations of the pupal density of the pine looper (log numbers per m^2) at Letzlingen, Germany, 1881-1940 (A) and correlation between successive pupal densities of the same population (See text.)

range of change between successive generations, variations in N_{t+1} are due both to variations in N_t and in R_t (equation 1). In these cases, predictions of the density of the defoliating stage in generation $t+1$ must be based on estimations of both N_t and R_t .

R is the product of the survival rates in the successive stages or age intervals of the insect and its reproductive rate. Thus, according to figure 3:

$$N_2 = N_1 \times R_1 = N_1 \cdot S_3 \cdot S_4 \cdot F \cdot S_1 \cdot S_2 \quad (2)$$

It has been found, in some species, that the variations in R are essentially determined

by the variations of one of these components (Morris 1959, Watt 1963). This component has been called the key factor of population fluctuation (Varley & Gradwell 1960). When the key factor operates during one of the later stages of the life cycle of the insect (pupa, moth), the inter-generation variation of the components affecting the earlier stages will be relatively small. This gives rise to a correlation between the density of the stage occurring after the operation of the key factor and the density of the defoliating stage following. For instance, if in figure 3 the population fluctuations are mainly due to variations of S_4 or F (or, when both are key factors), egg density and the density of the defoliating larvae will be correlated, and

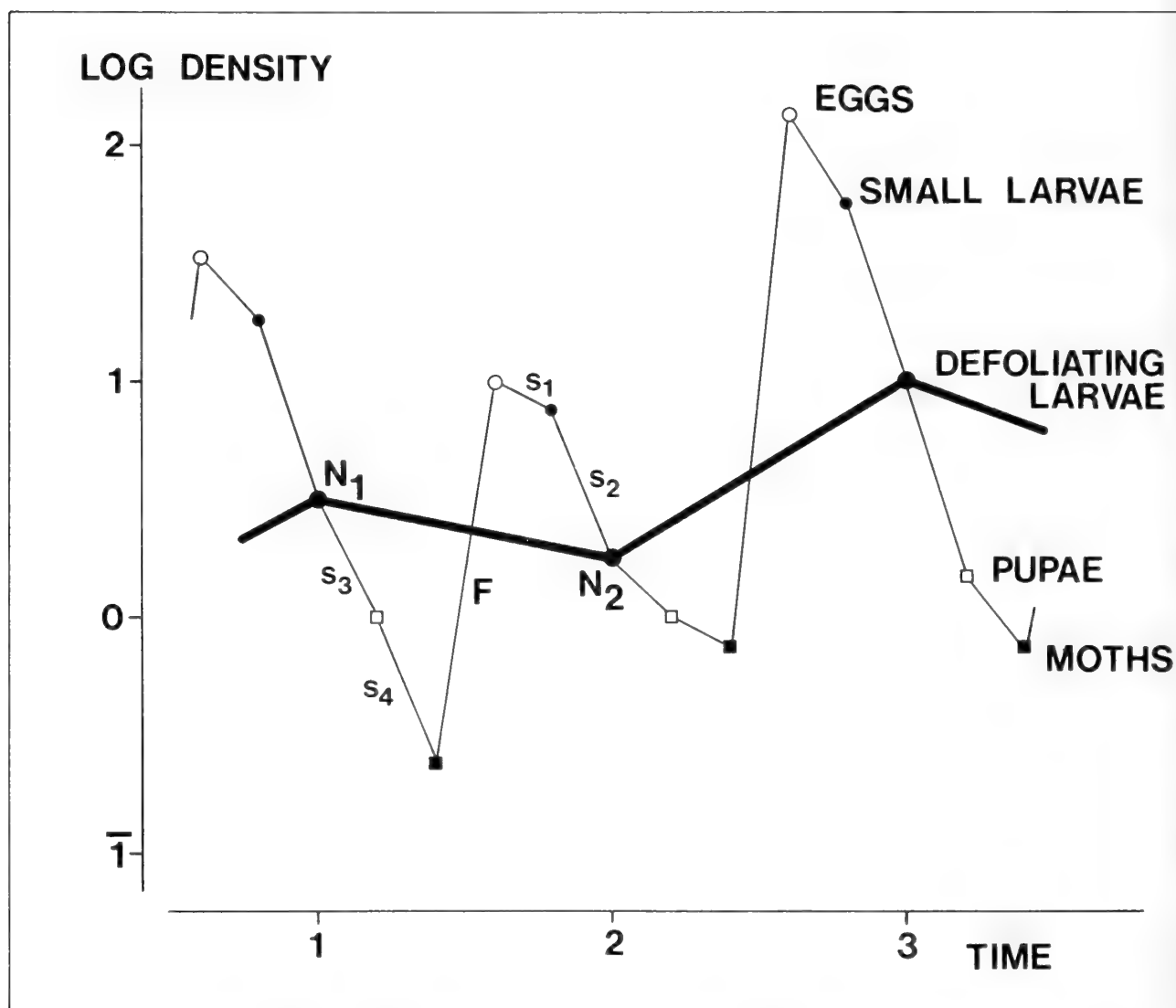


Figure 3.--Intra and inter-generation fluctuations of an imaginary population of an univoltine insect over nearly three generations, to show the relation between two successive generations of defoliating larvae: $N_2 = N_1 \cdot S_3 \cdot S_4 \cdot F \cdot S_1 \cdot S_2$, where S_1 to S_4 indicate survival rates in different age intervals, and F is the reproductive rate of the moths.

this relation may be used to predict the incidence of outbreaks.

This method was used for the white-fir sawfly, *Neodiprion abietis* Harr., by Struble (1959) to show that control may be necessary whenever the egg density exceeds 20 clutches in a 200-twig sample. However, he was unable to indicate the probability of this prediction being correct, because the correlation between egg and subsequent larval densities was based on only a 4-year census.

Another example of the use of the correlation between egg density and larval density to predict the latter was reported by Shepherd & Brown (1971) for the forest tent caterpillar, *Malacosoma disstria* Hbn., which defoliates trembling aspen in North America. Larval densities were expressed as defoliating classes (light, moderate, and severe), and the incidence of these classes was predicted on the basis of the number of egg-bands per sample. However, in testing the accuracy of the predictions in the field, only 65 percent of the larval populations proved to be in the correct class.

Locally, trees usually are defoliated 4 years in succession. This is possible because the trees recover their foliage during the first 2 years of an outbreak, but recovery is much less in later years. Owing to this declining recovery, the egg hatch rate and the larval survival rate decrease as the outbreak progresses. In consequence, at the same high egg density, the damage by larval feeding proves to be severe at the beginning of an infestation, but light to moderate at the end. In compensating for this effect by using "sliding class-boundaries," the accuracy of the prediction could be increased to 75 percent. However, this still leaves too great a possibility for a needless, and hence unjustifiable, application of insecticides.

In conclusion, prediction of the numbers of the defoliating stage can be based on the density of an earlier stage of the same generation when there is a high correlation between these densities. This is so, when the key factor(s) operate before the stage on which the prediction is based. Although this forecast is apparently based on density alone, in contrast to also using net reproduction rate, this is only seemingly so. The variable effects of the previous density of the defoliating stage (N_t) and of the key factor(s) are included in the variation of the density of the stage used for prediction.

For population fluctuations which are mainly due to variations in S_1 or S_2 (fig. 3), the correlation between egg density and the

numbers of the defoliating stage will be poor. Thus, for the pine looper in Holland, as shown for two generations in figure 4, the density of large larvae is primarily determined by the amount of juvenile mortality, most of which occurs during the first few days after hatching (Klomp 1966). As a result of variations in juvenile survival, the mortality from egg to defoliating larvae varied from 27 to 96.5 percent. This gives rise to a poor correlation between the densities of the two stages of the life cycle (fig. 5A). In contrast, the density of small larvae in the beginning of August, occurring after the operation of the key factor, is fairly well correlated with larval numbers later in the season (fig. 5B).

If the latter relation is used for the prediction of defoliation in September-October, it is necessary to census larval density in August every 2 or 3 years because in this species, epidemic levels are normally reached within 3 to 4 years (fig. 2A). This frequency of estimating density is perhaps practicable if large forested areas with virtually the same larval density are involved. However, as shown for Germany by Engel (1942), and for England by Bevan & Brown (1961) and Davies (1962), there may be considerable differences in density between the compartments of a pine forest, sometimes only 500 meters apart. This situation requires such an extensive census program that the available time interval ($t_0 - t_x$) of roughly 45 days could be limiting. This implies that, for species with fluctuations governed by key factors operating shortly before the defoliating stage, and having a highly patchy distribution pattern, predicting outbreaks with much precision seems to be an unattainable goal.

Predictions Based on the Size of the Key Factor

Instead of using measured densities of preceding stages of the same generation, estimates of the size of the key factors themselves may be used to predict the density level of the defoliating large-larval stage. This method was used by Morris (1959, 1963a, 1963b) in developing predictive equations for the black-headed budworm, *Acleris variana* Fern., the European spruce sawfly, *Diprion hercyniae* Htg., and the spruce budworm, *Choristoneura fumiferana* Clem.

In the first species, a univoltine defoliator of fir and spruce in Canada, larval density in generation $t+1$ is predicted from the larval density and the rate of larval parasitism in generation t . Parasitism is easily measured in this species by dissecting or

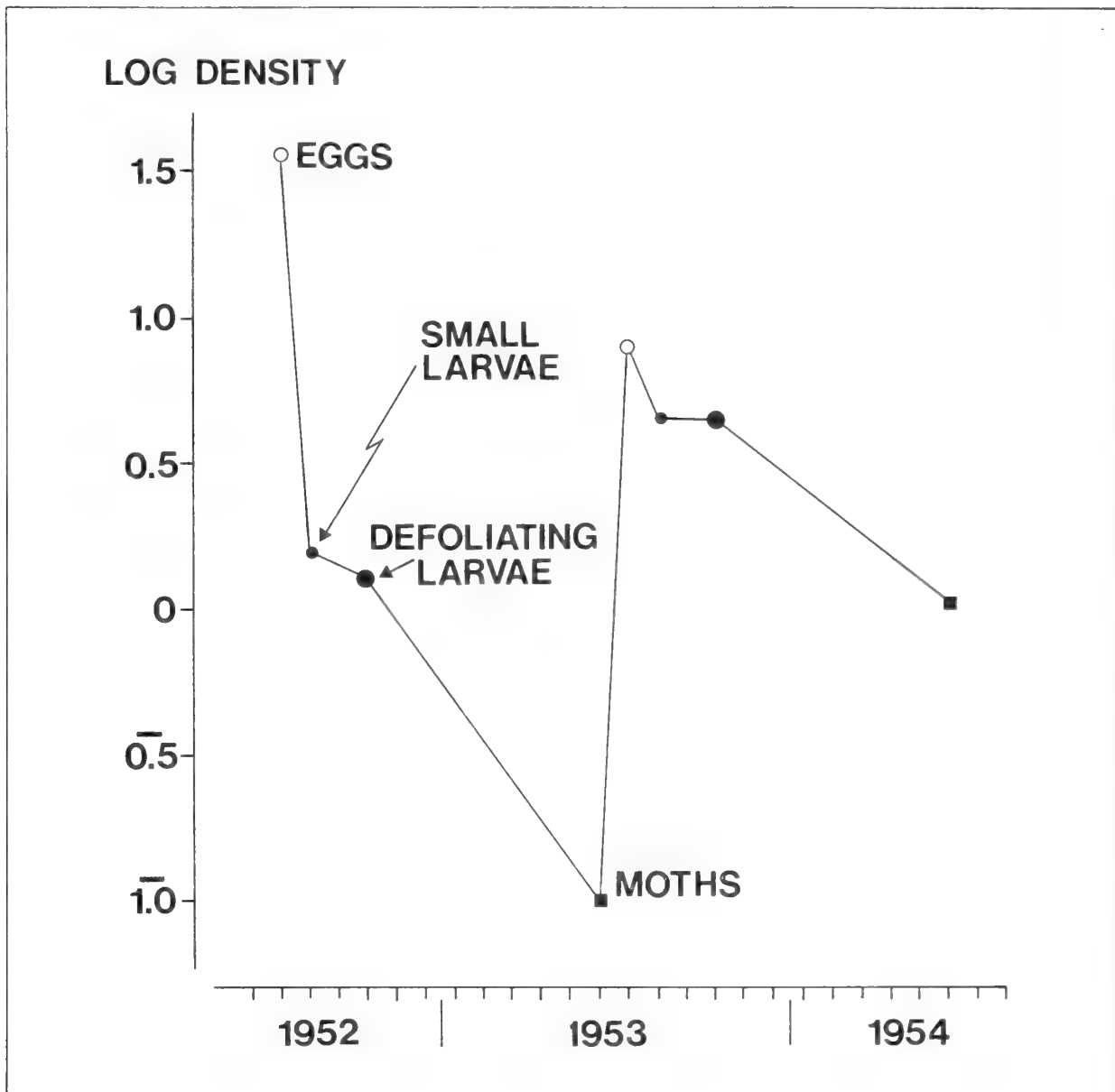


Figure 4.--Survivorship curves of the pine looper in Holland, showing the predictive value of juvenile mortality for the density of the defoliating larval stage.

rearing the larvae obtained in the population sampling.

This makes sense when larval parasitism is a key factor, i.e., when larval density (N_{t+1}) in generation $t+1$ is essentially determined by the rate of parasitism (p_t) in generation t , in addition to the contribution of larval density (N_t) in generation t . This was tested by Morris by comparing the correlation between $\log N_{t+1}$ and $\log N_t$ with the correlation between $\log N_{t+1}$ and $\log \{N_t(1-p_t)\}$, and appraising the effect of the assumed key factor by measuring the improvement it made in the correlation coefficient.

For this procedure, Morris used population data on N and p from a coniferous stand in New Brunswick collected over 12 successive years (fig. 6). He concluded, from the considerable improvement of the correlation coefficient, that parasitism was a key factor for this population during the period that the population was studied.

This method differs from those described above, in which densities of an earlier stage of the same generation have been used, because $\{N_t(1-p_t)\}$ is not a real density of larvae surviving parasitism; it is only an index. There is considerable mortality of both

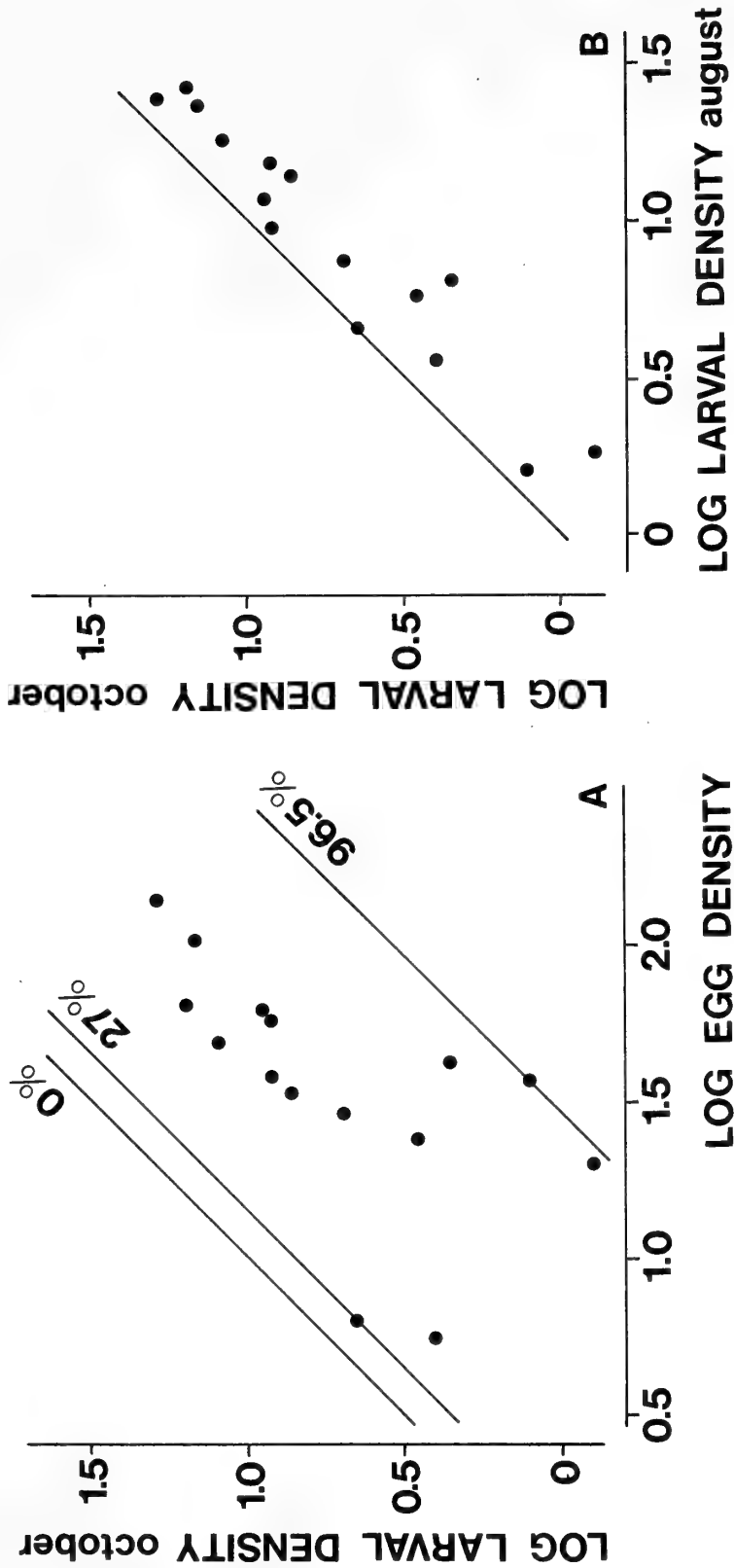


Figure 5.--Graphs showing the poor correlation between egg density and the density of fully grown larvae (A), and the high correlation between the densities of half grown and fully grown larvae (B) in the pine looper in Holland, 1950-1964. (See text.)

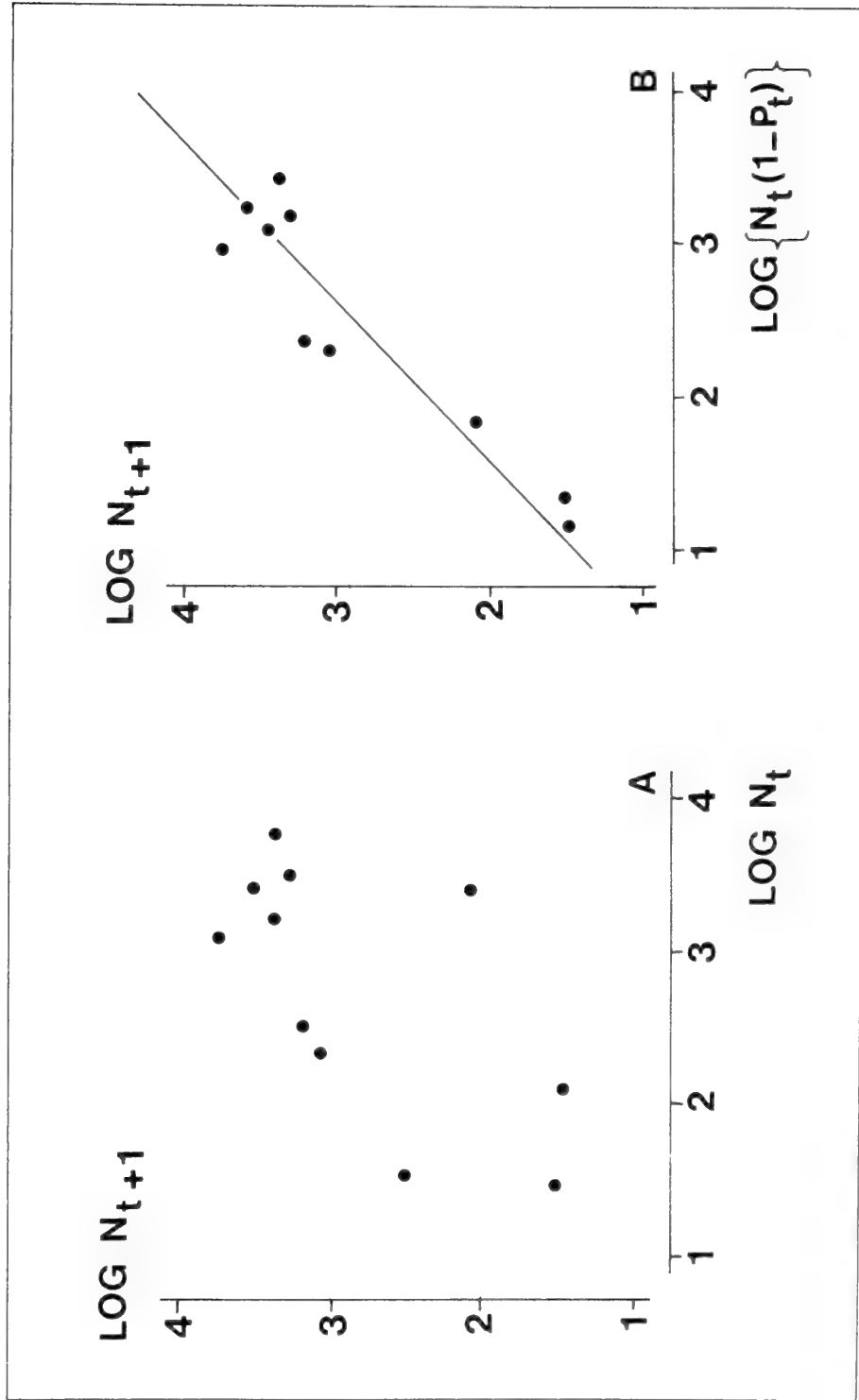


Figure 6.--The correlation between $\text{LOG } N_{t+1}$ and $\text{LOG } N_t$ ($r=0,67$) in a New Brunswick population of the black-headed budworm (A) and the correlation between $\text{LOG } N_{t+1}$ and $\text{LOG } N_t(1-p_t)$ in the same population over the same period ($r=0,93$) (B). Graph B has one point less than A, because parasite data are lacking for one generation. The line in B represents the linear regression line, the equation of which is given in the text. After data of Morris 1959.

parasitized and unparasitized larvae due to other causes, both during and after the period of activity of the adult parasites. Morris developed a method to correct larval survival for this mortality, but this correction will be omitted here, because the adjustment did not significantly improve the correlation.

Predictions of $\log N_{t+1}$ can now be based on the regression of $\log N_{t+1}$ on $\log \{N_t(1-p_t)\}$ giving the equation (fig. 6):

$$\log N_{t+1} = 0.53 + 0.93 \log \{N_t(1-p_t)\} \quad (3)$$

However, this equation seems to be of no use for the prediction of defoliation. Morris has reported that, in New Brunswick, populations of the black-headed budworm decline before food shortage becomes an important factor. This implies that equation (3) is based on data from an area where outbreaks of this species do not occur. Therefore, the question may be raised as to the validity of the predictive value of the equation for populations in other stands. In areas where the budworm periodically causes defoliation, the parasite's numerical response to increases in the host population is probably insufficient to bring about a downward trend in the numbers of the host. Under such conditions, food quantity and quality, rather than parasitism, are likely to be key factors, as is the case with the larch budmoth discussed earlier.

Another objection to the predictive value of equation (3) is that it is based on only 12 generations. Over this series of years, parasitism indeed proved to be a key factor, but there is some evidence from other species studied over longer sequences of years, showing that fluctuations of numbers may be governed by different factors over successive intervals.

Another species considered by Morris (1963a), the spruce budworm, was studied on several plots of an extensively forested area (Area I) in northwestern New Brunswick during the outbreak period of 1945-1960. Because the overall range of fluctuation in this period is considerably larger than the range of annual increases or decreases, there is a high correlation ($r = 0.67$) between $\log N_{t+1}$ and $\log N_t$.

In this species, unlike the black-headed budworm, there is hardly any improvement of the correlation coefficient between $\log N_{t+1}$ and $\log N_t(1-p_t)$ over that between $\log N_{t+1}$ and $\log N_t$. This shows that parasitism is not a key factor in this budworm, at least not during the outbreak period studied. There was some evidence suggesting an influence of weather on population development, and Morris showed that the deviations of individual

points (years) from the regression of $\log N_{t+1}$ on $\log N_t$ were related to an easily measured expression of weather: the mean maximum daily temperature during the main period of larval development (roughly June 1-July 13). Morris simply added the regression of deviations on temperature to the relation between successive larval densities, giving the predictive equation

$$\log N_{t+1} = 0.98 + 0.76 \log N_t + 0.18(T_t - \bar{T}) \quad (4)$$

where

T_t = mean maximum daily temperature June 1-July 13 in year t .

\bar{T} = the average value of T_t over a long period of years, being 66.5°F .

Morris tested the predictability of this equation by calculating the regression of observed values of N_{t+1} on those calculated from equation (4). This regression had a standard error of estimate of 0.41, which is too high to permit good predictions.

Equation (4) was based on data from various plots in Area I, including those that suffered from severe defoliation and others that did not. By restricting the analysis to the latter, thus eliminating effects of food shortage and possibly the mass dispersal of moths induced by overpopulation, Morris was able to improve the predictability of the equation considerably. The regression of observed values on calculated values in this case explained 79 percent of the variance and showed a standard error of estimate of 0.29.

However, the forest entomologist interested in predicting larval densities causing economic damage in situations where overpopulation phenomena may be expected to play a role before heavy defoliation occurs will have to await the development of predictive equations which incorporate these factors. Where some factors are largely weather dependent, such as moth migration, reliable prediction of economic damage for definite stands of forest will remain a wish for a long time.

The Change of the Key Factor over Long Intervals

For the prediction of population change with some precision, knowledge concerning the

key factor(s) causing this change is essential, unless the larval densities of successive generations are highly correlated and fluctuations are cyclic. In some species, prediction can be based on the density of a life stage occurring earlier in the life cycle than the defoliating stage, provided the key factor operates before that earlier stage. In all other cases, predictions have to be based on the size of the key factor. Thus, predictions of population changes of the winter moth in Wytham Wood, England are as yet impossible, because the main cause of the year to year changes is largely unknown (Varley & Gradwell 1971). The changes are thought to arise from variations in the degree of synchronization between bud burst and egg hatch, factors which are probably weather dependent.

Therefore, identification of the key factors is essential, and should be based on a detailed life table study of the species involved. With some exceptions, case studies of this kind have been limited to 10 to 15 generations or less. There is, however, some evidence that population change may be governed by different key factors over successive intervals of that length. This is illustrated by the long term population study of the pine looper in Holland.

We have studied the fluctuations of this moth in a pine plantation over a period of 26 consecutive years (fig. 7). Detailed life table analysis as described by Klomp (1966) and key factor analysis according to Varley & Gradwell (1960) have shown that fluctuations over the years 1950-1963 were mainly due to variation in juvenile mortality, most of which affects the tiny larvae just after hatching.

After 1963, there was a sudden increase of an ichneumon fly, *Poecilostictus cothurnatus*, killing an increasing proportion of the pupae up to the 1967-1968 generation, and causing a tremendous decline in host numbers. The proportion infected in 1968 is unknown, but from 1969 onward the parasite's numbers rapidly decreased, giving rise to a recuperation of the host population within 4 to 5 years.

This parasite was also present in the system during the 1950-1963 period, during which it killed a small, slightly variable proportion of pupae each year. It emerges from the host pupae in June, but does not attack pine looper larvae before their development is well advanced in September-October. Oviposition on earlier stages of the pine looper is refused, and the parasite has at

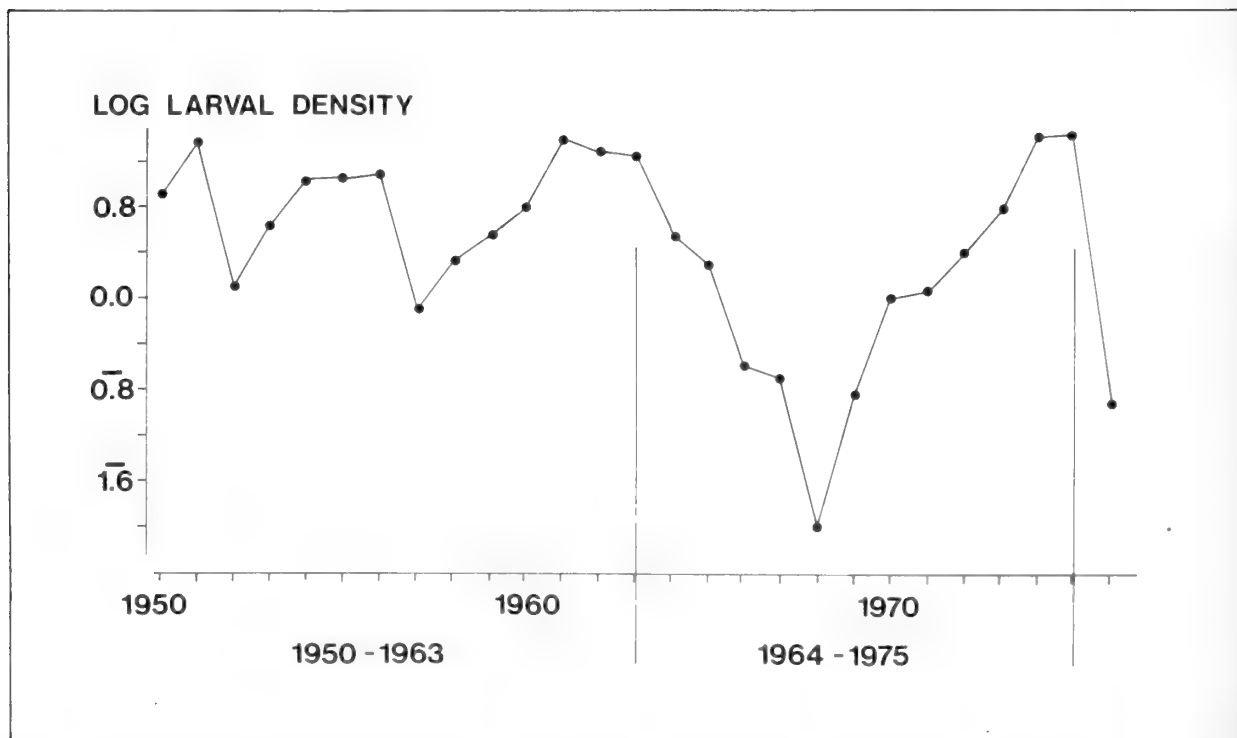


Figure 7.--Long-term fluctuations of a pine looper population in Holland. The year to year changes of density are mainly due to first instar larval mortality over 1950-1963, to a non-specific ichneumon fly over 1964-1974, while the crash 1975-1976 is caused by a polyphagous egg-parasite.

least two alternate hosts on birch which are infected in July. The new generation emerges from these alternate hosts in September. Birch trees do not occur in our study plot, but are present in large numbers at distances of 500 meters or more. Large numbers of the parasite probably invaded the study plot in the late summers of 1965, 1966, and 1967, because the low numbers emerging there in June could not have been responsible for the high proportion of larvae subsequently attacked in the autumn.

Variations in juvenile mortality still played a part over this period, as shown by the variation in the steepness of the decline in looper numbers from 1963 to 1967. The much more dominant effect of pupal parasitism is, so to speak, superimposed on the variable effects of the juvenile mortality.

Then, finally, there was a sharp decline of larval numbers in the 1976 generation. This was caused by a 98 percent kill of the eggs, due mainly to the polyphagous egg parasite, *Trichogramma embryophagum* Htg. With some exceptions, this parasite killed from 20 to 40 percent of the eggs in previous years. It is highly polyphagous and may have invaded the study plot from the surrounding deciduous forests; further, its host searching may have been favourably influenced by the extremely high temperatures (30-35° C) over a considerable part of June. Whatever the cause may be, the egg parasite acted as a key factor in that year and affected population change to an extent never before observed.

For trend prediction, an occasional switch of key factors over time has far-reaching consequences. For the pine looper, it implies that in outbreak areas, larval density in August should be intensively censused annually.

All this means that trend prediction in forest insects is of limited applicability, and this implies that as yet there is no good basis for decisionmaking with respect to control actions, because the principal data needed for maximization of the benefit/cost ratio given at the start are not available.

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Detecting Forest Insect Pests in Canada

Gordon M. Howse¹

The Forest Insect and Disease Survey is an operational unit within the Canadian Forestry Service charged with the responsibility of detecting and evaluating forest pest outbreaks on a nationwide basis throughout Canada. In 1956, Blair M. McGugan, who at the time was the Survey Coordinator attached to Divisional Headquarters at Ottawa, presented an excellent paper describing the origin and development of the Canadian Forest Insect Survey at the Tenth International Congress of Entomology in Montreal. The intent of this article is to review McGugan's paper briefly, to describe the present capability of detecting forest insect pests in Canada, and finally, to offer a few comments about the future.

Canada is a large country. It is the second largest country in the world, with an area of about 10 million km². It extends 9248 km from coast to coast, and shares a common border with the United States for 6400 km.

Much of Canada is covered by forests which stretch across the continent in an unbroken belt 960 to 2080 km wide. These forests are among our greatest renewable resources and provide raw material for the lumber, pulp and paper, plywood, and other wood-using industries that are so vital to our economy. In addition, the forests of Canada control water runoff and prevent erosion, shelter and sustain wildlife, and offer unmatched opportunities for human recreation and enjoyment. Productive forests cover nearly 2.6 million km². The total volume of wood in these forests is estimated at nearly 22 billion m³. Four-fifths of this wood is coniferous and one-fifth is deciduous.

The nature of the forests in any country is influenced by many factors, including climate, geology, and topography. In Canada, different combinations of these factors and

the post-glacial migration of tree species from the south have resulted in eight distinct forest regions (fig. 1), which may be subdivided further into 90 sections, each with its own ecological characteristics. The largest of these regions, occupying three-quarters of Canada's productive forest area, is known as the Boreal Forest, stretching in a broad belt from the Atlantic Coast westward and then northwest to Alaska. The forests of this region are predominantly coniferous, with spruces, balsam fir, and pines the most common species. Many deciduous trees are also found in the Boreal Forest, with poplar and white birch being the most widespread. The Great Lakes-St. Lawrence and Acadian regions are found in eastern Canada south of the Boreal Forest. Here the forests are mixed, with many species represented. The principal conifers are white and red pine, hemlock, spruce, cedar, and fir. The main deciduous trees are yellow birch, maple, oak, and basswood.

Entirely different in character is the Coastal Region of British Columbia. Here the forests are coniferous, and because the climate is mild and humid and rainfall is heavy, the trees are very large in comparison with those in the east. The principal species are cedar, hemlock, spruce, fir, and Douglas fir. In the Subalpine, Montane, and Columbia regions of western Alberta and the interior of British Columbia, lodgepole pine, Englemann spruce, and several true firs are found along with Douglas fir and other coast species. The only true deciduous forests in Canada occupy a relatively small area in the southernmost part of Ontario, which is predominantly an agricultural district.

The British North America Act (1867) is the core of the Canadian constitution. It specifies the major arrangements governing the organization of the government and the division of powers between the central (or federal) government and the provinces. Canada today consists of ten provinces and two huge northern territories (fig. 2). The provinces from east to west are Newfoundland, Nova Scotia, Prince Edward Island, New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, Alberta, and

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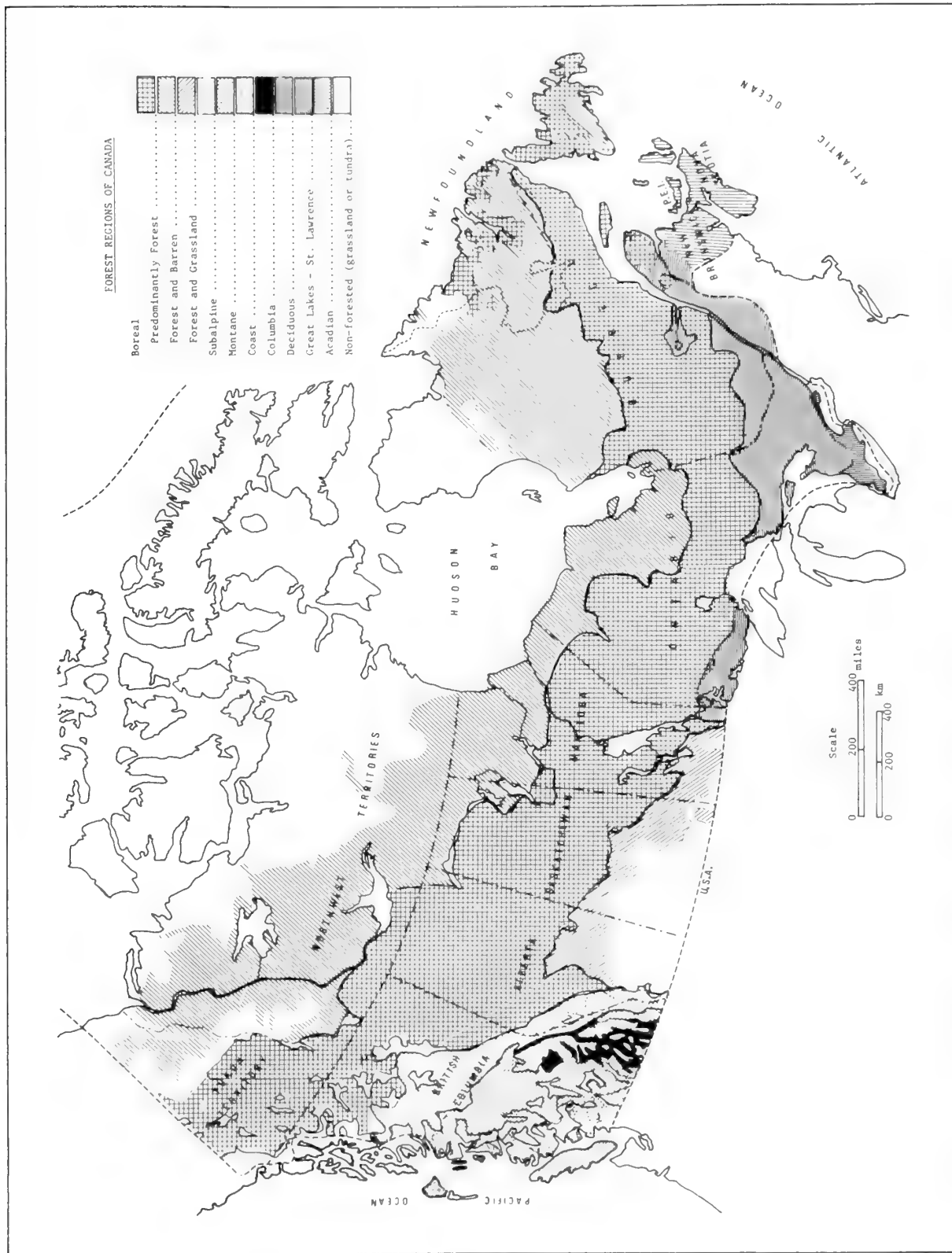


Figure 1.--Canada has eight distinct forest regions. The Boreal Forest is the largest region and covers about 75 percent of Canada's productive forest land. Within the eight forest regions, 90 forest sections have been designated. Some 140 tree species grow in Canada.

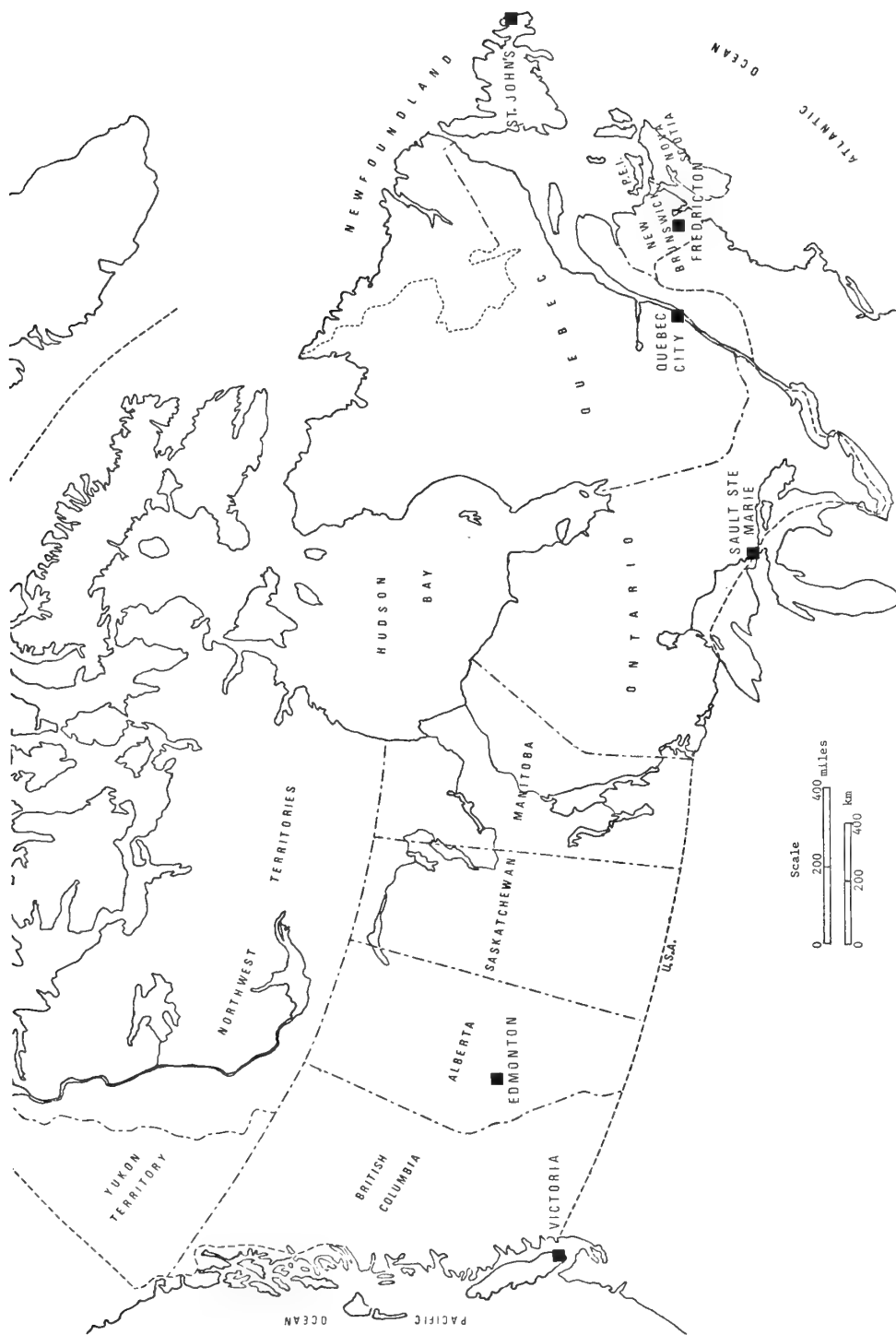


Figure 2.—Canada comprises 10 provinces and two northern territories. This huge area is covered by the Forest Insect and Disease Survey as part of the function of six regional forest research centres. (Black squares represent forest research centres.)

British Columbia. In addition, there are the Yukon and the Northwest Territories. Each province has its own governing structure whereas the territories still come under the jurisdiction of the federal government.

Eighty percent of Canada's productive forest land is publicly owned. This condition was established by the British North America Act, which assigned to the various provincial governments the exclusive right to enact laws regarding management and sale of public lands within their boundaries, including the timber and wood on those lands. In the northern territories, which contain only about 8 percent of the country's productive forest land, the forests are administered by the federal government.

For many years, the policy of both the federal and provincial governments has been to retain in public ownership all lands not required for agricultural purposes. In some of the older settled areas of Canada, however, the proportion of privately-owned land is high. This is especially so in the three Maritime (Atlantic) provinces where nearly two-thirds of the productive forest area is privately owned. Thus, the administration and protection of most of Canada's productive forest area is vested in the various provincial governments, which make the forests available to private industry through long-term leasing and other arrangements. With 11 different forest authorities in Canada, a great diversity of policies and forest laws might have been expected to develop; in fact, the similarities are far more significant than the differences. And furthermore, although most of the productive forest land in Canada is publicly owned, virtually all timber harvesting is carried out by private industry, an arrangement believed to be unique among the major wood-producing countries.

It is estimated that 99 million m³ of wood are cut each year from Canada's forests. About 90 percent of the wood harvested is coniferous while the remaining 10 percent is deciduous. In addition to the wood used by industry, it is estimated that more than 56.6 million m³ are lost to insects, diseases, and forest fires on an annual basis. Much of the effort to prevent losses by these major natural enemies is carried out through more intensive forest management, reforestation, basic and applied research, forest pest surveys, and control operations.

In Canada, the federal government concentrates much of its forestry effort on research, which is carried out by the Canadian Forestry Service of the federal Department of the Environment. Forest research is also conducted by

provincial governments and universities.

The Canadian Forestry Service operates laboratories, field stations, and experimental areas in six regions across the country, as well as a number of institutes in Ottawa and elsewhere. Extensive research, both basic and applied, is carried out on forest management, forest fire control, forest insects and diseases, and forest products. The Canadian Forestry Service is also responsible for conducting surveys of forest insect and disease conditions across Canada and for providing informational and educational material for the public on the wise use of the nation's forests.

With the foregoing summary serving as both an introduction to the topic and an overall framework, it is evident that the function of detecting forest insect pests, at least in the Canadian context, is not a simple task. The sheer physical size of the area presents a formidable challenge. A well-organized team of field and laboratory personnel possessing considerable knowledge, skill, and ingenuity is required to monitor pest situations effectively under conditions such as we face in Canada.

In 1931, the Division of Forest Insects of the Entomological Branch organized a service known as "Forest Insect Intelligence Service." A number of special circulars on the principal forest insects was published giving popular accounts of the life history and habits of the pests as well as colored illustrations showing the insects themselves and the nature and appearance of the damage caused by them. These circulars, together with printed questionnaires, were sent to the forest industry and provincial forestry services with the request that they be distributed to the men working in the forest and that these men be asked to make reports on the occurrence of insects in their respective districts. The plan met with general approval and valuable information was received.

In 1936, a regional survey was started in eastern Canada for the specific purpose of assessing the status and spread of the introduced European sawfly. The first receiving center for forest insect reports and collections was established in Ottawa in 1936. A national Forest Insect Survey was proposed in 1937 to include forest insects generally and other receiving centers were set up in 1937 at Fredericton, New Brunswick and Vernon, British Columbia, at Duschenay, Quebec in 1938, at Indian Head, Saskatchewan in 1940, and at Winnipeg, Manitoba in 1941.

In these early years, the Forest Insect Survey relied primarily upon observations and

collections provided by cooperators in the field. These cooperating personnel were highly fire-oriented, with little training or interest in biology or entomology, and the overall quality of the work was relatively poor -- though certainly better than nothing. After World War II, Forest Insect Survey Groups, including a ranger service (field) of subprofessional staff, were established at the following centres: Fredericton, New Brunswick, Sault Ste. Marie and Ottawa, Ontario, Indian Head, Saskatchewan, and Vernon, British Columbia in 1945; Calgary, Alberta in 1948; Victoria, British Columbia in 1949; Truro, Nova Scotia in 1953; Winnipeg, Manitoba in 1954; and Corner Brook, Newfoundland in 1955. In 1953, the Sault Ste. Marie laboratory accepted responsibility for all of Ontario, and the original Ottawa Survey Centre was disbanded. Survey activities of the Indian Head laboratory, which had dealt with prairie shelterbelt, were discontinued in 1954, and responsibilities were divided among the Winnipeg and Calgary laboratories. The province of Quebec operated an independent survey, cooperating closely with the federal laboratory in Quebec until 1973, when the Laurentian Forest Research Centre took over full responsibility for all aspects of forest insect and disease survey there.

Forest disease surveys were gradually incorporated into the organization throughout the 1950s, although development in this area was slow and most rangers required training in forest pathology.

A processing system for field data was inaugurated in the early 1950s using Remington-Rand equipment which was later converted to a fully automatic IBM system in the late 1960s. The original Remington system proved quite useful: it was employed, for example, in the preparation of regional summaries for major compilations such as the Forest Lepidoptera of Canada series initiated in 1958.

Although the general aims of the Forest Insect Survey have changed little over the years, the methods and emphasis have undergone considerable adjustment. The primary purpose of the Survey was, and still is, the detection of insect outbreaks and an annual census of important forest insect conditions. Initially, this was accomplished almost exclusively through the use of cooperators but results, while encouraging, allowed only broad qualitative interpretation. Following 1945, a small staff of forest biology rangers was hired for the purpose of instructing and working with cooperators. Before long, the rangers were providing most of the collections and observations, and these were of consistently good quality. As a consequence, ranger staffs were

increased, coverage and detection became more comprehensive and complete, and the use of cooperators was de-emphasized. As McGugan stated in 1956, "there was a trend from what might be termed the 'taxonomic phase' of the Survey to the 'ecological phase'." The ecological phase lasted from the mid-1950s until the late 1960s. We are now in an "economic phase" -- economic in the sense that our attention, in terms of detection and evaluation, is focused on the most important, or potentially important, insect pests known, and on their hosts. In retrospect, the change in emphasis from the "ecological phase" -- which was really a broad, faunistic survey -- to the "economic phase" was probably natural and realistic, although it was hastened considerably by events of the winter of 1969-1970. In 1969, severe budget constraints required a major reorganization and retrenchment, including the closing of the Winnipeg laboratory and the amalgamation of the three prairie provinces into the Prairie Region, with headquarters in the Northern Forest Research Centre in Edmonton. The various Survey Units across the country sustained major cutbacks in staffing, which required considerable reorganization and a consequent shift in emphasis. All regions were forced to reduce the number of forest biology rangers (technicians) on field assignment, thereby increasing travel time and the size of the survey districts under surveillance.

At present, the operational responsibilities of the Forest Insect and Disease Survey cover the whole of Canada, as part of the function of the six regional forest research centres (fig. 2). For survey purposes, the country is subdivided as follows: the province of British Columbia and the Yukon Territory are assigned to the Pacific Forest Research Centre in Victoria, British Columbia; the three prairie provinces and the Northwest Territories to the Northern Forest Research Centre in Edmonton, Alberta; the province of Ontario to the Great Lakes Forest Research Centre in Sault Ste. Marie, Ontario; the province of Quebec to the Laurentian Forest Research Centre in Quebec City, Quebec; the three maritime provinces (New Brunswick, Nova Scotia, and Prince Edward Island) to the Maritimes Forest Research Centre in Fredericton, New Brunswick; and Newfoundland-Labrador to the Newfoundland Forest Research Centre in Saint John's, Newfoundland.

The staff organization and resource required to conduct Survey functions within each region may be summarized as follows, although it must be borne in mind that there is some variation from region to region (see figure 3 for Ontario's organization structure). In each forest research centre, Survey operates under the general direction of a program man-

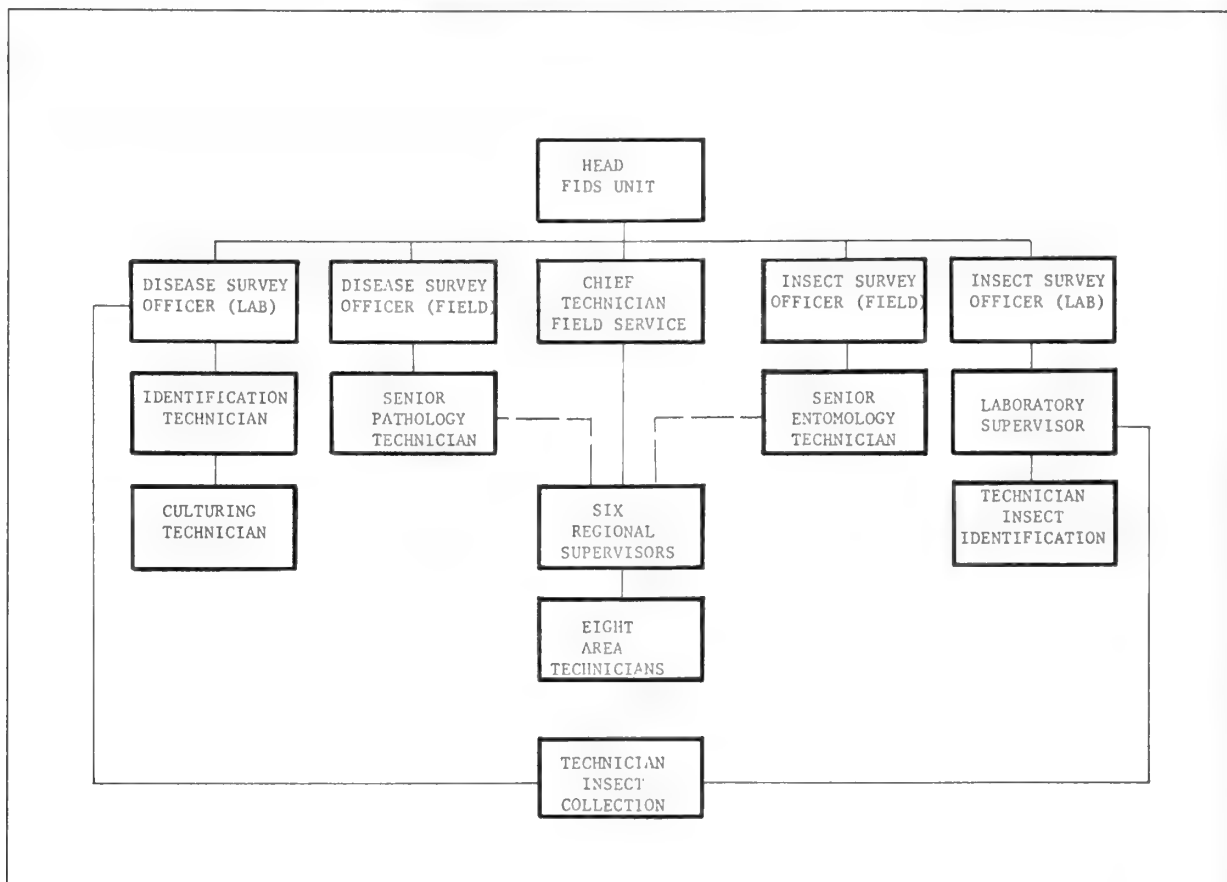


Figure 3.--Staff organization of a regional Forest Insect and Disease Survey Unit. This particular chart illustrates the organization of the Survey Unit in Ontario at the Great Lakes Forest Research Centre, Sault Ste. Marie.

ager in charge of forest protection. Survey is the largest single unit or project in each region and is headed by a professional with many years of experience in pest surveys. At the professional level, he is supported by an Insect and a Disease Survey Officer, an entomologist, and a pathologist, respectively. Professional officers also head up the insect and disease diagnostic and technical services in most centres. The professionals advise the Survey head in their particular disciplines and participate in planning and executing the program. The support professionals also carry out survey-oriented research as time permits.

Appropriate technical support is provided in all units. This support varies according to regional program priorities, but covers certain core areas. The backbone of the detection function is provided by the district-assigned ranger who also carries out major liaison and technical service duties and takes part in appraisals, usually in the off-season. Normally, the activities of one or more district rangers are supervised by a senior ranger who also covers a survey dis-

trict. A chief ranger is responsible for the overall supervision of the rangers. One or more technicians support each of the insect and disease diagnostic and taxonomic service groups, appraisal or research functions.

In all, the six regions have been allocated approximately 24 man years of professional staff and more than 90 man years of technical staff. In addition, varying amounts of student and casual support are allotted to Survey depending on their availability and on Survey requirements. Approximately \$2 million is required annually for salaries, travel, and supplies.

A fundamental question one might ask is: "Why do we want to detect forest insect pests?" In the author's opinion, the purpose of detection surveys is summed up in the following three objectives:

1. To determine the distribution of native insect organisms and their damage.

Pest distribution data have been gathered and recorded for some 40 years

or more. Much of the information has been published or otherwise made available but much still remains in files or on punch cards awaiting analysis.

The second, and perhaps most important, objective is to detect changes in population or damage levels of selected organisms known to be potentially damaging, especially to discover rising, and possibly threatening, populations and outbreaks. The delineation of outbreaks may be considered part of this objective as well as being the first step in the appraisal process.

Most of Survey's current efforts and resources are directed toward meeting this objective. Control or management actions usually result from this type of activity. For example, aerial control operations have been mounted against some 24 different forest insect pests in Canada in recent years. In the Ontario Region, forest insect pests have been classified according to a historical analysis of outbreaks and damage so that priorities have been established. For example, there are nine species in Category 1 (highest priority), which includes insects of major importance to forestry in Ontario because of their continuous or recurring abundance and their severe direct or indirect impact on trees. Among these insects are such well known pests as spruce budworm, jack pine budworm, larch sawfly, forest tent caterpillar, European pine sawfly, white pine weevil, native elm bark beetle, smaller European elm bark beetle, and saddled prominent. In Category 2 are insects or complexes of species causing appreciable damage to natural stands but usually over a period of several years or in a limited area, mostly with unknown impact. This category contains some 24 species such as large aspen tortrix, poplar leafroller, birch skeletonizer, oak leaf miner, etc. In Category 3 are insects causing appreciable damage primarily to plantings or nurseries and somewhat less damage to natural forests. Some 29 species are considered, including Leconte's sawfly, red pine sawfly, root and shoot weevils, bud and shoot miners, cutworms, aphids, spittlebugs, and June bugs. In Category 4 are insects known to have caused appreciable forest losses elsewhere in North America and considered to be potentially serious forest pests of Ontario. Included here are some 16 species, such as gypsy moth, European spruce sawfly, balsam woolly aphid, and hemlock looper. Category 5 contains 16

species that are important primarily because of damage done to shade trees; Category 6, species or groups causing damage to finished or partially processed wood (six families); Category 7, insects known to have caused limited damage in small areas (71 species); Category 8, species found commonly each year but only in low numbers in the history of Survey (105 species); Category 9, species causing damage to unimportant tree species such as alder, willow, cherry, etc. (46 species); and Category 10, species collected infrequently (2770 species).

The rangers concentrate their attention on those species in the first four categories. Emphasis is placed on the economically important tree species that occur within the Survey Region, and it is damage to those species that is of primary concern. When Survey was reorganized in 1969-1970, it was felt that since detection must now be carried on in larger areas than had been the case previously, field staff would not normally be able to detect changes in insect populations at low levels. Therefore, rather than look for insects (general collecting), they were instructed to look for damage. These, of course, are general instructions to the field staff, and, in some cases, special surveys designed to detect the presence, change in abundance, or spread of a particular insect are frequently organized.

- 3. The third objective is to detect the introduction of insects exotic to the region.*

While vigilance is maintained continually for introduced pests because they pose a special danger, specific attention to particular exotic species by specially designed surveys is the method most likely to succeed.

These objectives, therefore, represent the major reasons for detecting forest insect pests. The next question that needs to be dealt with involves our procedures and methods, or, in other words, our technical capability, for meeting our detection objectives. How are forest insect pests detected? The main reliance for detection is placed on the Survey rangers who carry out a series of planned or impromptu observations in their districts. These are frequently supported by quantitative sampling procedures designed to monitor, at their appropriate life stages, the populations of particular insects. Ground vantage point and aerial observation (fig. 4) are employed by the rangers seeking



Figure 4.--Prompt detection of forest pest problems in Canada's forests requires frequent and comprehensive aerial observations.

visible indication of the presence of pests. Sampling involves a variety of methods suitable to the particular pest stage sampled. Foliage may be removed from tree crowns (with pole clippers or a line thrower) and examined (fig. 5), or beating samples may be taken. Light traps and pheromone traps are used, although interpretation of numbers of insects trapped is uncertain. However, traps of this type are useful for detecting the presence of a particular species. They are relatively inexpensive and some limited conclusions may be drawn regarding numbers. Per-

manent sampling plots, while not as useful a detection procedure as "blind" or random sampling, do provide good information on year-to-year population trends; however, the high costs of permanent sampling plots require a close look at their cost/benefit status.

It is difficult to state just where remote sensing stands in relation to forest insect pest detection. There seems to have been some oversell concerning satellite capability for detecting forest insect outbreaks, and methods have not yet been developed for



Figure 5.--A forest research technician with the Forest Insect and Disease Survey is shown using a pole clipper and basket to collect spruce budworm infested foliage from the mid-crown of a balsam fir tree. A basket is used to prevent loss of active, later instar larvae (when they are in the later stages of growth).

operational application. In Canada, ERTS or Landsat imagery and high altitude photography are still in the experimental stage, at least as far as detection is concerned. It is to be hoped that this is primarily a question of technology and will eventually be resolved. Lower altitude aerial photography is fairly commonly used for purposes of delineating outbreaks or assessing damage. The detection aspect would not seem to be particularly significant.

What will the future bring to the function of forest insect pest detection? It is difficult to foresee how we can improve significantly upon the insect ranger with a good pair of eyes, an inquisitive nature, and a thorough knowledge of his district. Undoubtedly, technological advances will occur that will be useful or less expensive than existing methods. Satellite imagery and high altitude photography are examples that come to mind. But there is no replacement for the field man.

Apart from technological advances or standardized nationwide approaches to detection, prediction could become the principal tool of Survey personnel. The basic elements of prediction are available, although our knowledge of many is limited at the present time. Examples of these elements are knowledge of the insect (i.e., its life history, behavior, etc.), its abundance as determined by its environment and other factors, population behavior in relation to climate, cyclic patterns, knowledge of migratory patterns and behavior and monitoring thereof, knowledge of our forests, and so on. In other words, if we possess enough knowledge about the systems involved and can monitor or measure the appropriate parameters, it might be possible to predict when and where outbreaks will occur. This brings us back to detection. Appropriate management action dealing with

a pre-outbreak situation would probably be much more effective and much less costly. At the present time, we depend largely on, and respond to, visible symptoms such as damage or large numbers of insects. Management actions in this situation are costly and probably will not change the course of events.

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Survey of the Nun Moth, *Lymantria monacha* L.,
in the Swiss Alps by Means of Disparlure

J. K. Maksymov¹

The nun moth, *Lymantria monacha* L., is considered to be one of the most destructive pests existing today in the coniferous forests of Europe. Outbreaks have occurred periodically in Germany, Austria, Czechoslovakia, Poland, Rumania, the USSR, and Spain. In recent years, outbreaks have been reported from Sweden and Denmark, also.

In Switzerland, outbreaks occur only in the Alps. The last outbreak 11 years ago in the southwest Swiss Alps affected 300 ha (740 acres) at an altitude of 1100 to 1600 m (3600 to 4250 feet). The forestry service was taken by surprise at this turn of events, for the population buildup had remained unnoticed. For this reason, we are interested in an effective early survey method.

The attraction of nun moth males by females has been known for a long time; this behavior was put to practical use for the first time in 1931 (Ambros 1937). In 1949, the reciprocal attraction of the nun and gypsy moth males by the females of the other species was discovered (Görnitz 1949), and in 1955, this was confirmed by means of additional experiments (Schwinck 1955). Following the synthesis of disparlure in 1970 (Bierl *et al.* 1970), the first field experiments were carried out in Germany, Czechoslovakia, and Denmark to test the effectiveness of this product against the nun moth (Schoenherr 1972; Skuhravy *et al.* 1974; Schroeter and Lange 1975). Recent investigations have shown that the natural sexual attractant of the nun moth chemically is identical with disparlure (Bierl *et al.* 1975). The optical identity of these two substances has not been established, however.²

Tests with disparlure-baited traps were first carried out in the Swiss Alps in 1973, and systematic experiments have been conducted since 1974.

Table 1 shows the sites and number of traps. One site is in the Rhone Valley (Albenwald) while all others are in the Zermatt Valley. The type of trap used was the Pherocon 1 C Trap, manufactured by Zoecon of Palo Alto, Calif. In 1974, three traps were placed at each of the eight sites in the Zermatt Valley and six were placed at Albenwald. The following year, the number was doubled at the Zermatt Valley sites and nine were used at Albenwald. The traps were placed in a horizontal line along the slope of the mountain, 2 to 3 meters (6 to 10 feet) up on the trunks of trees, and 20 to 40 meters (65 to 131 feet) apart from one another. In the 1974 experiments, the traps at each site were baited with three different concentrations of disparlure: 0.1, 0.2, and 0.4 mg. As no significant difference in the number of males attracted resulted from the use of different concentrations, only two concentrations were used in 1975, 0.1 mg (A) and 1 mg (B). The lower disparlure concentrations in 1974 and 1975 were applied in cotton rolls -- much like those used by dentists -- along with 3 mg of Trioctanoin in order to retard the release of the attractant. The higher concentration in 1975 was placed in plastic caps with no additional ingredient, with the caps themselves taking over the function of the carrier.

Table 2 shows that in 1975 the traps containing the stronger concentration attracted significantly more moths than those with weaker concentrations in all sites. This is

¹ Swiss Federal Institute of Forestry Research, 8903 Birmensdorf/Zurich, Switzerland.

² Results of field experiments in Germany support in the meantime the opinion that *L. dispar* secretes (+) -disparlure,

whereas *L. monacha* produces both (+)- and (-)-disparlure [Klimetzek, D., Loskant, G., Vite, J.P., Mori, K., 1976: Disparlure: differences in pheromone perception between Gypsy Moth and Nun Moth. - Naturwiss. 63, 581-582].

Table 1.--Distribution of disparlure-baited traps in the Albenwald and the Zermatt Valley, 1974/75

Site	Tree species	Aspect	Altitude m	1974	1975 A ³	1975 B ³	
						+	
Albenwald	Fir,Spr,La,Pi ²	N	1150	6	6	+	3
St. Niklaus	Spr,La,APi	NW	1400	3	3	+	3
Herbriggen R ¹	La,Spr	W	1350	3	3	+	3
Herbriggen L	La,Spr	E	1300	3	3	+	3
Randa R	La,Spr	W	1400	3	3	+	3
Randa L	La,Spr	E	1400	3	3	+	3
Täsch R	La,Spr	W	1450-1500	3	3	+	3
Täsch L	La,Spr	E	1450-1500	3	3	+	3
				27	27		24

- 1 R and L designate opposite sides of the valley
 2 Fir = Silver fir
 Spr = Norway Spruce
 La = European larch
 Pi = Scotch pine
 3 APi = Alpine pine
 A = 0.1 mg and B = 1 mg concentrations of disparlure

Table 2.--Number of *L. monacha* males in disparlure-baited traps in the Albenwald and the Zermatt Valley, 1974/75

Site	Number of males 1974		Disparlure 0.1 mg Number of males 1975A		Disparlure 1 mg Number of males 1975B	
	Total	Per trap	Total	Per trap	Total	Per trap
Albenwald	293	48.8	183	30.5	237	79
St. Niklaus	100	33.3	69	23	198	66
Herbriggen R	99	33	52	17.3	217	72.3
Herbriggen L	65	21.7	81	27	161	53.7
Randa R	99	33	69	23	96	32
Randa L	66	22	14	4.7	63	21
Täsch R	56	18.7	17	5.7	30	10
Täsch L	35	11.7	8	2.7	29	9.7

also evident from figure 1, showing the catches at Albenwald in 1975.

Upon looking at the male catches by the lower disparlure concentrations in 1974 and 1975, it is noted that with one exception the catches in 1975 were lower than those of 1974 (table 3). This may be due to the competitive effect of the traps with the higher concentration. In the case of the one exception (a gain of 24 percent per trap in Herbriggen L), this might be pure chance, but a local increase in population might have been the cause.

If one similarly compares the results of 1975 using 1 mg disparlure with those of 1974 using 0.1 to 0.4 mg, one notices that at only four sites were significantly better catches obtained using the stronger concentration. At four other sites in the upper part of the valley, the number of males caught per trap using the stronger concentration

remained below that of the previous year. This might be explained by the fact that there were approximately the same number of moths in this area as in the previous year, and the males simply were distributed over more traps.

Table 4 is an attempt to correlate the total number of males attracted in each of the two years with the estimated forested area below the line of traps, whereby the following assumption was made: The males react to the disparlure only toward evening (Schroeter and Lange 1975). At this time of day, the wind is moving downward along the slope of the mountain. Since the source of scent can only be detected downwind, this makes the forested area below the traps a potential source of moths which can be attracted. The area assumed to be affected by the attractant was increased at all sites in 1975 due to the increase in number of traps used that year as compared with 1974. The percent increase in

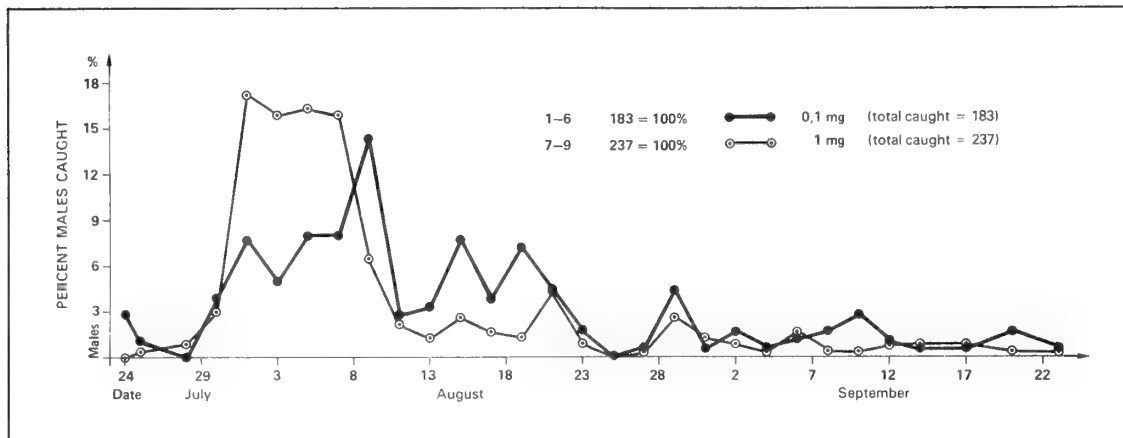


Figure 1.--Percentage of male moths caught in disparlure-baited traps by date, with total number caught in the low and high concentration traps -- Albenwald 1975.

Table 3.--Mean number of *L. monacha* males per trap with two disparlure concentrations

Site	Mean number of males per trap			Change in mean number of males per trap		
	1974	1975A	1975B	1975A/74	1975B/74 Percent	1975B/75A
Albenwald	48.8	30.5	79	-37.5	+ 61.9	+159
St. Niklaus	33.3	23	66	-30.9	+ 98.2	+187
Herbriggen R	33	17.3	72.3	-47.6	+119.1	+317.9
Herbriggen L	21.7	27	53.7	+24.4	+147.5	+ 98.9
Randa R	33	23	32	-30.3	- 3	+ 39.1
Randa L	22	4.7	21	-78.6	- 4.5	+346.8
Täsch R	18.7	5.7	10	-69.5	- 46.5	+ 43
Täsch L	11.7	2.7	9.7	-76.9	- 17.1	+259

Table 4.--Comparison of the number of *L. monacha* males in disparlure-baited traps and the forested area possibly influenced by the attractant

Site	Total number of males in traps		Estimated forested area below the traps (ha)		Change 1975 compared to 1974	
	1974	1975	1974	1975	Total no. Males	Forested area Percent
Albenwald	293	420	3.5	7	+ 43.3	+ 100
St. Niklaus	100	267	2	5.8	+167	+ 190
Herbriggen R	99	269	0.6	2.6	+171.7	+ 333.3
Herbriggen L	65	242	0.5	1.2	+272.3	+ 140
Randa R	99	165	0.2	0.4	+ 66.7	+ 100
Randa L	66	77	0.2	0.4	+ 16.7	+ 100
Täsch R	56	47	0.3	1.0	- 16.1	+ 233.3
Täsch L	35	37	0.08	0.4	+ 5.7	+ 400

male moths attracted, however, was markedly less than the increases in forested area. In Täsch R, there was even a decrease. Herbriggen L is again an exception. There the percent increase in moths attracted was almost twice the increase in forested area! This is an additional indication (other than the

evidence of table 3) that the nun moth population had probably increased locally at this particular site.

Table 5 shows the flight period and maximum catch period, as well as the proportion of the male moths caught during this maximum at

Table 5.--Flight period based on moth catches and percent caught during maximum catch period

Site	Flight period							Percent of total catch		
	1974		End	1975		End	1974	1975 A	1975 B	
Begin	Max. Date	Begin		Max. A Date	Max. B Date					
Albenwald	25.7.	27.7.- 8.8.	20.9	24.7.	1.- 9.8.	1.- 9.8.	23.9.	74.1	44.2	70.5
St. Niklaus	25.7.	1.- 6.8.	26.8.	24.7.	6.-20.8.	6.-20.8.	23.9.	73	92.8	84.3
Herbriggen R	23.7.	30.7.- 5.8.	24.9.	30.7.	6.-20.8.	6.-20.8.	23.9.	66.7	76.9	75.6
Herbriggen L	24.7.	30.7.- 2.8.	28.8.	25.7.	6.-20.8.	6.-20.8.	23.9.	76.9	91.4	77.6
Randa R	3.8.	3.-19.8.	28.8.	30.7.	6.-20.8.	6.-20.8.	10.9.	87.9	82.6	82.3
Randa L	3.8.	9.-19.8.	28.8.	30.7.	12.8.	6.-20.8.	10.9.	80.3	28.6	82.5
Täsch R	3.8.	9.-19.8.	28.8.	30.7.	12.8.	12.-20.8.	10.9.	85.7	41.2	70
Täsch L	3.8.	9.-19.8.	9.9.	30.7.	12.8.	12.-20.8.	10.9.	71.4	37.5	62.1

Note: Dates written European style (day, month).

the various sites. The flight period varied from 1 to 2 months over both years. A shorter flight period was characteristic of the upper valley areas. The maximum catch period ranged from 4 to 16 days in 1974 and from 8 to 14 days in 1975. Sixty-seven to 88 percent of the males were attracted during this period in 1974, whereas 44 percent to 93 percent (traps with 0.1 mg disparlure) and 62 percent to 84 percent (traps with 1 mg disparlure) were caught in this period in 1975. In the latter year, no outstanding maximum could be discerned for the traps with the lower concentration (A) in the uppermost sites in the Zermatt Valley (where only 8 to 17 males were attracted).

We intend to extend the experiments for an additional 3 years, and hope to improve the distribution of traps to provide more information on relative numbers and variation in nun moth populations in the Albenwald and Zermatt Valley areas.

I would like to emphasize that the interpretation of the figures given in this paper (tables 1 to 5) should be understood as an indication of tendencies. We hope to present statistically sound figures at a later stage of the experiments.

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II. ASSESSMENT AND PREDICTION OF PEST INSECT IMPACTS ON FOREST USES AND VALUES

214 One Aspect of Damage to the Forest Caused by Insects 214

Keiji Kanamitsu¹

Introduction

The forest ecosystem encompasses a vast number of plants and animals living together. Many insects feed on living trees, which inevitably causes some detrimental effect upon tree growth. There is a concept of threshold density of insect pests (Waters 1971), and most entomologists agree that only when an insect population exceeds a certain threshold density, is the insect considered a pest. Discussion will start with this noxious level of pest density or the level of resulting loss to the forest.

Noxious Pest Density

Yoda (1971) described a relationship between the amount of tree leaves eaten by insects (L) and the amount of their fecal droppings (F), estimated by:

$$L = 1.15 F \text{ (in dry weight)}$$

Thus, about 90 percent of the leaves eaten by insects were returned to the ground as excrement. This excrement contains a great amount of soluble nitrogen and other substances that are nutritious to the tree. Furthermore, some insect cadavers and corpses of secondary animals will also be added to the ground. Thus, comparing this gain of nutrients with the loss of leaves, some low-level density of leaf eating insects may have a beneficial effect upon the forest by recycling nutrients. It is generally accepted in Japan (Furuno 1964, Yamaguchi 1973) that defoliation of less than 30 percent has little effect, while defolia-

tion of more than 50 percent usually causes some serious effect upon trees. The threshold of noxious pest density will then be between 30 percent and 50 percent defoliation.

Yield tables for timber production in managed forests give an indication of normal decrease in tree density by artificial thinning. The following figures were tentatively picked from a yield table for an intensively managed stand of a Japanese cedar, *Cryptomeria japonica* D. Don, at an average site in Japan (Sakaguchi *et al.* 1965), where tree density decreased at a rate of 20-40 percent every 10 years.

Age of Trees	10	20	30	40	50
Trees per ha.	3,000	1,900	1,300	900	700

These figures indicate that the annual decrease in tree numbers is roughly 3 percent. Apparently, this percentage decrease is not a real loss to the forest, but a necessary sacrifice for the remaining trees to attain better growth. Many insects have usually aggregated distributions in the forest, and tree mortality is often patchy. However, if some low percentage mortality of trees were not to be very aggregated, the death of these trees would not be taken seriously, even though it might be caused by insects. Trees injured by insects are usually felled at the time of thinning in a practical management program. The noxious level of pest density can now be explained as causing more than 30 percent tree mortality in 10 years, if stands are normally stocked.

Real Damage to the Managed Forest

The managed forest is not entirely natural, but it usually resembles a natural ecosystem and thereby maintains some degree of natural stability. Real damage to the managed

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forest is mortality exceeding the normal loss (30 percent or less) caused by the normal abundance of insects. Loss of trees below the noxious level of pest density discussed previously is not the real damage to the forest. In forest management, the commercial value of trees killed by insects is usually lower than that of living trees. However, dead trees have some commercial value. Economic loss to the forest is then the reduced value of dead trees that exceed normal decreases in tree density. This interpretation of loss seems extremely important when applying an artificial pest control method, since control costs should be weighed against the commercial losses caused by real damage to the forest.

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* English translation by author.

Measuring Damage to Lodgepole Pine, Caused by the Mountain Pine Beetle (2)

William H. Klein¹

Introduction

The single most important enemy and killer of lodgepole pine is the mountain pine beetle, *Dendroctonus ponderosae* Hopk. During the past two decades, this bark beetle has killed more than 100 million lodgepole pine, and to a lesser extent, ponderosa, western white, and whitebark-limber pines in the intermountain States. During 1958 to 1970, an estimated 18 million dollars was spent to control individual outbreaks, but these efforts were unsuccessful.

Forest managers now face the formidable task of managing vast areas of heavily depleted lodgepole pine forests. As a base for sound planning, there is a need to determine the intensity and extent of tree losses, the recuperative capabilities and growth trends of the beetle-depleted stands, and the overall effect of these stands on resource uses and values; in effect, impact.

With these objectives in mind, an impact survey was planned in 1971, conducted in 1972 and 1973, and repeated in 1975. Four criteria were used for the selection of the survey area and sampling system: First, the infestation had to be recently terminated; second, the area must contain other significant and measurable resources than just timber; third, the area should be small and homogeneous enough to afford efficient sampling, but large enough that whatever changes occurred, they would impact management decisions and practices; and finally, the sample plots must be permanently established and conducive to remeasurement.

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Methods

The survey was conducted on the Ashton Ranger District of the Targhee National Forest in southeastern Idaho; covering an area slightly less than 120,000 acres, including 86,000 acres of lodgepole pine type ranging in elevation from 5,700 to 7,500 feet. The outbreak started during the early 1960s, peaked during the period 1967 to 1969, then rapidly declined. Infestation development progressed from southwest to northeast. Control, using the individual tree standing spray method, was started in the west portion of the survey area in 1964, continued for three consecutive years, then terminated because of ineffectiveness.² Salvage logging is now underway in part of the area.

The basic survey design was a systematic, randomized, double sampling system using 35mm color aerial photography, photo ground truth, and a series of on-the-ground sampling methods (fig. 1). In 1971, 60 stereo triplets at a scale of 1:5000 were taken from a light aircraft in a grid pattern of approximately 1 to 1 1/2 mile intervals. A 4-acre square plot was delimited on the best stereo pair and examined stereoscopically for dead lodgepole pine. These plots served as a base for supplemental sampling:

1. Ground truth for a correlation between photo and actual mortality counts were recorded on 21 randomly selected plots.
2. Stand structure was determined from variable plots (BAF 10) established in the center of each 4-acre plot. All tree species 5-inches dbh and over, living and dead, were recorded. All

² Personal communication with John J. Kincheloe, Toiyabe National Forest. Mr. Kincheloe was Project Director of the mountain pine beetle control program on the Targhee National Forest from 1964 to 1970.

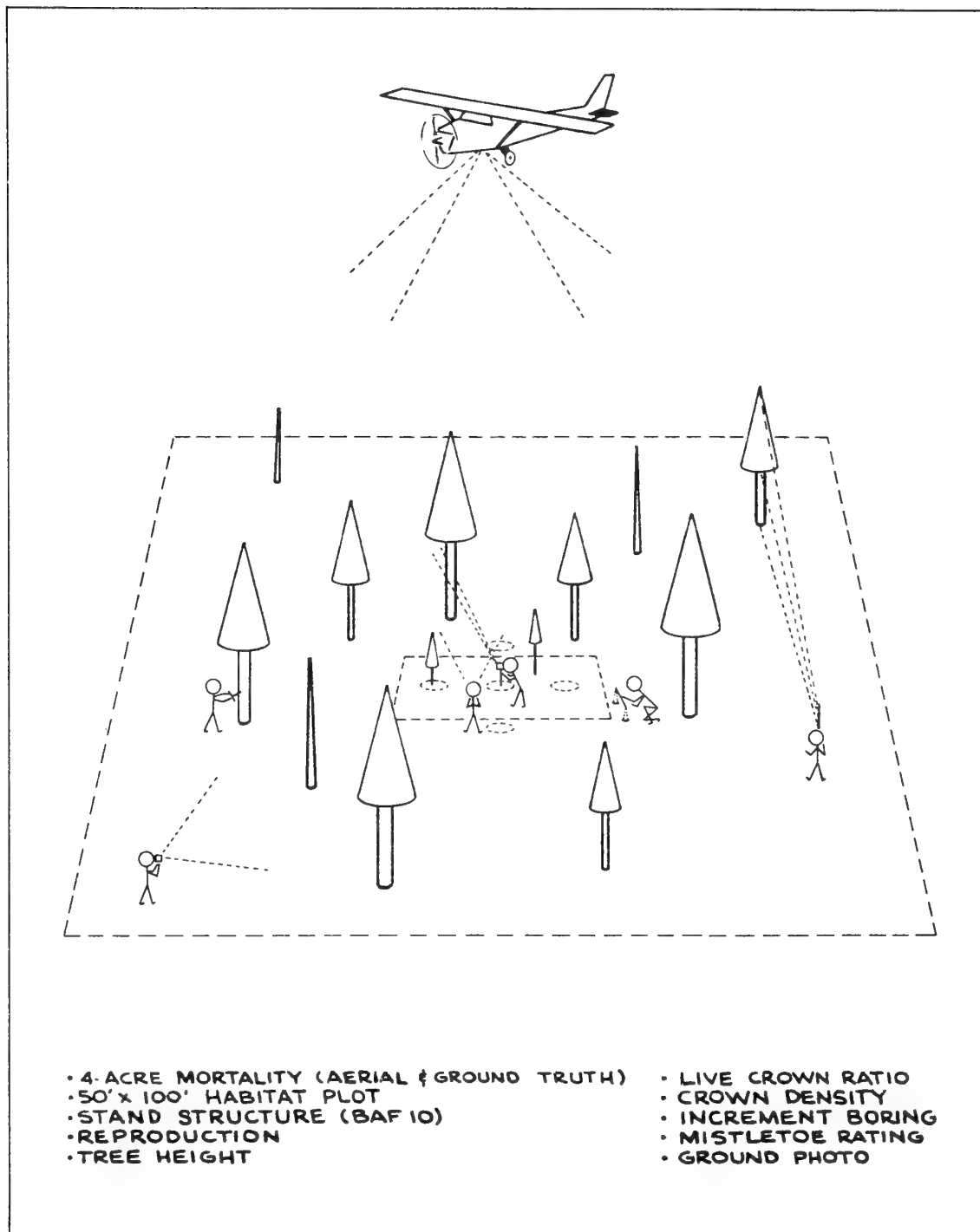


Figure 1.--The basic plot sampling design.

trees were permanently tagged for future reference. Additional data was taken on tree height, live crown ratio, mistletoe occurrence, growth rates, crown density, reproduction, habitat type, and herbage yield. Each plot was permanently marked and photographed on the ground for future comparisons and remeasurements.

Results

Lodgepole pine mortality was estimated two ways: by aerial photography interpretation, and by the variable plot method. Estimates of the number of lodgepole pine per acre killed by the mountain pine beetle by both of

these methods follow:

METHODS	>5 inches dbh	>7 inches dbh
Aerial photos	113.2	71.3
Variable plot	97.7	79.6

Considering the high level of mortality, there was generally good agreement between the two methods. For the photo interpretation portion, the R^2 values for all trees and those 7 inches dbh and greater were 0.80 and 0.94, respectively. The photo method is believed to best describe the overall tree losses as well as diameter distribution, and although there is a disparity between the two methods in the small diameter classes, they are closely in accord with trees greater than 10 inches dbh.

Figure 2 depicts the stand structure, living and dead, following the outbreak in 1972-73 while figure 3 shows the 1972-73 live stand component compared to that measured in 1975. Initial stand mortality of merchantable lodgepole pine 9 inches dbh and greater amounts to 62 percent of the trees and 65 percent of the volume for the lodgepole component and 56 percent of the trees and 55 percent of the volume for the stand (tables 1, 2).

There is a very little overall difference between the two sampling periods. Approximately, six lodgepole pines per acre died, mostly from windthrow (tables 3, 4). However, ingrowth practically nullified this difference. The decrease of approximately eight trees per acre in the 6-inch class may be partially due to ingrowth into the 7-inch class.

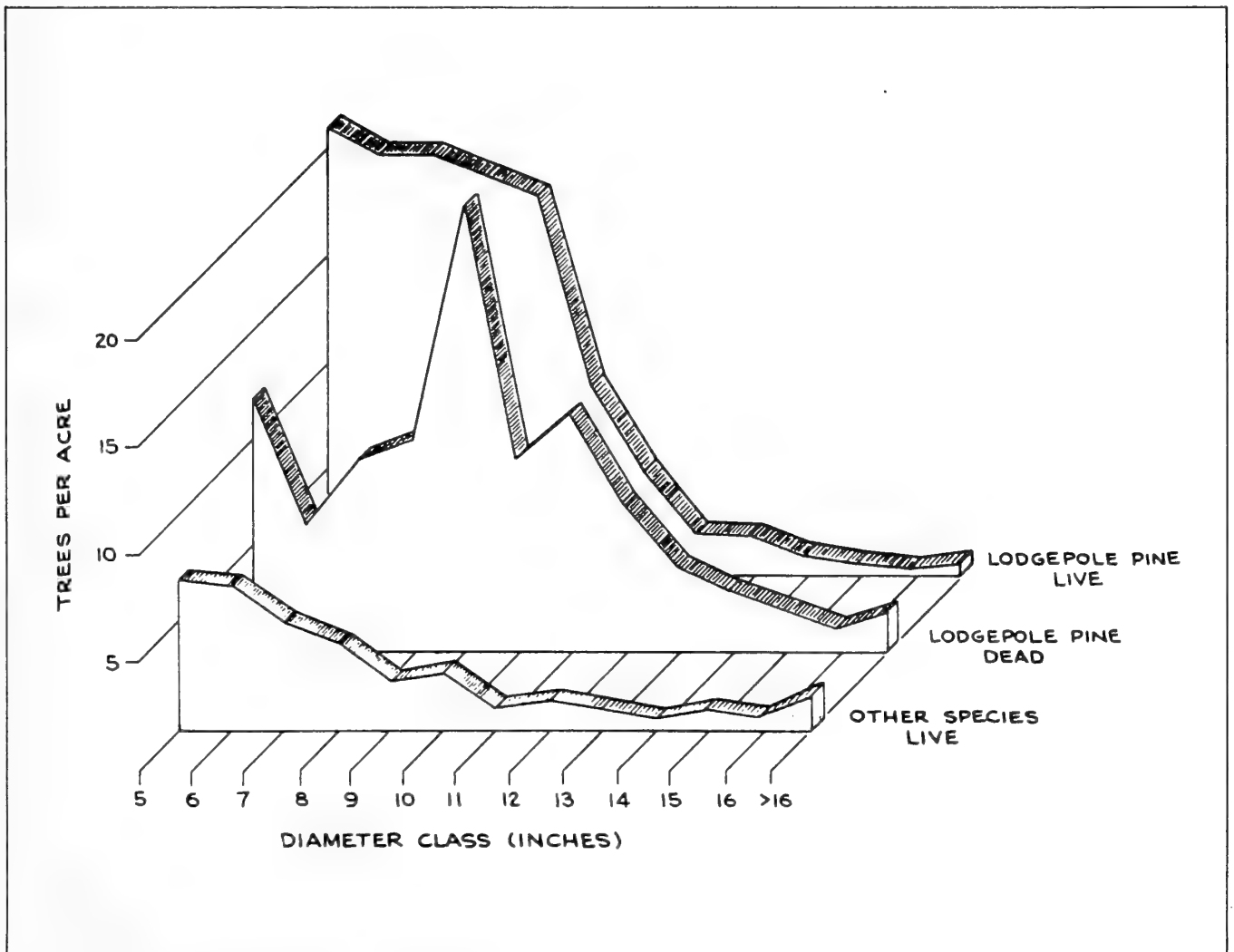


Figure 2.--Stand structure of lodgepole pine forest following an outbreak of the mountain pine beetle, 1972-73.

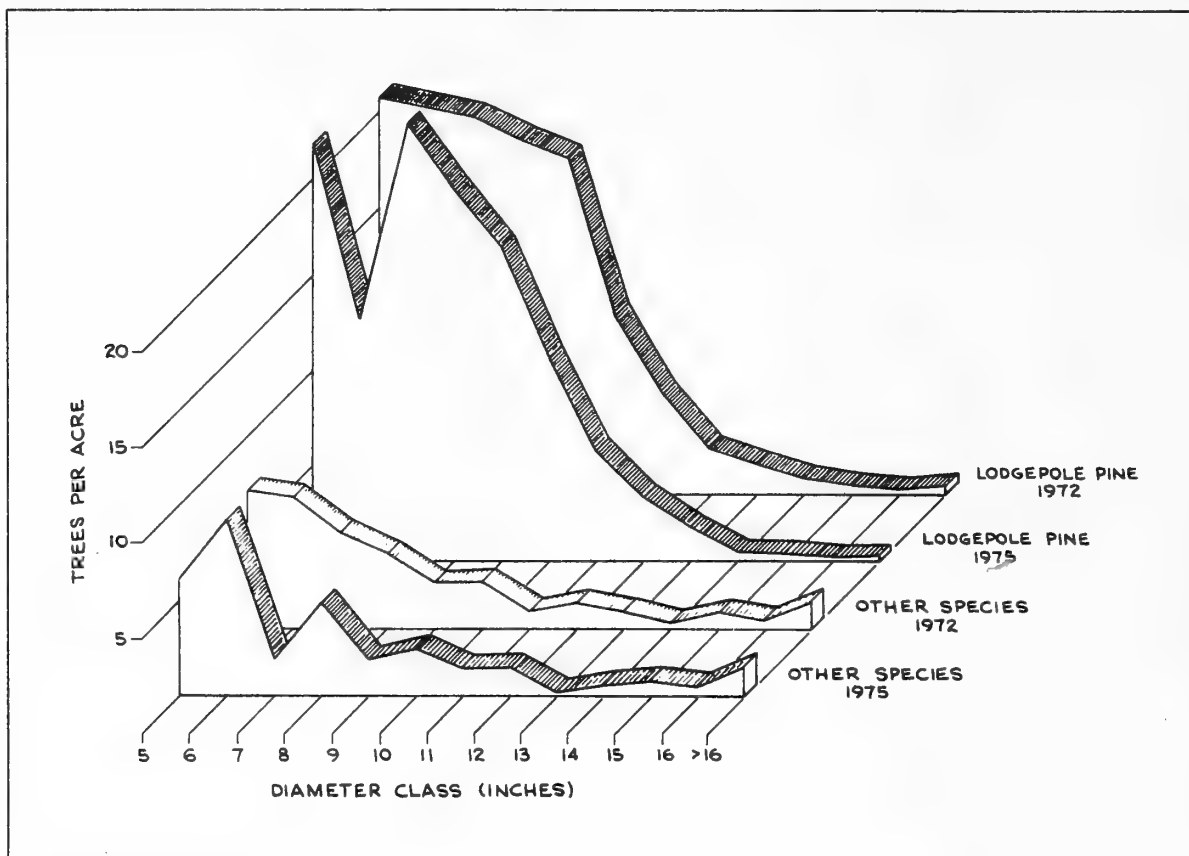


Figure 3.--Comparison of stand structure of mountain pine beetle depleted lodgepole pine forest following an outbreak, 1972-73, and three years later, 1975.

The difference between the two cruises is greater when the data are converted to board feet volume 5 inches dbh and more:

Board feet volume in trees >5-inches dbh

Year	Lodgepole pine		
	Live	Dead	Total
1975	5103	7050	12153
1972	4894	6110	11004
Diff.	+209	+940	+1149

Year	Other species		
	Live	Dead	Total
1975	1797	173	1970
1972	1705	835	2540
Diff.	+92	-662	-570

Year	Total		
	Live	Dead	Total
1975	6900	7223	14123
1972	6599	6945	13544
Diff.	+301	+278	+579

The important factor here is that although some trees, particularly lodgepole pine, continued to die (mostly windthrow and secondary insects), there was a net increase of 301 bd. ft., with lodgepole volume increasing by more than 200 bd. ft. Now that the stand has stabilized somewhat, and barring a natural catastrophe, gains should continue to outstrip the losses.

The implications of this exceptionally heavy tree mortality on forest fire hazard and management is evident. These data eventually will be converted to tons of fuel per acre as criteria for on-the-ground fuel loading and other fire hazard classifications.

Table 5 shows the reproduction component as estimated during the 1972-73 and 1975 surveys. The overall level of stocking for all tree species is more than adequate, but personal observations indicate large variations in both distribution and abundance between areas. Some form of supplemental stand examination may be required to specifically identify those areas inadequately stocked or in need of conversion.

Table 1.--Stand structure (trees per acre) of a lodgepole pine forest following a mountain pine beetle outbreak, Targhee National Forest, 1972-1973

Area	Diam. Class (In.)	Trees per acre						Total	
		Lodgepole pine		Other spp. ²		All spp.			
		Live (No.)	Percent ¹	Dead (No.)	Percent ¹	Live (No.)	Percent ¹	(No.)	Percent ¹
Porcupine	5	20.8	8.2	12.2	4.8	8.6	3.3	41.6	16.3
Targhee N.F.	6	20.4	8.0	5.9	2.3	6.8	2.7	33.1	13.0
	7	19.9	7.8	8.7	3.4	6.9	2.7	35.5	13.9
Basal Area/acre	8	18.6	7.3	10.0	3.9	5.3	2.1	33.9	13.3
	9	17.7	6.9	21.1	8.3	2.6	1.0	41.4	16.2
Live Lpp. 40.0	10	9.2	3.6	9.2	3.6	2.7	1.1	21.1	8.3
Dead Lpp. 51.2	11	5.1	2.0	10.8	4.2	1.3	0.5	17.2	6.7
Other Spp. 15.7	12	2.3	0.9	7.2	2.8	1.5	0.6	11.0	4.3
	13	1.6	0.6	4.3	1.7	0.9	0.4	6.8	2.7
Total 106.9	14	0.8	0.3	3.1	1.2	0.5	0.2	4.4	1.7
	15	0.3	0.1	1.8	0.7	1.1	0.4	3.2	1.2
	16	0.1	0.1	1.3	0.5	0.7	0.2	2.1	0.8
	>16	0.3	0.1	2.1	0.8	1.6	0.7	4.0	1.6
TOTAL		117.1	45.9	97.7	38.2	40.5	15.9	255.3	100.0

¹ Percent of total stand

² Douglas-Fir, Subalpine Fir, Englemann Spruce, Limber Pine, and Quaking Aspen

Table 2.--Stand structure (volume per acre) of a lodgepole pine forest following a mountain pine beetle outbreak, Targhee National Forest, 1972-1973

Area	Diam. Class (In.)	Volume per acre scribner						Total	
		Lodgepole pine		Other spp. ²		All spp.			
		Live (Bd.Ft.)	Percent ¹	Dead (Bd.Ft.)	Percent ¹	Live (Bd.Ft.)	Percent ¹	(Bd.Ft.)	Percent ¹
Porcupine	5	499	3.9	252	1.9	63	0.6	814	6.4
	6	480	3.8	140	1.1	36	0.3	656	5.2
	7	455	3.6	168	1.3	60	0.5	683	5.4
	8	669	5.3	272	2.1	77	0.6	1018	8.0
	9	925	7.3	873	6.9	61	0.5	1859	14.7
	10	643	5.1	588	4.6	126	1.0	1357	10.7
	11	419	3.3	791	6.2	66	0.5	1276	10.0
	12	311	2.4	788	6.2	106	0.8	1205	9.4
	13	213	1.7	528	4.1	85	0.7	826	6.5
	14	124	1.0	496	3.9	68	0.5	688	5.4
	15	60	0.5	296	2.3	162	1.3	518	4.1
	16	14	0.1	257	2.0	135	1.1	406	3.2
	>16	82	0.6	661	5.2	660	5.2	1403	11.0
TOTAL		4894	38.6	6110	47.8	1705	13.6	12709	100.00

¹ Percent of total stand

² Douglas-Fir, Subalpine Fir, Englemann Spruce, Limber Pine, and Quaking Aspen

Table 3.--Stand structure (trees per acre) of a lodgepole pine forest following a mountain pine beetle outbreak, Targhee National Forest, 1975

Area	Diam. Class (In.)	Trees per acre						Total All spp.	
		Lodgepole pine		Other spp. ²		Total All spp.			
		Live (No.)	Percent ¹	Dead (No.)	Percent ¹	Live (No.)	Percent ¹	(No.)	Percent ¹
Porcupine	5	22.0	8.5	14.7	5.6	6.1	2.3	42.8	16.4
Targhee N.F.	6	12.7	4.9	6.8	2.6	11.0	4.2	30.5	11.7
	7	23.1	8.9	8.7	3.3	3.1	1.2	34.9	13.4
Basal Area/Acre	8	19.6	7.5	11.0	4.2	6.2	2.4	36.8	14.1
	9	16.6	6.4	21.5	8.3	2.3	0.8	40.4	15.5
Live Lpp. 41.3	10	10.7	4.1	9.2	3.5	2.7	1.0	22.6	8.6
Dead Lpp. 52.8	11	5.8	2.2	11.6	4.5	1.8	0.7	19.2	7.4
Other Spp. 15.8	12	3.4	1.3	7.2	2.8	2.1	0.8	12.7	4.9
	13	1.8	0.7	4.3	1.6	0.4	0.2	6.5	2.5
Total 109.9	14	0.5	0.2	3.1	1.2	0.9	0.3	4.5	1.7
	15	0.4	0.2	1.8	0.7	1.0	0.4	3.2	1.3
	16	0.1	0.1	1.3	0.5	0.7	0.3	2.1	0.9
	>16	0.2	0.1	2.2	0.8	1.7	0.7	4.1	1.6
TOTAL		116.9	45.1	103.4	39.6	40.0	15.3	260.3	100.0

¹ Percent of total stand

² Douglas-Fir, Subalpine Fir, Englemann Spruce, Limber Pine, and Quaking Aspen

Table 4.--Stand structure (volume per acre) of a lodgepole pine forest following a mountain pine beetle outbreak, Targhee National Forest, 1975

Area	Diam. Class (In.)	Volume per acre scribner						Total All spp.	
		Lodgepole pine		Other spp. ²		Total All spp.			
		Live (Bd.Ft.)	Percent ¹	Dead (Bd.Ft.)	Percent ¹	Live (Bd.Ft.)	Percent ¹	(Bd.Ft.)	Percent ¹
Porcupine	5	560	4.0	308	2.2	18	0.1	886	6.3
	6	300	2.2	160	1.2	80	0.6	540	4.0
	7	531	3.8	210	1.5	29	0.2	770	5.5
	8	720	5.2	352	2.5	68	0.5	1140	8.2
	9	854	6.1	1142	8.2	57	0.4	2053	14.7
	10	762	5.5	630	4.5	144	1.0	1536	11.0
	11	477	3.4	1009	7.2	109	0.8	1595	11.4
	12	394	2.8	816	5.9	160	1.2	1370	9.9
	13	241	1.7	576	4.1	39	0.3	856	6.1
	14	76	0.6	503	3.6	142	1.0	721	5.2
	15	85	0.6	325	2.3	144	1.0	554	3.9
	16	38	0.3	286	2.0	135	1.0	459	3.3
	>16	65	0.5	733	5.2	672	4.8	1470	10.5
TOTAL		5103	36.7	7050	50.4	1797	12.9	13950	100.00

¹ Percent of total stand

² Douglas-Fir, Subalpine Fir, Englemann Spruce, Limber Pine, and Quaking Aspen

Table 5.--Summary of reproduction survey, Targhee National Forest, 1972-73 and 1975

Year	Species	Seedlings		Saplings			
		Trees/acre	Percent	Live		Dead	
				Trees/acre	Percent	Trees/acre	Percent
1972-73	Lodgepole pine	425.0	49.8	104.0	69.4	35.0	66.0
	Subalpine fir	67.0	7.9	8.0	5.3	0.0	0.0
	Douglas-fir	125.0	14.6	18.0	12.0	8.0	15.1
	Englemann spruce	10.0	1.2	2.0	1.3	0.0	0.0
	Quaking aspen	205.0	24.0	7.0	4.7	10.0	18.9
	Limber pine	21.0	2.5	11.0	7.3	0.0	0.0
	All Species	853.0	100.0	150.0	100.0	53.0	100.0
1975	Lodgepole pine	398.0	42.3	75.0	56.4	47.0	75.8
	Subalpine fir	136.0	14.5	21.0	15.8	1.0	1.6
	Douglas-fir	78.0	8.3	20.0	15.0	6.0	9.7
	Englemann spruce	18.0	1.9	3.0	2.3	0.0	0.0
	Quaking aspen	294.0	31.2	3.0	2.3	8.0	12.9
	Limber pine	17.0	1.8	11.0	8.2	0.0	0.0
	All Species	941.0	100.0	133.0	100.0	62.0	100.0

There was relatively high mortality of lodgepole pine saplings between the two surveys (47 per acre) which is primarily due to secondary bark beetles, particularly *Ips* spp.³ which characteristically follow in the aftermath of a mountain pine beetle outbreak (Evenden and Gibson 1940).

The plant association or habitat type analysis is incomplete at this time, but a preliminary scan of the data indicates that more than half of the site study plots were classified as being in the *Pseudotsuga menziesii/Colamogrostis rubescens* (Douglas-fir/pine grass) habitat type. By far the most severe lodgepole mortality occurred in this lower elevation vegetational zone, which differs from that reported by Roe and Amman (1970) who measured the most intense beetle activity in the *Abies lasiocarpa/pachistima mysinites* habitat type or middle elevational zone. It is now known, however, that the severity of mountain pine beetle outbreaks in lodgepole pine is inversely related to elevation (Amman and Stipe 1972). The plant classification and abundance data, coupled

with crown density, may provide some insight into change in forage capacity.

These results are preliminary and stem from only a portion of the data collected during the survey. They are being reported to show the drastic and obvious changes in a lodgepole pine forest caused by the mountain pine beetle. The immediate changes are in stand structure, species abundance and composition, volume, reproduction, and other readily measurable factors that will aid in the identification of major impact areas. Subsequent compilation and analysis of other data such as tree growth rates, mistletoe intensity, habitat relationship, fuel loading, and the collection of supplemental, corroborative data including recreation use trends, streamflow records, changes in road, trail, and fence construction costs, and their analysis and interpretation will be incorporated into a subsequent report. In the meantime, however, it is hoped that this preliminary information will provide the base upon which the final analysis can be built.

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Economic Impact of Mountain Pine Beetle on Outdoor Recreation^{1 2}

E. L. Michalson and Jill Findeis³

This study estimates the economic impact of outdoor recreation as a contributor to total value of forest resources in an area which has been heavily infested by mountain pine beetle. The area of study was the Island Park area in the Targhee National Forest in eastern Idaho. This National Forest includes a popular recreation area west of Yellowstone and Grand Teton National Parks. Recreationists use this area for both destination and nondestination purposes. The recreation opportunities include water sports, hiking, and related outdoor activities. It is classified as one of the major recreation areas of Idaho.

The Island Park area has been heavily infested with mountain pine beetle since 1960.⁴ The major tree species involved is lodgepole pine, which at present is utilized for poles, fence posts, roundwood, cordwood, and pulpwood. The recreation resources of the area are directly impacted by the mountain pine beetle as was indicated by the large number of dead trees observed in infested campgrounds. The question which is uppermost in the minds of the resource managers is: To what extent is the mountain pine beetle affecting recreational and other resource values in the Targhee National Forest? Secondly, how did recreationists react to the large number of dead trees in the infested areas?

¹ The work herein reported was funded in part by an IPM sponsored project entitled, "The Principles, Strategies, and Tactics of Pest Population Regulation and Control in Major Ecosystems." Journal No. 7513, Idaho Agricultural Experiment Station.

² This paper was published previously using estimated rather than actual campground use data in the Southern Journal of Agricultural Economics, December 1975, p. 43-50.

Objectives

The purpose of this study is to estimate the economic impact of the mountain pine beetle infestation on the recreational resources of the area and project this economic impact on the future recreational use of the area. The specific objectives were to:

1. Survey recreational users in selected campgrounds in the Targhee National Forest to obtain information on recreational patterns and uses
2. Develop recreational demand models to estimate the economic impact of mountain pine beetle on recreational use in the Targhee National Forest.

Data

The basic data used in this study were obtained from personal interviews with approximately 500 recreational users in six campgrounds in the Targhee National Forest during July and August of 1973. The campgrounds were selected for this study based upon the degree of mountain pine beetle infestation evident. Three of them were defined as infested (over 50 percent of the trees affected by mountain pine beetle), and three as noninfested (under 50 percent of the trees infested). All areas of the Targhee National Forest exhibit some degree of mountain pine beetle infestation.

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⁴ Rivas, A., 1974. "Economic Evaluation of Mountain Pine Beetle Control on the Targhee National Forest," unpublished report presented at Twenty-fifth Annual Western City, Utah.

The interview procedure was to visit the campgrounds in the evening, leaving questionnaires with the recreationists and allowing them to fill them out overnight. In order to obtain a representative, unbiased sample of the user population, a systematic method of stratified sampling was used. The sample was stratified by campground, and users of each campground were sampled systematically. Questionnaires were collected at different campsites in each campground each day so as to assure a representative sample. Of the 500 questionnaires handed out, 90 percent were returned and 307 were useful in the analysis.

The information obtained from the questionnaires consisted of a profile of recreational users of the area, a catalog of the activities in which they participated, origin-destination data, and the transfer costs of the recreation trip. The transfer costs included the cost of transportation and costs directly related to participating in the recreational experiences.

The tabulated questionnaires indicated that approximately 86 percent of the recreationists were repeat visitors and only 14 percent were first time visitors. Recreation was the major purpose of the trip for the majority (53 percent), and it was a vacation trip for most of them (49 percent). Only 30 percent of these recreationists visited areas besides the Targhee compared to 60 percent who did not, and 90 percent indicated that they planned to return to the area in the future. The activities most frequently participated in were fishing, camping, sightseeing, canoeing or rafting, hiking, photography, swimming, and waterskiing. The average length of stay in these campgrounds was 6.4 days and the average size of group was 3.8 persons. Information on the user's average mileage, travel time, and trip cost is shown in tables 1 to 3.

The differences in the average mileage traveled, average travel time, and average costs of recreating between residents and nonresidents were not very large. The reasons for this were related to the fact that many of the residents visiting the area came from western and northern Idaho which is 500 to 800 plus miles distant by highway. Secondly, when out-of-State people indicate that the major purpose of their recreation trip was to visit some other area, the mileage charged to their visit to the Targhee was computed from the last stop prior to their Targhee visit and on to their next stop. This was done in order to allocate travel costs in a reasonable manner between destination and nondestination recreation. A third factor was that the majority of the out-of-State recreationists who use this area come from northern Utah (approximately a 300-mile trip).

Table 1.--Average miles traveled to and from the Targhee National Forest, 1973

User group	Average mileage to	Average mileage from
Idaho residents	517	465
Nonresidents	612	642
Total sample	550	527

Table 2.--Average travel time in hours to and from the Targhee National Forest, 1973

User group	Average hours to	Average hours from
Idaho residents	47.2	58.5
Nonresidents	57.6	63.9
Total sample	50.7	60.0

Table 3.--Average trip expenditures made to recreate in the Targhee National Forest, 1973

User group	Average total cost	Average expenditure in Idaho
Idaho residents	\$188	\$151
Nonresidents	191	141
Total sample	188	147

Methodology

The procedures used to evaluate economic impact would logically compare two situations. The first step would be to hypothesize what the situation in the Targhee National Forest would be without the mountain pine beetle and compare this with the situation where the beetle infestation exists. The difference measures the economic impact of the mountain pine beetle on outdoor recreation. Equation (1) below indicates a simplified model:

$$R \text{ w/o mpb} - R \text{ w/mpb} = E.I. \quad (1)$$

where: $R \text{ w/o mpb}$ = economic value of recreation without the presence of mountain pine beetle

$R \text{ w/mpb}$ = economic value of recreation with mountain pine beetle infestation

$E.I.$ = economic impact of the mountain pine beetle

The evaluation procedure relies upon separation of campgrounds in order to compare those

infested with those not infested. Where the economic impact of recreation was estimated, it was done by interviewing recreationists camping in infested and noninfested campgrounds.

The evaluation technique involved developing a statistical demand model which estimates the number of visitor-days of outdoor recreation as a function of round trip mileage, estimated travel time, and cost per visitor-day.⁵ Once an equation was developed, it was then possible to determine the average transfer costs and the average consumer surplus per visitor-day.

The general form of the demand curves developed is shown in Equation (2) below:

$$Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \epsilon \quad (2)$$

where: Y = number of visitor-days per group

X_1 = round trip mileage⁶

X_2 = estimated travel time⁶

X_3 = costs per visitor-day per person

$\alpha + \beta$ = constants

ϵ = error term

The above general model utilizes a multiple regression least squares analysis. The usual assumptions of this estimating technique are made.

Analysis

The demand equations developed in the analysis are shown in the tabulation below.

⁵ For a more detailed discussion see Clawson, M. and Knetsch, J.L., "Economics of Outdoor Recreation." Resources for the Future, Johns Hopkins Press, 1966, and Nawis, F., "The Oregon Big Game Resource: An Economic Evaluation." Unpublished Ph.D. Thesis, Oregon State University, Corvallis, Oregon, 1972.

⁶ Both round trip mileage and estimated travel time variables were included so as to improve the predictability of the model. The inclusion of both variables simultaneously in the model inevitably results in some degree of multicollinearity, but both variables were deemed necessary to the model, and, therefore, both were included.

The R^2 statistics in the three equations varied from 0.435 to 0.564. The estimated economic values are shown in table 4. Demand relationships were estimated for: (1) All campgrounds, (2) campgrounds which were heavily infested with mountain pine beetle, and (3) campgrounds which were lightly infested with mountain pine beetle. For purposes of convenience, the terms infested and noninfested are used to describe (2) and (3). Table 5 indicates average number of visitor-days per group, average cost per visitor-day, and average consumer surplus per visitor-day values. The average consumer surplus per visitor-day was obtained by integrating the equation between the average cost per visitor-day and the highest reported cost per visitor-day estimate. The consumer surplus is defined in the usual sense as the benefit which consumers receive but do not pay for. It can be interpreted as a net resource value for publicly owned properties if the assumptions are made that the marginal utility equals the marginal cost at each point on the curve above the average cost per visitor-day, and that the government is a discriminating monopolist. Equations used to estimate the demand for outdoor recreation in the Targhee National Forest, 1973:

1. All campgrounds: $N = 181^b$, $R^b = 0.499$,
 $F = 58.54$

$$Y^n = 13.732 + 0.005X_1^* + 0.632X_2^* - 1.142X_3^{*a}$$

(1.0617)(0.0012) (0.0140)²(0.2701)

2. Infested campgrounds: $N = 113$, $R^b = 0.435$,
 $F = 28.00$

$$Y^n = 13.920 + 0.004X_1^* + 0.732X_2^* - 1.083X_3^{*a}$$

(1.2592)(0.0017)¹(0.2125) (0.3703)

a Y^n = number of visitor-days per trip,
 X_1 = round trip mileage,
 X_2 = hours traveled to recreation in area, and
 X_3 = cost per visitor-day per person.

b Although 307 questionnaires were useful in analyzing the socioeconomic characteristics of the users, only 181 were useful in statistically estimating demand. Only complete questionnaires in regard to variables, Y^n , X_1 , X_2 and X_3 (i.e., no missing data) were included in the statistical analysis.

* Coefficient significant at the 5 percent level, and estimates of the standard errors of the coefficients are given in parentheses.

3. Noninfested campgrounds: $N = 68$, $R^b = 0.54$,
 $F = 27.60$

$$Y^n = 12.869 + 0.006X_1^* + 0.555X_2^* - 1.083X_3^{*a}$$

(1.9803) (0.0018) (0.2027) (0.4224)

It is evident that there were differences between the estimates of value derived for the three demand equations. The average cost per visitor-day was \$2.95 per day in all campgrounds; \$2.85 per visitor-day in infested campgrounds, and \$3.10 per visitor-day in noninfested campgrounds. The average consumer surplus values were \$7.80 per visitor-day in all campgrounds, \$7.75 per visitor-day in infested campgrounds, and \$8.95 per visitor-day in noninfested campgrounds.

Table 4.--Estimated economic values for outdoor recreation in selected campgrounds in the Targhee National Forest, 1973

Campground categories	Average visitor-days per group	Average cost per visitor-day	Average consumer surplus per visitor-day
All	16.8	\$2.95	\$7.80
Infested	15.8	2.85	7.75
Noninfested	18.3	3.10	8.95

The above results indicate that there was a difference in recreationist responses between infested and noninfested campgrounds. It is assumed that this response measures the desirability of recreating in campgrounds which do not have a large proportion of dead trees. The demand curves are measuring the response of recreationists to the environment by the length of their stay, and by the amount of money they spend.

Estimation of Losses

The losses were determined by calculating the differences between the estimated average consumer surplus and recreation costs for the infested and noninfested campgrounds. The average consumer surplus values were estimated by holding the other variables in the estimating equations at average levels; and the recreation costs were the estimated average cost per visitor-day. The method used to develop the loss values is indicated in table 5. The calculation is to subtract the consumer surplus value of the infested campgrounds from that estimated for the noninfested campgrounds ($\$8.95 - \$7.75 = \$1.20$ /

Table 5.--Estimated losses of recreational values resulting from mountain pine beetle infestation in the Targhee National Forest, 1973

Item	Average number of visitor-days per group	Average cost per visitor-day	Average consumer surplus per visitor-day
Noninfested campgrounds	18.3	\$3.10	\$8.95
Infested campgrounds	15.8	2.85	7.75
Net difference	2.5	0.25	1.20

visitor-day). A similar calculation was made for the cost per visitor-day expenditures ($\$3.10 - \$2.85 = \$0.25$ /visitor-day). These residuals were then summed to determine the total value (marginal value per visitor-day) of \$1.45 per visitor-day. This value is an estimate of the economic cost of the mountain pine beetle infestation in terms of its impact on recreational values.

The values generated above were aggregated to determine the magnitude of the total losses caused by the mountain pine beetle in the Targhee National Forest. This was done first for the campgrounds which were studied, then for all campgrounds in the forest, and, finally, for all the campgrounds in the forest assuming the average level of infestation which currently exists in the Targhee National Forest.

In the case of the campgrounds which were studied, the estimated losses reflected the existing situation with regard to the infestation levels of mountain pine beetle in the six campgrounds studied. The loss estimates were based on U.S. Forest Service estimates of recreational use in these campgrounds. This estimated use was 177,600 visitor-days. The estimated losses were \$257,520 based on the average loss per visitor-day of \$1.45 estimated from the demand equations developed previously. This value can be allocated as follows, \$44,400 in reduced expenditures, and \$213,120 in reduced consumer surplus (table 6).

Additional data on campground use were available from U.S. Forest Service records. These data indicated that the total number of visitor-days in all campgrounds in the Targhee National Forest during 1973 was 252,000 visitor-days. In making loss projections, it was assumed that the level or degree of mountain pine beetle infestation would be the same as that observed in the campgrounds

Table 6.--Estimated potential economic losses in outdoor recreation values assuming that the campgrounds studied were infested with mountain pine beetle, 1973

Item	Value
All campgrounds studied (177,600 visitor-days)	
1. Not infested	
a. Expenditures	\$ 550,560
b. Consumer surplus	1,589,520
Total	<u>\$2,140,080</u>
2. Infested	
a. Expenditures	\$ 506,160
b. Consumer surplus	1,376,400
Total	<u>\$1,882,560</u>
3. Not infested - infested (difference of above figures)	
a. Expenditures	\$ 44,400
b. Consumer surplus	213,120
Total	<u>\$ 257,520</u>

previously studied. This assumed an infestation level of 0 to 50 percent in the noninfested campgrounds and a 50 to 100 percent infestation level in the infested campgrounds.

The first projection was made by assuming that all 19 campgrounds in the Targhee National Forest were infested and the economic losses were calculated as shown in table 7.

Table 7.--Estimated potential economic losses in outdoor recreation values assuming that all campgrounds in the Targhee National Forest were infested by mountain pine beetle, 1973

Item	Value
Total campground use (252,000 visitor-days)	
1. Not infested	
a. Expenditures	\$ 781,200
b. Consumer surplus	2,255,400
Total	<u>\$3,036,600</u>
2. Infested	
a. Expenditures	\$ 718,200
b. Consumer surplus	1,953,000
Total	<u>\$2,671,200</u>
3. Not infested - infested (difference of above figures)	
a. Expenditures	\$ 63,000
b. Consumer surplus	302,400
Total	<u>\$ 365,400</u>

The total losses were \$365,400. This was determined as follows: a) Expenditure losses were \$0.25/visitor-day x 252,000 visitor days = \$63,000, and b) consumer surplus or net resource benefit losses were \$1.20 x 252,000 visitor-days = \$302,400.

A second estimate was made which assumed that only half of all the campgrounds in the Targhee National Forest would be infested at any one time. This relationship was assumed because there were no empirical data available to verify a greater or smaller level of campground infestation. What this assumption does is to introduce an aspect of marginality into the analysis in a gross way. The loss values estimated were half the value of those estimated for the previous estimate (table 8). The calculations were: a) ($\$0.25/\text{visitor-day} \times 252,000 \text{ visitor-days}$)/2 = \$31,500 loss of expenditures, and b) ($\$1.20/\text{visitor-day} \times 252,000 \text{ visitor-days}$)/2 = \$151,200 loss of consumer surplus. These values sum to \$182,700 in terms of annual economic losses of recreation values in the Targhee National Forest.

Table 8.--Estimated potential economic losses in outdoor recreation values assuming that half of all campgrounds in the Targhee National Forest would be infested by mountain pine beetle at any one time, 1973

Item	Value
Half of the total campground use (126,000 visitor-days)	
1. Not infested	
a. Expenditures	\$ 390,600
b. Consumer surplus	1,127,700
Total	<u>\$1,518,300</u>
2. Infested	
a. Expenditures	\$ 359,100
b. Consumer surplus	976,500
Total	<u>\$1,335,600</u>
3. Not infested - infested (difference of above figures)	
a. Expenditures	\$ 31,500
b. Consumer surplus	151,200
Total	<u>\$ 182,700</u>

Investment in Control Program

If a recreational management agency is interested in developing a control program, an obvious question is, given the estimated losses caused by mountain pine beetle, how

much money can the agency justify spending on control measures? This question can be thought of as how present losses are evaluated in terms of future losses. The present value of all future losses needs to be determined. This can be done by assuming that the estimated losses are an opportunity cost and discounting them at an appropriate discount rate. The rate used in this analysis was 7 percent. The formula used to develop these capitalized values was:

$$V = \frac{L}{r}$$

where: V = capitalized value
L = aggregate annual economic losses
r = discount rate of 10.0 percent

The present value of the economic losses for each of the three examples discussed above is shown in table 9. The total capitalized value for each example was: \$2,575,200 for the campgrounds studied; \$3,654,000 for the potential loss due to infestation by the mountain pine beetle in all campgrounds in the Targhee; and \$1,827,000 value for loss of half of the campgrounds or visitor-day use in the Targhee National Forest. These values may seem high until compared to present investment in controlling infestation in the Targhee National Forest.

"The present infestation began in 1960 and large scale control efforts started in 1962. Control efforts were undertaken to protect multiple use values which were never quantified. Control costs through 1970 were 10.3 million dollars."

The capitalized values are the present value of the recreational losses resulting from the mountain pine beetle infestation in the Targhee National Forest. These values can also be used to determine the upper limit on the amount of investment which could be justified for a pest management control program. The difficulty is that the decision-maker needs to know what his potential losses may be before he can determine the amount of investment he should be using, or if he should be concerned with a control program at all.

Summary

This study used recreational demand models to estimate the economic impact of mountain pine beetles on recreational use in

⁷ Rivas, A., *op. cit.*, p. 40.

Table 9.--Present values of economic losses in outdoor recreation values in the Targhee National Forest, 1973

Item	Capitalized value
1. Studied campgrounds, 177,600 visitor-days	
a. Expenditures	\$ 444,000
b. Consumer surplus	2,131,200
Total	<u>\$2,575,200</u>
2. All campgrounds, potential losses, 252,000 visitor-days	
a. Expenditures	\$ 630,000
b. Consumer surplus	3,024,000
Total	<u>\$3,654,000</u>
3. Half of all campgrounds, potential losses, 126,000 visitor-days	
a. Expenditures	\$ 315,000
b. Consumer surplus	1,512,000
Total	<u>\$1,827,000</u>

the Targhee National Forest. The procedure followed was to estimate the demand for both infested and noninfested campgrounds and compare the consumer surplus and transfer cost estimated derived from the demand models. These estimates were then used to simulate various infestation conditions to determine the magnitude of average annual losses from mountain pine beetle infestation. These losses were then capitalized to determine the total value of damages, and this value was interpreted as the upper limit for investment in control measures for the mountain pine beetle pest control program in the Targhee.

There are several concerns which should be recognized when using transfer costs as a surrogate for prices in estimating consumer surplus values for outdoor recreation. First, an adjustment was made to account for nondestination use, because in some cases the hours and mileage traveled were incidental to the Targhee visit. A second factor affecting the estimation of consumer surplus was that the data used for this study were obtained during the summer of 1973, a period of rapidly rising gasoline prices. These price increases had the effect of dramatically increasing the average cost per visitor-day compared to earlier years. A third factor was that the consumer surplus values are point estimates. These point estimates are assumed to have wide and unknown bounds, and computation of these bounds is difficult if not impossible.

This paper is an attempt to use demand models to measure the economic impact of mountain pine beetle on outdoor recreation in

the Targhee National Forest. The results imply that such measurement is possible, and that the loss estimates developed in this analysis may be compared to losses of other resources in the forest. More research is needed to develop models for other resources to obtain loss values related to mountain pine beetle damage.

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Impact Analysis, Interpretation, and Modeling

William A. Leuschner¹

Living in a world of scarce resources which have competing uses should lead the forest resource manager to question those actions which use these resources, including his when he acts as a pest manager. Therefore, one may ask: (1) Why should resource managers make impact analyses? (2) How can they usefully interpret them once they are made? and (3) Why bother with impact models?

Why Make Analyses

We have just had an excellent discussion by Dr. Stark on the concept and definition of impact. The major thrust of his and most definitions is that impact is the net effect of an insect upon the physical ability to produce goods and services which are desired by man. The key phrase in this sentence is ". . . which are desired by man." Insect impact has meaning only to the extent it affects something which man desires.

Let me more fully explain what I mean by "something desired by man" lest I be accused, as many economists are, of knowing the price of everything and the value of nothing. There is a very broad spectrum of goods and services produced from our forest resources. These include not only the more tangible and easily quantified items, such as timber and grazing, but also those less easily quantified, such as recreational and esthetic services. All of these goods and services

which are affected by an insect or insect complex should, to the extent possible, be included in an impact analysis.

I would like to clarify another point and that is that "net effect" of impact may be either positive or negative. The term "pest management" is negative because the word "pest" by definition means something detrimental to man. However, we should recognize, at least philosophically, that the net effect of an insect or insect complex could be beneficial to man. I will be speaking in the negative context because that is why most forest control activities take place.

The reason, then, for making an impact analysis is to discover whether an impact is positive or negative and also to discover or predict the amount of the positive or negative effects. Now, to be realistic, few impact analyses will be made until a resource manager first perceives that there is an interaction between an insect and what man wants from the forest. Further, the impact must be perceived to be large enough to make some kind of difference. The reason for this is obvious -- impact analyses cost money; they take time and effort away from other desirable activities and there should be a good reason for incurring these costs.

The reason for incurring the cost is to provide the forest manager with information needed for him to decide upon which course of action to take. He must decide whether to do nothing or to initiate a control activity, and, if the latter, he must decide upon which activity or combination of activities to use and how large a program to initiate. But this brings us to the second question, how are impact analyses interpreted to help the manager make these decisions?

Interpreting the Analysis

After impact is first perceived, the forest manager -- sometimes almost intuitively

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tively -- decides whether it is small enough to be acceptable. This in itself is an interpretation which may be based on casual observations, experience or the results of some extensive surveys. The conclusion may be that: (1) The impact is acceptable and will be ignored henceforth, therefore, no further interpretation is needed; (2) the impact is currently acceptable but that it should be monitored frequently, therefore, further interpretation and decision is postponed to a later date; or (3) the impact is presently unacceptable, therefore further interpretation and decision is needed at once.

A second judgment must usually be made if the impact level is unacceptable about whether or not a control activity is available or can be developed. Lack of control activity can force acceptance of otherwise unacceptable impacts. However, in most cases, a control activity exists even if that activity is to fund research to find better control activities.

If control activities are desired, I would let my economic bias come to bear and suggest that impact and other data be used in a benefit-cost analysis to help interpret the impact analysis and to provide a more complete guideline for decisionmaking. A benefit-cost analysis framework is one of the more useful methods of interpreting the results of an impact analysis. Its framework is quite general and the basic principles are applicable to many cases.

The general framework is this: The benefits of a control program are the damages which that program prevents from occurring. Estimating benefits usually requires estimating the damages without the program, and then either estimating the proportion of these damages which the program will eliminate or estimating a second damage level with the program and subtracting it from the estimated damages without the program to obtain damages prevented.

Valuing damages may be very difficult because either the quantities are unknown, such as the impact on an elk herd caused by the mountain pine beetle, or because the impact is not valued in the market place, such as the value of one head of elk. In some cases, we may just have to be satisfied with establishing that an impact exists and indicating whether it is positive or negative instead of putting the value of the impact in a benefit-cost analysis.

However, to be useful for decisionmaking, a great deal more information is needed. It

is not only desirable to know the amount of damage reduction which a new control program will cause, but it would also be desirable to know how much more the damages would be reduced if the program size were increased or how much the damages would be increased if program size were reduced. This information is needed to provide guidelines for deciding on the most efficient program size.

Finally, an analyst must estimate the costs of a particular control program. The cost analysis is usually easier than the benefit analysis because most costs are labor or materials for which estimates are readily available. Of course, nonmarket costs which do occur, such as adverse environmental effects of insecticides, should also be included just as nonmarket benefits should be included.

The interpretation of the estimated benefits and costs is fairly straightforward. One simply adopts the control activity which has the greatest positive difference between benefits and costs, and a program is not adopted if the benefits are less than costs. This means that if the damage reduction is less than the control costs, the indicated course of action is to allow the insect to continue unchecked for the time being.

Benefit-cost analyses are not, however, a complete guideline to forest management decisions. First, there are the obvious imprecisions in benefit-cost estimates. Second, there are those items omitted from the analysis because of our inability to quantify them, for example, the impact of insects on esthetic values. Finally, there are some areas which benefit-cost analysis is not designed to cover, most notably the impacts of insect damage on income and wealth distribution. This latter area is concerned with shifts of income and wealth from one group to another. A recent example which came to my attention is the possible shift in the county tax burden in the western United States due to mountain pine beetle attacks on residential properties. Here the homeowners obtained reduced personal property assessments because mountain pine beetle killed trees on their house lots and hence lowered the market value. This meant that the tax was shifted to property owners who had no attacked trees and who consequently were paying relatively more tax than before the attack, assuming the total amount of tax collected in the county remained the same. This type of shift may be relevant to pest management decisions but is not included in a benefit-cost analysis.

The remaining question is: Why model impact? The reason is to predict the impact (or damages) for use in making control activity decisions. Note that there are other reasons for modeling, for example, population dynamics models which may lead to better understanding of life processes and hence allow improved control tactics. However, we are discussing impact and its analysis, and I would maintain the major reason for modeling impact is to provide information for control activity decisions.

But why are impact models needed? Don't we know what the impact is? The answer in many cases is no. Not only do we lack accurate estimates of the past impact of many forest insects but we certainly do not have estimates on what the future impact will be. It is this latter information that is needed because decisionmaking is for control activities taking place in the future. For example, we would not plan control activities for the coming field season if we thought an insect population was going to collapse under its own weight. Similarly, the benefits of many control activities, particularly those that prevent rather than suppress impacts, take place over a number of years in the future. Assessing the benefits of these prevention programs, therefore, requires predicting the damage reduction in future years which, in turn, requires predicting future impacts. An understanding of risk and uncertainty and how to treat them will help do this.

The management team for the Expanded Southern Pine Beetle Program has outlined four major types of impact models which they feel are important, but which are not yet developed. These models are defined by the geographic area covered and the use to which

the results are put. I would like to present them to you here because I believe they help to define the context of impact modeling (table 1).

The first type of model is used to predict impact over wide geographical areas for the next 5 to possibly 50 years. Here, wide geographical area is defined as an area which covers several counties or a forest survey unit sized area and which may contain hundreds of thousands or millions of acres (or hectares) of forest land. Impact information is desired to predict the benefits of long-term prevention programs for use in benefit-cost analyses.

A second type of impact model would also predict impacts over wide areas but only for 1 year in the future. Hopefully, this model would give more precise estimates of damage and be better able to account for annual fluctuations than a model which predicts decades into the future. It would be used to plan the next field season's activity and to make budget requests for submission to legislatures.

The third model also predicts wide area impact but only for a month or so into the future. This model would be used to plan field operations during the season, for example, intensification of detection or control efforts. We would also hope to have a hazard index available for use with this model to indicate the general areas on the ground where increased activity might occur.

The fourth and final type of model would predict the likelihood of a severe outbreak on a specific area. It would seek to predict how large a specific spot will grow if left uncontrolled. The purpose of this type of impact model is to guide operational decisions for suppression activities. It comes closest to

Table 1.--Types of impact models

Model number	Area covered	Information predicted	Use of prediction
I	Wide area	Impact over next 5-50 years	Estimate benefits of long-term prevention programs
II	Wide area	Impact next year	Plan budget request for coming field season
III	Wide area	Impact next month	Plan field activities
IV	Specific spot	Growth if uncontrolled	Plan suppression activities on outbreak

predicting what is commonly called the "economic threshold" of control activity.

We have also found it useful to think in terms of two different impact modeling techniques. The first may be called a population dynamics, or life table technique and the second a probability, stochastic, or actuarial technique. Note that, as with many categorizations, these are not mutually exclusive, and that some models may have elements of both categories.

The population technique models, which may contain probability elements, simulate insect population numbers throughout their life cycle and translate these numbers to trees attacked and hence to impacts. The emphasis is on modeling the insect. The actual models may be much more complex than this, for example, they may model tree physiology in order to determine the next tree attacked. Population modeling has the advantage of usually including basic physiological processes which cause attacks and hence can cope better with changes in exogenous causal variables. One would speculate that the population technique would be most useful for Type IV models and least useful for Type I models, in descending order, because of difficulties in aggregating results over wide areas and long time periods.

Probability technique models take a more empirical approach and seek to relate the probabilities of attack and spread to observable abiotic and biotic factors affecting the host material. The emphasis is on modeling the host. Probability modeling has the advantage of requiring less detailed knowledge of basic biological processes and the disadvantage of being less able to cope with changes in exogenous causal variables. One

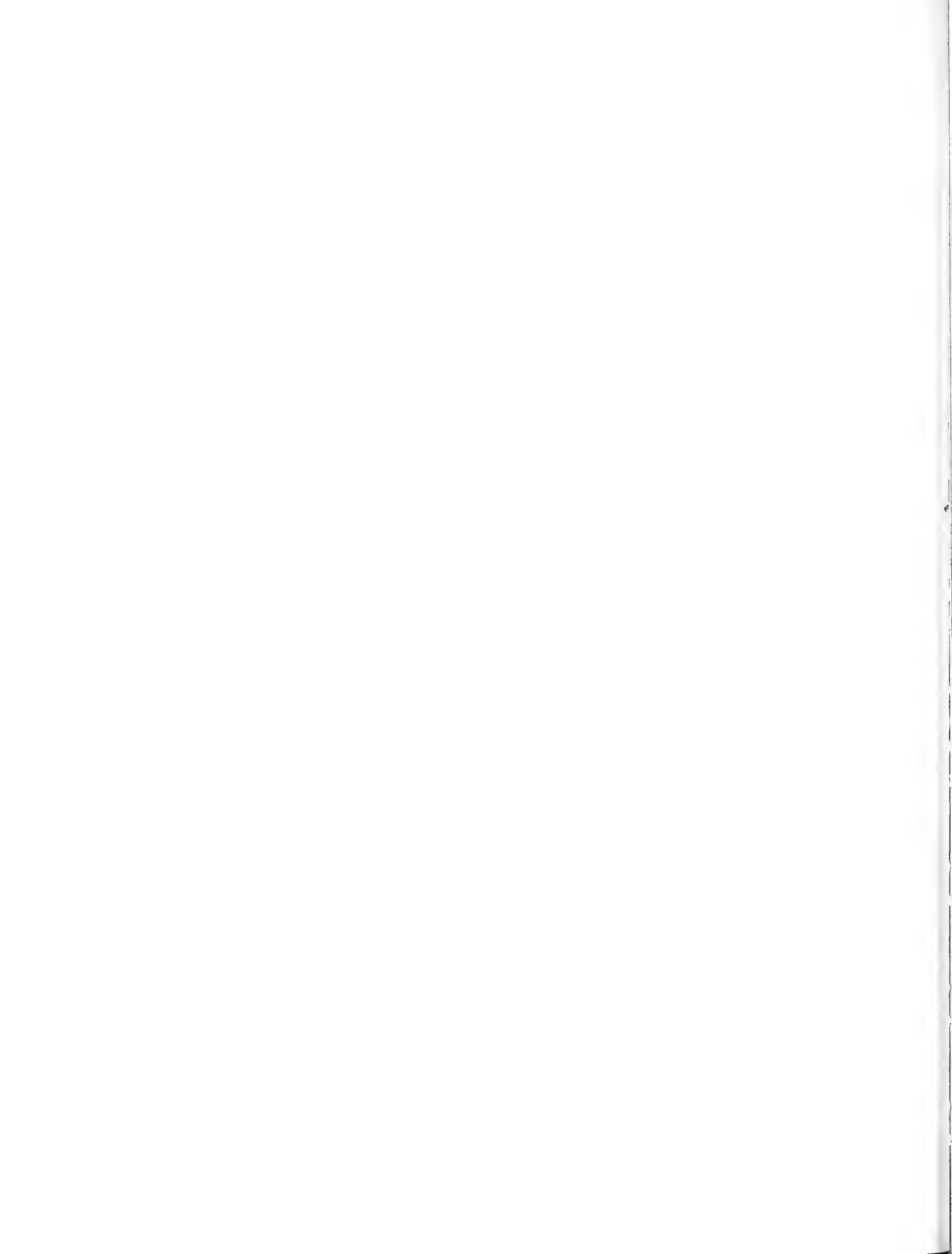
would speculate that the probability technique would be most useful for Type I models and least useful for Type IV models, in descending order, because it is based on probabilities of attack and spread rather than variables affecting biological processes which can be measured for an individual spot.

Summary and Conclusions

To summarize: (1) Impact analyses are made to supply information for deciding which course of action to take; (2) the analyses can be usefully interpreted within a benefit-cost analysis framework; and (3) models are needed to better predict future impacts and hence potential control program benefits.

The need for better impact analyses and prediction models is becoming quite evident to many forest and pest managers. I detect, at least in the U.S., increased scrutiny of pest management expenditures and requests to demonstrate that the benefits of proposed control activities exceed their costs. There appears to be less willingness to accept control proposals on the basis of: "bugs are bad because they kill trees" or "we better get them now before they eat the whole forest," and an increased desire for quantified costs and results.

I personally endorse this trend because it can lead to better decisions and more efficient use of resources, whether in the public or the private sector. However, these estimates require more knowledge, which, in turn, will require better records of past impacts and the development of more models to predict future impacts.



III. CONCEPT AND PRACTICE OF INTEGRATED PEST MANAGEMENT IN FORESTRY

214 Night Application of Aerial Sprays Using Multi-Engine Aircraft, Inertial Guidance Equipment, and Incremental Application Technology for Insect Control, with Special Reference to the Spruce Budworm C. 1.2 ?

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The relationship of aerial spray deposits on a coniferous forest and the degree of spruce budworm, *Choristoneura fumiferana* (Clem.), control based on ground sampling devices was established in the early 1950s by Hurtig *et al.* (1953) at 10+ drops/cm² for a coarse (MMD-250 μ) DDT spray. These values were modified by Fettes (1962) and Randall (1969) to include 20-40 drops/cm² for ultra low volume concentrate sprays in insecticides. Research by Himel and Moore (1967 and 1969) showed that the highest degree of mortality to the western spruce budworm *Choristoneura occidentalis* (Freeman) was achieved by contact with drops of less than 50 μ diameter, thus confirming the effectiveness of a fine droplet spectrum. Researchers over the years have used the above ranges of drop deposit para-

meters as an index for equipment calibration prior to use on operational budworm sprays. Calibration trials undertaken on a Douglas DC-7B spray aircraft (Randall and Zylstra 1972) indicated the potentiality of multi-engine aircraft for incremental spray technology using swath intervals of 3000 feet based on a deposit coverage of 40 drops/cm².

The basic concept of multi-engine use was predicated on an economical but effective swath width, large payload capability, electronic navigation for swath lane alignment, and effective spray coverage for optimum insect mortality. The calibration trials were conducted using the Porton Method of crosswind spray application whereby the height/wind product determined the degree of downwind displacement of the drop spectrum to ensure the desired degree of spray coverage (Gunn *et al.* 1948). From these early trials, the spray dispersal (and hence, proposed droplet distribution) on the target site was based on the concept of incremental spray application (Randall and Zylstra 1972). The first semi-operational trials using the DC-7B spray aircraft equipped with the Litton LTN-51 inertial guidance system for spray block location and swath lane offset of 3000 feet confirmed the reliability of multi-engine aircraft, electronic swath guidance navigation, incremental application technology, and efficacy of deposit distribution for spruce budworm control (Randall 1974 a,b; 1975). The success of these early incremental spray applications trials prompted the Quebec Department of Lands and Forests to embark on a program of incremental drift application in 1973, using multi-engine spray aircraft operating under electronic guidance control for swath lane location and automatic swath

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lane offset of 3000-foot intervals, thus eliminating the spray block system of visual terrain boundaries that constituted hazard zones for multiple spray application (Desaulniers 1973 and 1975; Paquet and Desaulniers 1974).

During the period of 1972 to 1976, an active cooperative program of research and development on application technology, swath lane navigation, pesticide formulation, and spray efficacy was undertaken to improve the Quebec spray operation and maintain an effective spray program in the face of rising costs.

The successful adaptation of a high capacity aircraft to produce a ULV droplet spectrum of MMD of 90 to 100 μ at volume output of 100 to 200 gallons (US)/minute and the subsequent improvement of the Litton LTN-51 navigation system to maintain a high degree of performance (Boivin and DeCamp 1975) opened up the potentialities for night application of pesticides for large scale spraying against the spruce budworm.

Aerial Application Techniques

As early as 1930, it was recognized that the most suitable weather for applying dust formulations by aircraft occurred during calm days when upward thermal air currents were minimal (Swain 1930). These findings were adapted and used with the introduction of oil formulations for the control of forest defoliators (Stewart 1949) and led to the practice of aerial application during the early morning and late evening hours of the day when wind velocities, air temperatures, and inversion conditions were conducive to maximum spray deposition. The findings that the earliest sprays in the morning and the latest sprays in the evening usually provided the best deposits and hence insect control results, led to speculation that night application of pesticides would be extremely advantageous. This concept has been successfully adopted in agricultural spray programs in the United States using high intensity light beams for visual guidance (anonymous, 1966) but is hardly acceptable for forest spraying over uncharted terrain quite unlike agricultural fields. Furthermore, Federal regulations would require 700-foot altitude clearance above the highest point of land over the spray area. The introduction of the multi-engine aircraft and electronic guidance system, however, provided the means to test the concept.

During the course of equipment development and modification of spray systems, numerous calibration trials were conducted at remote airports and late in the evening after sunset, thus providing the occasions to undertake "ad hoc" night trials.

The first attempt to obtain deposit data during a night application occurred late in September 1973 at Val D'Or, Quebec, using a CL-215 converted water-bomber aircraft. Two crosswind spray runs were made at 1000 feet above a 20-mile layout of card samples. Meteorological conditions were extremely unfavorable for spray deposition with a high pressure region over the test area and wind velocities of up to 18 knots at spray height. Results were very disappointing with a deposit recovery of 1 large drop across the 18 miles of deposit cards. This was attributed to a malfunction of a nozzle. The results, however, indicated the unsuitability of #2 fuel oil for high level spraying, and led to the development of a less volatile oil formulation (unpublished data) comprised of number two and number four bunker fuels. The trial also confirmed the findings of Mount *et al.* (1970) that wind velocity increases with increased altitude.

The second opportunity occurred later in 1973 during a series of calibration trials with a Douglas DC-6B spray aircraft to determine ULV droplet spectrum characteristics and effectiveness of low volume output on spray droplet deposition. Meteorological conditions were ideal (cool with winds at 0 to 0.5 mph at ground level and 0.5 to 1 above tree tops). Because of delays in equipment adjustment and rate of flow calibrations on the final calibration trial and fog conditions on the runway, the available daylight hours were exceeded. Rather than abort the last trial, the pilot elected to make the final run under night conditions at 250 feet above the layout with the aid of ground flares and radio communication to ensure proper track orientation. During spray emission, wind speeds of 15 knots were encountered by the aircraft above the layout whereas ground and treetop wind conditions as indicated by smoke flares were 0 to 0.5 mph at 180° to the upper air stream. Maximum drop size (D_{max}) of the spray deposits were displaced 700 yards downwind from the point of spray emission and covered the entire 3 miles of the sample layout. Results from this trial under night conditions illustrated the misconception of so-called ideal spray weather based on ground and treetop observations and stressed the need for meteorological equipment (Pibal or Radiosonde)

to sample the weather profile from ground to spray height emission. The data from the day (FTX=14) and night (FTX=19) calibration runs when plotted on a theoretical incremental deposit basis for a swath interval of 3000 feet, illustrate the effect of wind speed and altitude upon spray deposition (fig. 1).

By the spring of 1974, the new low volatile oil formulation (a 50/50 ratio of non-volatile to low volatile liquid fractions) was in operational use on daylight spray application programs against the spruce budworm. Simultaneously, a program of pilot training and equipment use of the LTN-51 was instigated to eliminate in-flight errors of navigation.

Early in the spring of 1974, a preliminary series of night trails was established

at Lac des Loups, Quebec to ascertain the practicability of night operations. A 50-mile layout was established in order to provide two flight swaths across the area for comparison of spray deposition of dissimilar spray formulations (fig. 2). Low level (200 feet) and high level (1500 feet) flight lines were established at right angles to the layout to provide crosswind deposit characteristics. The program, unfortunately, was plagued by adverse meteorological conditions associated with late spring snowstorms and further compounded by installation problems of one of the Litton LTN-51 guidance systems in one of the experimental aircraft. By the time all problems were resolved, the aircraft were required on the operational spray program and the night trial was shelved until after completion of the spray project. At midnight,

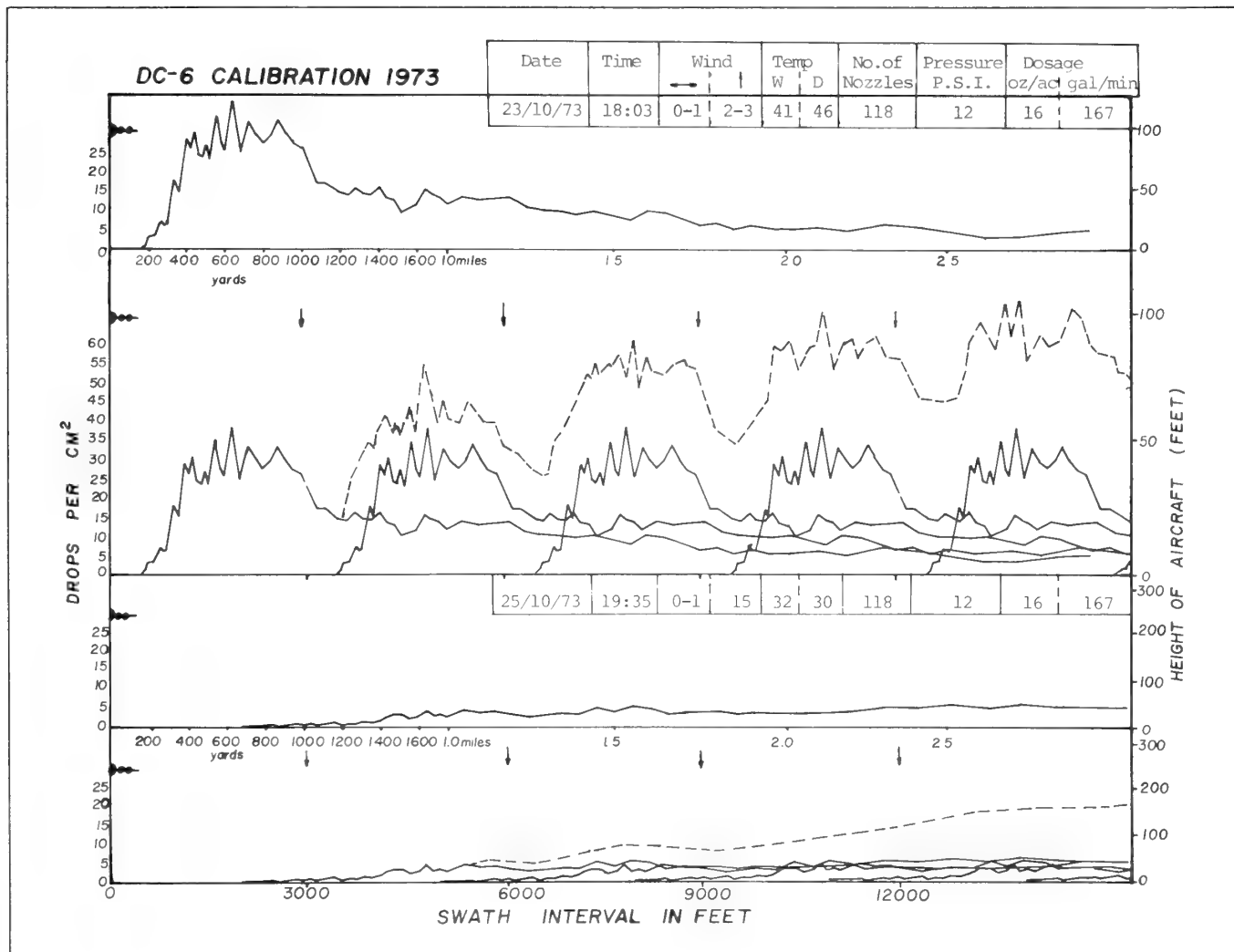


Figure 1.--Douglas DC-6b calibration trials (1973) under ideal day emission (FTX-14) and night emission conditions (FTX-19) showing a theoretical incremental cumulative spray deposit over 4-5 swath intervals. For maximum effectiveness a total of 8 to 12 swath intervals are required.

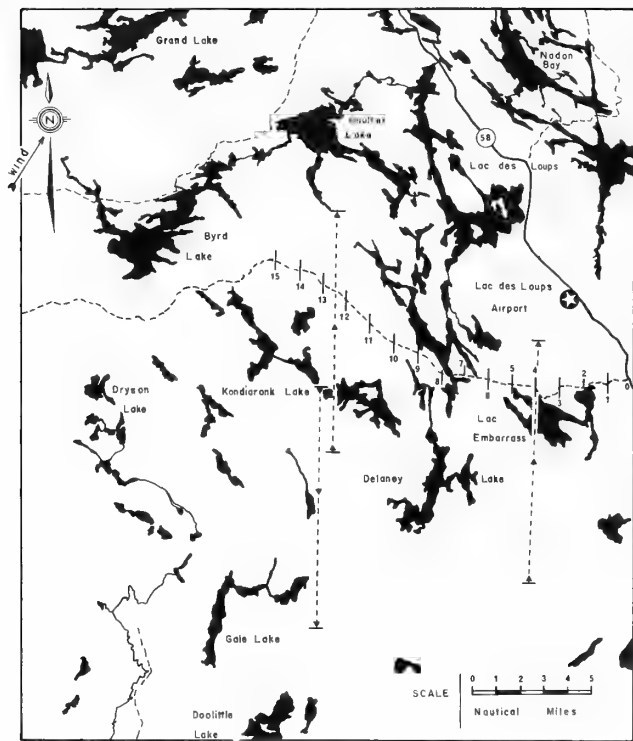


Figure 2.--Map of the lower end of the 1974 experimental night spray layout showing the location of the low level spray pass (mile 4) and high level spray pass (mile 13).

June 12, 1974, a DC-6B aircraft was released to provide a single spray run across the layout. Results of a single-line emission run at 1500 feet above and across the layout plus an aborted run are presented in figure 3. Spray deposits were recorded from both passes across a 6 mile area of the layout with a maximum deposit of 6 drops/cm² occurring at a position 1.5 miles from the point of emission (fig. 3). Drop sizes as small as 20 microns (μ) were collected on the kromekote cards and glass plates, thus confirming the relative low-volatility of the #2/#4 oil formulation. Projected cumulative deposits from a series of successive spray swaths at 3000-foot intervals indicated that a potential toxic deposit of 20 spray droplets/cm² could be deposited on the target site of spruce and fir foliage to kill early instar budworm larvae or adult moths (Kettela 1975). Plans were, therefore, established to undertake a night spray application of a pesticide against early instar larvae of the spruce budworm in 1975.

In the spring of 1975, an experimental site of 35,000 acres was selected at Maniwaki, Quebec, a distance of 60 miles from the air field. Two sampling lines were established across the area to provide spray deposit and biological data on transects at 1/20 mile intervals. A cross section of the experi-

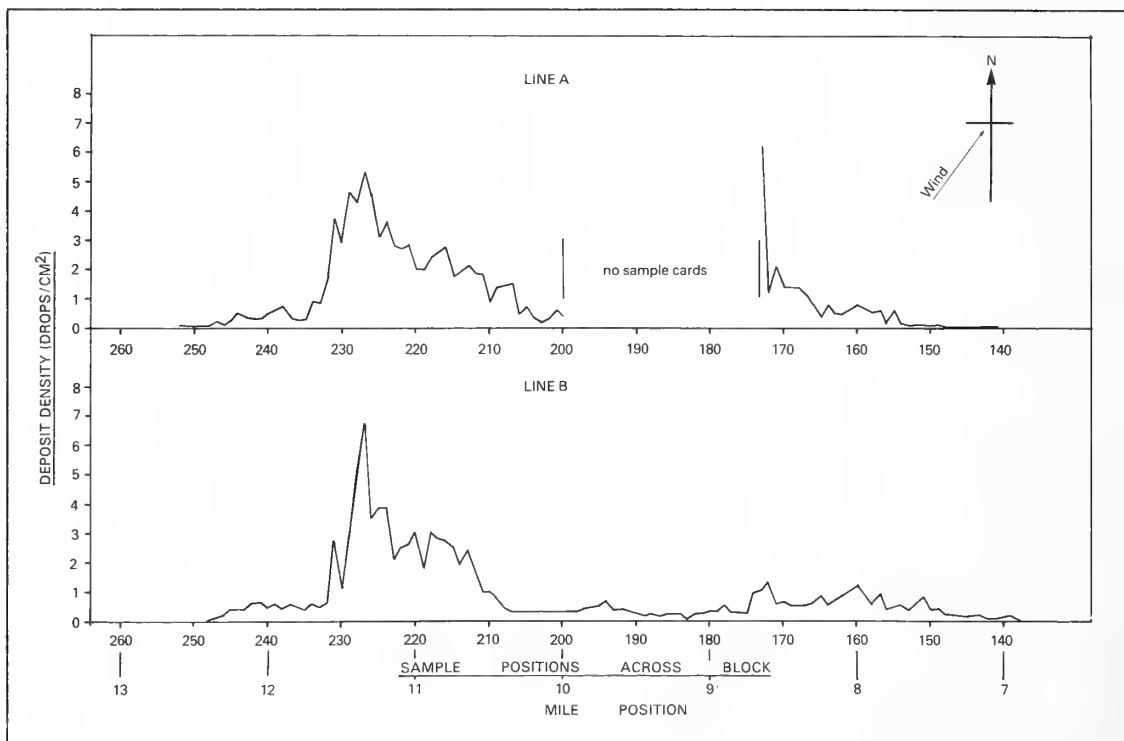


Figure 3.--Transect of spray deposit (drops/cm²) collected downwind from a single high level pass (1500 ft) across the layout plus an aborted run are presented for lines A and B.

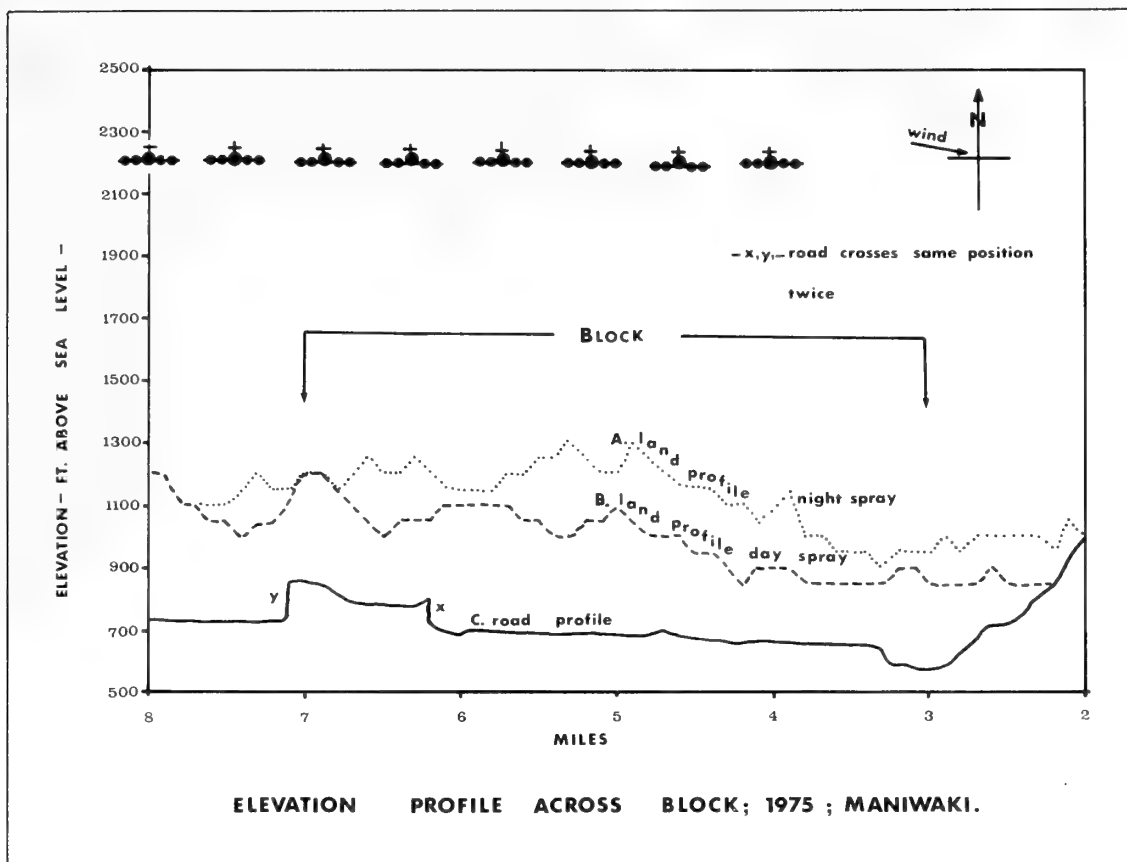


Figure 4.--Transect of experimental night spray block showing the profile of road elevation, day and night land profile and spray emission altitude.

mental block is shown in figure 4 in terms of the road profile, the day land profile (based on the highest point of land 2 miles on either side of the road), and the night land profile (based on the highest point of land on the swath lanes within the block). Spray emission altitude was set at 700 feet above the highest point of forest terrain bounding a 5-mile zone surrounding the spray block. All profiles are shown with reference to elevation above sea level.

The first attempt to spray the experimental block on June 4 under ideal weather conditions was aborted due to improper programming of the LTN-51 and a malfunction of the spray system on the Constellation 749 spray aircraft. Meteorological conditions during the next 4 days were extreme, with a low centered over the experimental site. Ground winds were 3 to 5 kilometers/hr. Since the spray aircraft was scheduled to depart on the morning of June 10, it was decided to spray the experimental site on June 9 taking into consideration the high altitude winds. Pibal readings were taken before, during, and after spraying to provide a profile of wind speed and direction across the experimental block

(fig. 5). Because of the high winds at emission altitude, the aircraft swath lanes were offset 6000 feet upwind of the block. An oil/fenitrothion formulation containing 9.25 percent active ingredient, 25.82 percent arotex cosolvent, 24.98 percent #2 fuel oil and 40.15 percent # 4 fuel oil was applied at a dosage rate of 15.36 oz. (U.S.)/acre under starlight conditions using a Constellation 749 spray aircraft. The abovewing mounted boom and open nozzle system was operated at 14.5 PSI at a spray emission rate of 167 gallons (U.S.) per minute. All sampling units were collected 4 hours after spray completion to provide adequate time for deposition of the small drops within the target area. A transect of the deposit data in terms of drops/cm² and volume (oz/ac) is shown in figure 6.

Spray deposit data indicated that the Dmax spray droplets were carried 3 miles downwind before encountering the forest canopy. Maximum deposits over one drop/cm² were recorded 2 miles downwind beyond the block boundary thus indicating the bulk of the spray was deposited well downwind of the block. Preliminary assessment of deposit data

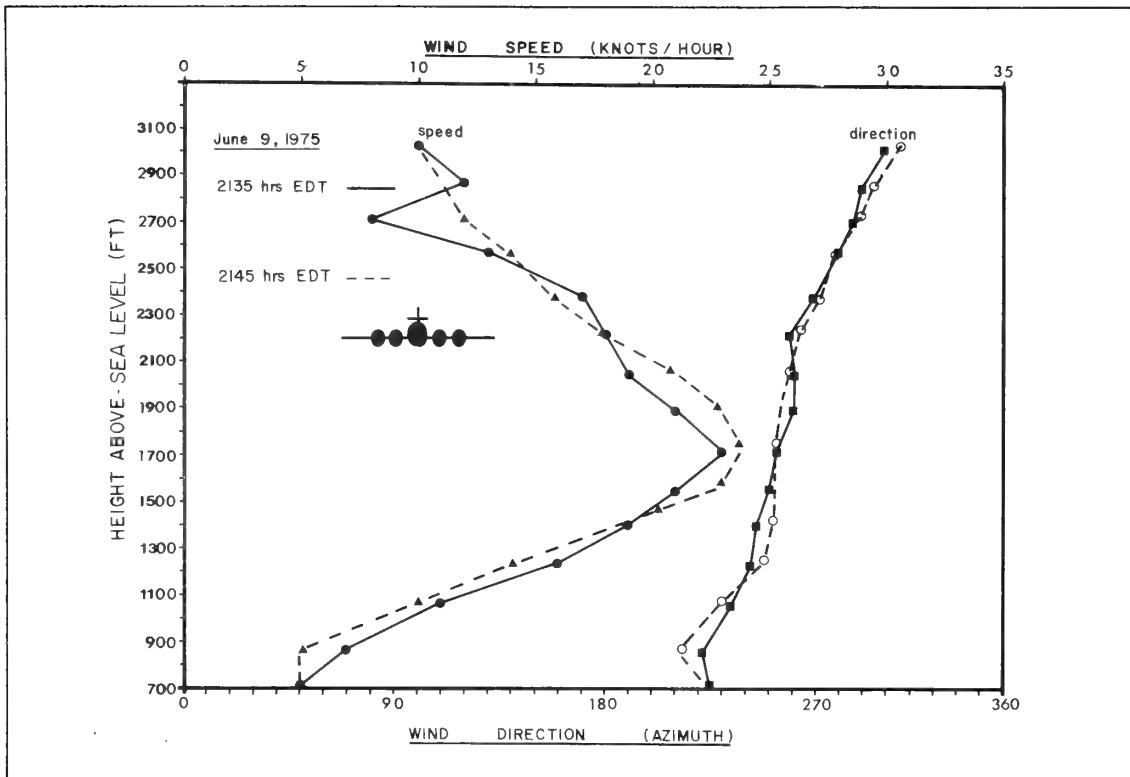


Figure 5.--Pibal recording of wind speed and direction during night spray trial, 1975.

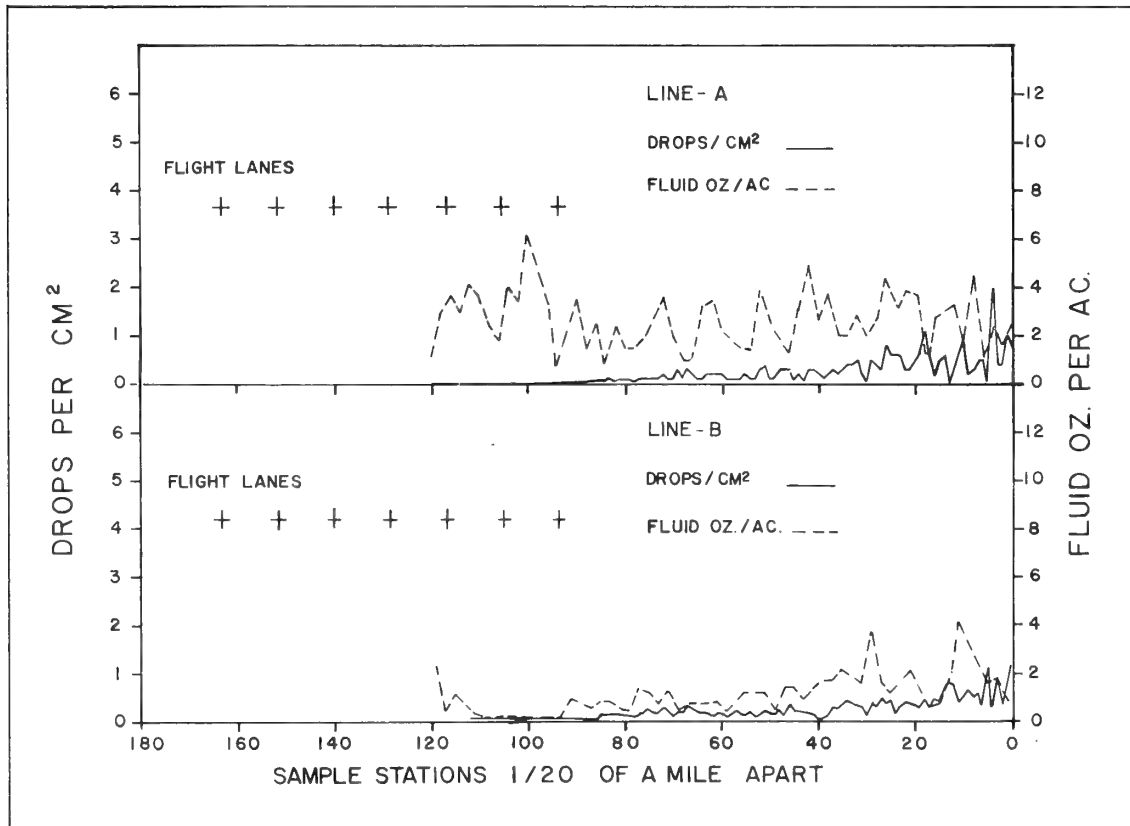


Figure 6.--Transect of spray deposit density across the experimental layout.

indicated a droplet spectrum with a maximum drop size of over 300 microns (μ) and mass median diameter of approximately 130 μ . A value for the number median diameter of 105 μ was recorded for the spray within the block; this value, however, would not be representative of the NMD for the entire application.

Tentative results of the efficacy of this single application of 2 oz. fenitrothion indicated a larval mortality of spruce budworm approximating 25 percent-30 percent with 0 percent foliage protection.

Results and Discussion

The night spray trials were exploratory trials designed to provide some parameters of spray deposit in an attempt to extend the favorable spray weather period on spruce budworm projects. It was recognized that with night operations, spray emission altitudes would have to be raised to 700 feet above points of highest terrain in the spray blocks and in the turning area at the ends of the block.

The majority of the trials were undertaken under adverse conditions of timing and meteorological conditions of high altitude winds. Meteorological conditions at ground level, however, were acceptable for spray application. In spite of adverse conditions a good deposit in terms of drop numbers and volume/cm² was recorded that was not unlike those obtained during daylight hours. These results, therefore, could well represent the upper end of spray application parameters for high altitude spray emission.

The success of spray operations under daylight conditions depends to a large extent on the meteorological conditions during the critical period of spray release and subsequent deposition of the spray droplets onto the target site and beyond. Failure to consider the wind component, temperature gradient, and heat turbulence during spray release seriously jeopardizes the success of the operation, particularly when the target site is a small woodlot or spray block (Hurtig *et al.* 1953). This effect is well illustrated on a grand scale in figure 6 where the winnowing effect of the crosswind component and spray altitude has resulted in the deposition of the largest (Dmax) drop sizes onto the target area in low numbers but in relatively high volume deposits per unit area. It is well recognized that coverage (drops/cm²) and not volume (oz/ac) is responsible for maximum larval mortality (Hurtig *et al.* 1953).

It is therefore not surprising that, under these conditions, a mortality of only 25 percent was recorded against the late instars of the spruce budworm. One could expect a higher mortality, however, beyond the downwind boundary of the block where spray coverage is higher as shown by the increasing slope of the drop deposit graph.

Of greater significance, however, is the potential use of incremental application techniques based on the findings of the uniformity of deposit across a wide area and deposition of droplets as small as 20 μ from spray emission heights of 1500 feet. Because of the nature of the night trials, scientific equipment to record droplets below 20 μ were unavailable. Mount *et al.* (1970), however, using bioassay techniques, reported excellent control of caged mosquitoes 3 to 5 miles downwind from spray emission altitudes of 1000 feet thus indicating the presence of droplets below 20 μ . These findings are in agreement with those of Yule and Cole (1969) who reported airborne spray particles miles downwind of operational sprays.

Conclusions

During the course of studies of night meteorology, it was found that wind velocity increased with increase in altitude and that the altitude of calm conditions above the forest canopy was influenced by the surrounding terrain. Droplet deposition is directly affected by high altitude winds which in turn determine the degree of spray drift according to drop size.

Results from these trials suggest that for operational use of high altitude (700 to 1500 feet) night spraying, a rapid system of meteorological data retrieval would have to be developed in order to utilize the optimum weather conditions for spray deposition. The present system is not sufficiently advanced for the control of spruce budworm larvae, but could be readily adapted for large-scale spraying of flying insects that are susceptible to uniform deposits of insecticides at low dosage rate on a cumulative deposit basis.

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Organization and Implementation of Comprehensive Research and Development Programs on the Gypsy Moth, Douglas-Fir Tussock Moth, and Southern Pine Beetle in the United States

bc.1.2.3.4

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The Problem

The Douglas-fir tussock moth (*Orgyia pseudotsugata* McD.), the gypsy moth (*Porthetria dispar* L.), and the southern pine beetle (*Dendroctonus frontalis* Zimm.) are among the most destructive forest pests in the northwestern, northeastern, and southern United States, respectively. Major outbreaks of the tussock moth occur every 7 to 10 years and cause severe defoliation and tree mortality in Douglas-fir, grand fir, and white fir forests over extensive areas for periods of about 3 years. In 1974, over 2.3 million acres of forest were infested in Washington, Oregon, and Idaho. Over 400,000 acres were treated with DDT to avoid extensive tree mortality.

Gypsy moth populations reached a peak in the northeast in 1973 when defoliation of hardwood forests occurred on about 1.75 million acres. Oaks, birch, and maple suffered significant growth loss and, under intense or repeated defoliation, large numbers of trees, principally white oaks, died.

During the 3-year period 1972-74, an outbreak of the southern pine beetle in 10 Southeastern States caused losses exceeding 1.5 billion bd. ft. of pine sawtimber and 350 million cu. ft. of pulpwood. Less than 25 percent of the dead timber was salvaged.

Decision to Act

In response to strong expressions of concern over continuing losses from land managers, owners, and other interested groups,

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Robert W. Long, then Assistant Secretary for Conservation, Research and Education, U.S. Department of Agriculture, called upon four Federal agencies -- Agricultural Research Service (ARS), Animal and Plant Health Inspection Service (APHIS), Cooperative State Research Service (CSRS), and Forest Service (FS) -- in August 1973 to pool their resources and develop a coordinated program to provide means for reducing losses from the three insects within a relatively short time period. Continuing damage from the three pests emphasized the urgency of developing more effective control methods.

Planning, Funding, and Implementing the Program

Field and Washington Office agency staff members, working closely with the Department, organized research and development programs of 3- to 5-years duration for the tussock moth, the gypsy moth, and the southern pine beetle. Because of the complexity of the problems and the need to accomplish specific tasks within definite time periods, a new approach to program planning was used. This planning technique, called Adapted Convergence Technique for Agricultural Research (ACTAR), provided: 1) Clearly stated, well defined program objectives, 2) a logically ordered plan to reach those objectives, 3) flexibility which allowed for the inherent uncertainty of accomplishment associated with research and development, and 4) a chronological scheduling of planned activities. ACTAR also provided bases for developing benefit/cost analyses, appraising the most effective way to organize the overall programs, and monitoring progress.

Each of the three programs was designed to accomplish two common objectives: 1) To more fully utilize available knowledge to reduce damage caused by the insects and 2) to develop improved or new methods and materials for

preventing or suppressing damaging outbreaks.

Although the three programs were to differ slightly in structure and in the manner in which they were to be handled, three major areas of investigation were to be pursued: 1) Measurement and prediction of pest population trends and their impacts on forest ecosystems; 2) development of methods for preventing or suppressing pest population outbreaks; and 3) development of integrated pest management strategies.

The ultimate goal was to provide an integrated pest management system within which the damage caused by each insect would be prevented or reduced to tolerable levels. An array of tactics and strategies would be developed which would be compatible with forest management objectives and environmental conditions and could be used by forest land managers and pest control specialists.

Planning was completed by March 1974, reviewed within the Department of Agriculture, and approved by the Office of Management and Budget. Testimony before the House and Senate Appropriations Committees by Federal agency and key organizational representatives from the problem areas resulted in a Budget Amendment which was signed by the President in August 1974.

Research and development efforts in what was to be collectively referred to as the Combined Forest Pest R&D Program was activated in the Department of Agriculture in FY 1975 with an appropriation of \$6 million. This, plus regular (base) funds available to the Federal agencies, brought total funding in that fiscal year to \$9.3 million -- \$2.0 million for Douglas-fir tussock moth, \$4.8 million for gypsy moth, and \$2.5 million dollars for southern pine beetle. Comparable funding was subsequently provided in FY 1976 and is anticipated in FY 1977. The Douglas-fir tussock moth and gypsy moth programs were scheduled for 3 years and the southern pine beetle program for 5 years. Though each program is expected to make major advances in providing means for coping with each of the pests, it is also anticipated that there will be a need for followup work to complete, report on, and implement the new technology.

Organization and Administration of the Program

The Combined Forest Pest R&D Program is administered from the Office of the Secretary, U.S. Department of Agriculture. This departs from the usual pattern in which Federal agencies conduct research or action programs.

A Staff Officer assigned to the Secretary's Office provides staff support and coordinates activities among the three insect programs. Each program is directed by a Program Manager, also assigned to the Secretary's Office. All four individuals report directly to a nine-member Program Board chaired by the Deputy Assistant Secretary for Conservation, Research, and Education.

Each Program Manager is located in a headquarters office in the field and is assisted by a Research Coordinator and an Applications Coordinator. The Program Manager is responsible for selecting, scheduling, and approving funding for activities described in an Annual Plan of Work and Budget. Research and development proposals are solicited both on a competitive and non-competitive basis from a broad array of Federal, State, university, and private research and action organizations. Much of the work currently underway was initiated in the first year of each program, but new studies have or will be undertaken in subsequent years.

Each proposal is reviewed by a peer group of specialists (*ad hoc* Technical Review Panel) and recommendations made to the Program Manager regarding acceptability based on scientific merit and likelihood of contributing to program goals. Publication and activity records of the proposed investigators are also reviewed to determine the potential productivity of these individuals. In other words, every effort is made to select investigators with good "track records."

Each year, Program Management submits Annual Plans of Work and Budgets for review by the Program Board. The Board provides a national overview, guidance, and advice. During each review, accomplishments during the past year are assessed, progress toward objectives evaluated, and any needed program adjustments recommended to the Program Managers. With the recommendation of the Board, the Annual Plans are approved by the Assistant Secretary for Conservation, Research, and Education, and serve as guiding documents for each insect program.

In the field, once projects are accepted, detailed study plans may be requested from the investigators if their original or revised proposals do not contain sufficient detail to serve as operating documents.

Projects may be of one to several years duration, may be funded entirely out of one fiscal year's money (entire agreements) or on a year-to-year basis (open-ended agreements), and may take the form of cooperative agreements, grants, or contracts. Funds are

provided through CSRS and FS for the Douglas-fir Tussock Moth and Southern Pine Beetle programs, through APHIS, ARS, CSRS, and FS for the Gypsy Moth Program. Allocations to these agencies or their field units are made based on recommendations from the Program Managers. Final negotiations on the details of work and funding are made with the performing organizations -- federal forest experiment station, state forestry organization, state agricultural experiment station, university, industrial firm -- by Program management working closely with the funded Federal agencies and appropriate Federal or State representatives. Continuing control over approval and assessment of work and funding is maintained by each Program Manager.

To establish and maintain a coordinated effort within each program, investigators in closely related studies (e.g., sampling, population dynamics, behavioral chemicals, site/stand attributes) have been grouped into working or subject area groups, each with a leader. Examples of these working groups are as follows:

Douglas-fir Tussock Moth Program

- Insect Dynamics
- Effect on Ecosystem Components
- Site, Tree, and Stand Dynamics
- Socio-Economic Evaluation
- Direct Control Methods
- Indirect Control Methods
- Survey Methods
- Integration
- Technology Transfer

Southern Pine Beetle Program

- Impact
- Insect Sampling and Population Dynamics
- Mortality and Competition Factors
- Site, Stand, and Climatic Characteristics
- Host, Insect, and Symbiotic Factors
- Behavioral Chemicals
- Toxicants
- Forest Manipulative Practices
- Integration

These working (or subject area) groups periodically meet with Program management to review status of accomplishments and any work in progress or planned. Study plans and progress reports are exchanged between investigators in each group each year.

In addition to coordination efforts within the programs, closer ties and coordination have been developed through periodic meetings of the Program Managers or entire Program management staff with the Staff

Officer. In addition, interprogram working meetings are also held within various specialty areas in which there is involvement in similar work in two or more programs (e.g., nucleopolyhedral viruses, *Bacillus thuringiensis* chemical toxicants, behavioral chemicals, pesticide application techniques). A wide range of current or anticipated problems is discussed; accomplishments, experience, plans and/or ideas shared; outside technical input solicited; and responsibilities for continuing work assigned where appropriate.

Program management continuously monitors and evaluates progress and needs for redirection, additional or new effort, and termination of unproductive or lower priority work. This is accomplished through review of semi-annual and/or annual progress reports, attendance at working group meetings, on-site visits to projects, solicitation of reviews, comments and criticisms from outside experts or special interest groups, annual program workshops, and other contacts with organizational administrators and investigators. Proposed administrative actions relating to strengthening, reducing level of effort, and redirection or termination are reviewed with technical peer groups prior to implementation. Similarly, continued support for acceptable work, broad reviews of accomplishment, and needs for changes in program priorities or direction are discussed with an administrative advisory group.

Although a large number of projects are funded for more than a year, all organizational administrators and investigators have been informed that continued support for multiple year studies or the initiation of followup studies is dependent upon accomplishment, availability of funds, and needs of the programs to maintain flexibility in making shifts in emphasis. Support for more fundamental work varies between the programs based on the state of knowledge, length of program, and estimated probability of success but, in all cases, overall program emphasis is scheduled to shift from a research to an applications orientation over time. This tends to be both a source of frustration and a challenge to many scientists in the life sciences who have not been accustomed to accomplishing results within a time limit nor considering ultimate practical use in their total planning.

Where appropriate, procedures have been established for data sharing and analysis in closely related lines of work. Consideration has also been given to the release of interim or final results through various outlets (e.g., in-house publications, referred journals). These actions are intended to focus

attention on the selection of critical parameters for measurement, the need for standardization of data capture and analysis procedures where appropriate, the early and continuing analysis of results and refinement of study approaches, the timely release of information, and protection of author rights.

As might be expected in any large-scale program, adjustments in level of support and emphasis have changed with time. Initially, full funding was not allowed for each of the programs and certain tasks were specifically deleted from funding consideration. This necessitated some internal adjustments in level of support to accommodate the activities to be funded in each program. Later on, as research and development results were obtained, along with more experience in managing large, interdisciplinary programs, the 3 to 5 year activity schedules were revised one or more times to accommodate changes in R&D opportunities, reflect progress in developing new knowledge, better utilize available expertise, and improve the organizational structure of the respective programs. Similarly, levels of pest activity have varied in the respective regions necessitating shifts to new areas for some tests while, at the same time, permitting initiation of studies of endemic populations in other areas.

The Douglas-fir tussock moth and gypsy moth programs are scheduled to be completed in FY 1978. Plans are being made to conduct final field and pilot tests, summarize program accomplishments in the form of updated "state of the art" compendiums and user guides, and to identify resources -- manpower, dollars, facilities -- no longer needed in the programs and tasks that remain to be completed by the Federal agencies and others. Similar plans will be developed in approximately 2 years for the southern pine beetle program.

Finally, it would seem appropriate to make some early observations on the apparent effectiveness of conducting programs in the manner I have described to solve major forest pest problems. First, I would note that the approach permits a concerted effort with sufficient resources to accomplish significant results. No single organization could expect to accomplish similar results with more limited resources except over a very long time period and, possibly, at greater total cost. Secondly, the use of a competitive approach has generally fostered a healthy atmosphere and led to a much more concentrated R&D effort by individuals and groups both within and between the Federal, State, and private sectors. Thirdly, investigators and many of their administrators have shown keen interest and enthusiasm in participating in such a

program to meet the needs of a larger user public. Individuals are able to grow professionally, to produce results that are acceptable both to their parent organizations and in the broader scientific community and to mingle, compete, and interact with other disciplines. Finally, many investigators have come to a fuller realization of the contribution that their individual work can make in achieving a larger goal, the development of an integrated pest management solution to a major forest pest problem.

Summary

I have attempted in these few minutes to describe three major forest pest problems which have led to a U.S. Department of Agriculture action program. Four of the Department's agencies are working closely with state agricultural experiment stations, universities, colleges, state forestry organizations, and industry in an accelerated research and development effort.

The Program is administered from the Office of the Secretary, USDA, and is directed in the field by program managers for each of the pest problems -- Douglas-fir tussock moth, gypsy moth, and southern pine beetle.

Common objectives and goals have been established and the three programs have been underway since FY 1975. Studies have been undertaken which will ultimately improve pest control specialist and land manager abilities to understand and predict pest population trends and their impacts. Site, tree, stand, and climatic characteristics influencing outbreak incidence and severity are under intensive investigation. Field and laboratory work is underway which will provide new toxicants, behavioral chemicals, and forest manipulative practices as well as increased understanding of mortality and competition factors, and insect/forest interactions regulating pest populations. Criteria and methods are being developed for implementing and evaluating pest management strategies.

A large number of investigators are working together within and across organizational and disciplinary lines in each of the programs to accomplish the goal of providing new or improved control methods and materials. Rapid progress is being made. The success of this approach to problem solving is expected to affect the future and direction of urgently needed research and development efforts on other forest problems.

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Discontinuous Stability in a Sawfly Life System and Its Relevance to Pest Management Strategies c 274

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Evidence is accumulating that many ecological systems are discontinuously stable, i.e., they possess more than one domain of attraction (Holling 1973). Southwood and Comins (1976) cite evidence for multiple equilibria phenomena in a number of insect systems, including eucalyptus aphids, sugar cane borers, cereal aphids, and a spruce sawfly.

Holling *et al.* (1977) have recently developed a powerful simulation model for management of the spruce budworm/balsam fir (*Choristoneura fumiferana* Clem./ *Abies balsamea* Mill.) ecosystem, at the base of which are multiple equilibria concepts, outlined by Morris (1963) in an exquisitely detailed population study of that insect. The fisheries literature is full of examples of stocks which have collapsed to extremely low levels following intensive exploitation, and which have remained at low levels for extended time periods, even when fishing pressures were released (Beeton 1969). Noy-Meir (1975), using the graphical techniques of Rosenzweig and MacArthur (1963), discussed the theoretical implication of discontinuously stable grazing systems as related to plant characteristics, to herbivore characteristics, and, most important, to management practices. He presents evidence that some real pasture and grazing systems are discontinuously stable (Perry 1968; Morley 1966).

The consequences of discontinuous stability are relatively sudden and unexpected shifts in numbers or productivity when systems are stressed, i.e., the collapse of a valuable resource, or a major outbreak of a pest. Although such events are usually viewed as catastrophic, the reverse may be true. Using an example from an insect/forest system, I here show how a pest manager may reap unexpected benefits in managing a system which possesses multiple stability domains.

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System Description

The insect is a sawfly, *Neodiprion swainsoni* Midd., a defoliating pest of jack pine, *Pinus banksiana* Lamb. (fig. 1).

The system has been partly described (McLeod 1968, 1970, 1972, 1973, 1975a), and a more complete description and a detailed process simulation model are in preparation.

This sawfly is a colonial defoliator, a discrete generation, univoltine insect, which feeds from early August through September on the previous year's growth of the host plant. It leaves the current foliage intact, except at high population levels if the supply of "old" foliage is exhausted. In September and early October, larvae drop from the trees and spin cocoons in the soil, where they pass the winter. The following spring, in early June, the insect transforms to the pupa while still in the cocoon, and the adults emerge in early July. The female deposits her total complement of about 65 eggs on a single current shoot of jack pine, and the eggs require 1 month to hatch.

A number of natural enemies attack the sawfly. The most important of these are shrews, *Sorex cinereus*, which feed on the sawfly in the cocoon stage throughout the fall and winter (McLeod 1966); birds which feed on large larvae in late summer and fall, and on emerging adults in July (McLeod 1974); and a complex of univoltine, synchronous, larval parasitoids which attack young larvae in early August and emerge from the cocoon the following summer in time to attack sawfly larvae of the succeeding generation (McLeod 1975a).

Larvae are strongly affected by weather (fig. 1). Development of larvae, especially in northern latitudes, may be so retarded by cold temperatures that they are unable to complete their feeding in the fall (Tripp 1965). Optimum conditions for sawfly development and survival are found in a narrow band between latitude 46° and 48° in the southern

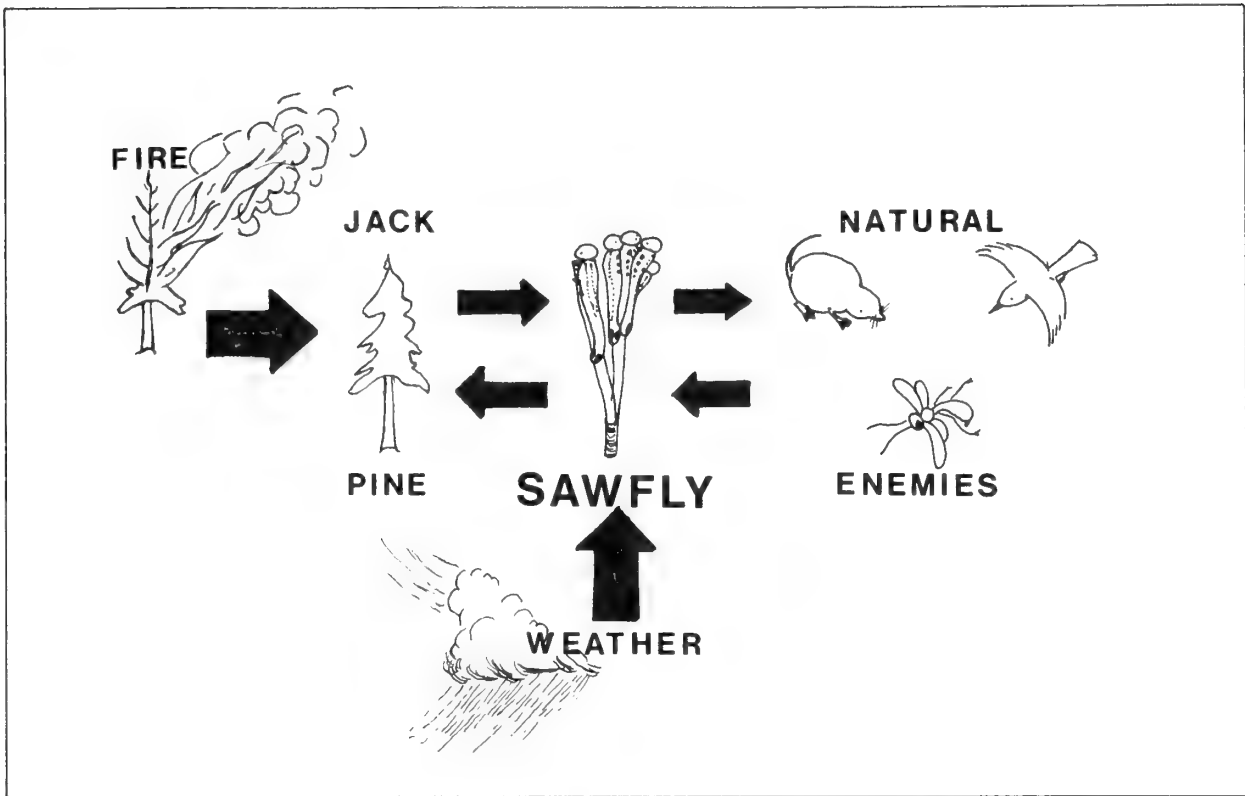


Figure 1.--Major components of the Swaine jack pine sawfly life system. There are feedbacks between the forest and the sawfly and between the sawfly and its natural enemies. Principal driving variables are fire (for the forest) and weather (for the sawfly).

extremity of the host plant's distribution (McLeod 1970).

Jack pine is the only host of *Neodiprion swainei*. Forests of jack pine are typically pure and even aged, and originate from fires (fig. 2). Cones are retained on the tree and will not open to release seeds unless exposed to temperatures in excess of 52° C. In its early years jack pine is one of the fastest growing of Canadian conifers, but the growth rate declines appreciably after about 35 years, and stagnation follows. If undisturbed, jack pine forests would usually be slowly succeeded by black spruce; but historically, repeated fires have assured the maintenance of jack pine in climax on poor, sandy, outwash soils where this species grows best (Rudolph 1958; Rowe 1971).

Insect survey literature gives a clear impression of strong discontinuities in space and time in the distribution of numbers of sawflies (McLeod 1970). Usually, this insect is a rare component of the jack pine forest. In certain favoured sites, however, repeated outbreaks have occurred at intervals of about 8 to 10 years, especially as trees approach maturity (fig. 2). During outbreak peaks,

severe and general defoliation and some top killing may occur, and in the troughs, some defoliation may be noticeable in the upper crowns of dominant trees only. Rarer still are truly catastrophic outbreaks, where whole forests may be killed over thousands of hectares. In fact, the qualitative behavior of sawfly populations is analogous to the qualitative changes observed by range managers cited by Noy-Meir (1975), which he attributes to discontinuities in the range's stability domains.

Detailed Historical Data and Perturbations

Further evidence for the existence of multiple stability domains in the sawfly's life system are obtained from precise historical records of population trends in Quebec between 1956 and 1974 (McLeod 1972; 1975a). The data are presented as a number of sawfly eggs per square metre of ground surface and were obtained annually from each of seven 4-hectare permanent plots, as the product of the following:

1. the number of sawfly egg clusters per tree from 75 to 100 randomly selected living whole trees per sample,
2. the number of eggs per cluster obtained from approximately 50 randomly selected egg clusters from (1),
3. the number of living jack pine trees per chain-square (20 x 20 metres) block measured annually in each of 25 blocks per plot.

$S_{\bar{x}B}$ = standard error of B
 C = number of living jack pine trees per unit area (404.68 sq. metres)
 $S_{\bar{x}C}$ = standard error of C

A brief history of the population trends and events in each of the plots follows (fig. 4):

Plots 1 and 2 -- Aged 51 and 70 years respectively in 1974, these two areas were in outbreak condition in 1964, and in 1965 were treated with the insecticide Phosphamidon at 4 oz. per acre (0.28 kg/ha). Populations of sawflies dropped to extremely low levels in 1966, the year following the one-shot application of insecticide, and have remained at low levels ever since.

Plot 3 -- Seemingly out of phase with the majority of *Neodiprion swainei* infestations in the mid- to late 1960s (McLeod 1970), the infestation in this 60-year-old stand reached extremely high levels and collapsed in 1965 owing to starvation and a polyhedral virus. Tree mortality was cumulative following collapse, and by 1966, virtually all the trees over 2000 hectares had died. This study was terminated in 1967 following a salvage cut.

Plots 4 and 6 -- Sawfly populations were maintained at moderately high levels in these two 51-year-old stands (in plot 4 from 1962 to 1974 and in plot 6 from 1967 to 1974). At the peak of the infestation in plot 4 in 1968, severe defoliation and some tree mortality (<2 percent) did occur, but the trees rapidly recovered as sawfly populations dropped in subsequent years. In plot 6, although absolute numbers of insects were only moderate throughout the study, the impact on the forest was greater than in plot 4 owing to the small number of trees per unit area (table 1). Severe defoliation persisted from 1967 to 1973 with some top killing but insignificant tree mortality. In 1974, insecticide contamination during an operation against the spruce budworm (McLeod 1975b) caused an abrupt collapse of this sawfly infestation.

Plot 5 -- Two sawfly outbreaks occurred in this 51-year-old jack pine stand between 1951 and 1974. The first collapsed dramatically in 1960 following high mortality through shrew predation and larval parasitism. Although defoliation at the outbreak's peak was severe, no top killing occurred and the trees recovered quickly. The second outbreak

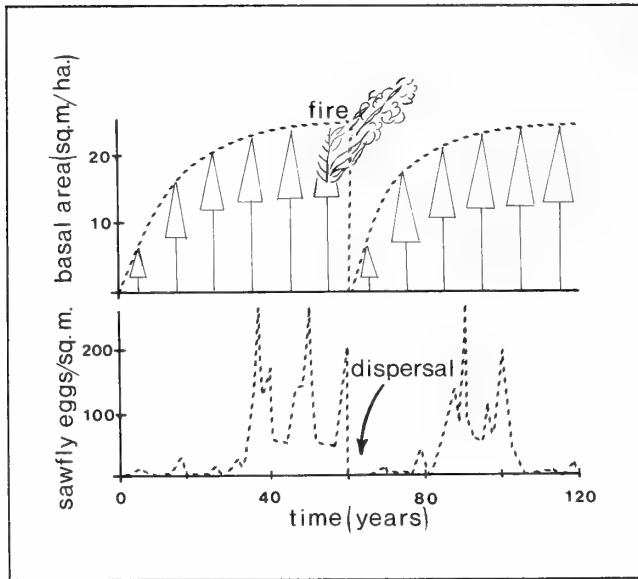


Figure 2.--Time bounding of the Swaine jack pine sawfly life system. Jack pine forests are pure and even aged and usually regenerate after fire. Sawfly populations are usually low but may suddenly erupt and persist at higher levels for years, especially as forests reach maturity. Periods between outbreaks are frequent (about 10 years).

The means and standard errors of each sample are shown (table 1), as well as the combined errors (fig. 3).

Calculated by propagation of error, the combined error estimate is:

$$S_{\bar{x}t} = \sqrt{[A^2 \cdot (S_{\bar{x}B} \cdot S_{\bar{x}C})] + [B^2 \cdot (S_{\bar{x}A} \cdot S_{\bar{x}C})] + [C^2 \cdot (S_{\bar{x}A} \cdot S_{\bar{x}B})]}$$

where

A = number of sawfly egg clusters per tree
 $S_{\bar{x}A}$ = standard error of A
 B = number of sawfly eggs per cluster

Table 1.--Basic statistics for calculating *N. swainei* eggs per square metre

Plot	Year	Egg clusters per tree ¹	Eggs per cluster ²	Living jack pine trees per unit area ³ (404.68 metres sq.)
01	1964	005.540 + 01.290	--	163.800
01	1965	017.293 + 02.466	053.717 + 01.629	157.300
01	1966	000.013 + 00.013	--	152.900
01	1967	000.000 + 00.000	--	132.840 + 06.624
01	1968	000.060 + 00.034	--	126.000
01	1969	000.085 + 00.051	--	119.560 + 06.453
01	1970	000.000 + 00.000	--	113.240 + 06.343
01	1971	000.000 + 00.000	--	108.240 + 05.370
01	1972	000.000 + 00.000	--	105.080 + 05.730
01	1973	000.000 + 00.000	--	102.520 + 05.834
01	1974	000.000 + 00.000	--	102.400
02	1964	018.580 + 03.369	--	065.100
02	1965	051.311 + 06.770	054.771 + 01.844	063.200
02	1966	000.053 + 00.032	--	061.840 + 03.913
02	1967	000.102 + 00.044	--	054.880 + 03.366
02	1968	000.160 + 00.066	--	051.900
02	1969	000.640 + 00.136	061.562 + 03.125	049.000 + 03.025
02	1970	000.300 + 00.091	--	045.320 + 02.885
02	1971	000.400 + 00.110	--	045.440 + 03.094
02	1972	000.167 + 00.069	--	043.640 + 02.867
02	1973	000.060 + 00.034	--	041.280 + 02.791
03	1962	009.533 + 01.841	068.383 + 02.228	119.000
03	1963	018.219 + 02.826	081.180 + 02.151	114.400 + 05.832
03	1964	106.980 + 12.973	051.038 + 01.852	099.840 + 0.576
03	1965	009.240 + 01.754	036.220 + 01.304	071.600 + 04.800
03	1966	000.000 + 00.000	--	019.840 + 04.760
03	1967	000.000 + 00.000	--	006.357 + 03.385
04	1962	003.350 + 00.676	--	117.400
04	1963	001.693 + 00.348	--	113.640 + 08.805
04	1964	006.253 + 01.053	063.260 + 01.571	112.300
04	1965	018.373 + 02.959	066.069 + 01.683	109.600
04	1966	020.274 + 02.655	060.603 + 00.834	108.280 + 08.130
04	1967	013.160 + 01.390	070.320 + 02.278	102.240 + 07.782
04	1968	039.210 + 05.092	071.200 + 01.891	092.520 + 07.243
04	1969	008.733 + 01.055	063.940 + 02.283	094.240 + 07.605
04	1970	004.387 + 00.626	063.060 + 02.163	085.800 + 06.661
04	1971	006.160 + 00.825	061.877 + 02.697	077.600 + 06.220
04	1972	009.540 + 01.290	057.456 + 02.141	072.360 + 05.761
04	1973	008.240 + 01.155	064.480 + 01.667	070.640 + 06.074
04	1974	004.300 + 00.838	069.559 + 03.341	069.400
05	1961	001.449 + 00.371	065.147 + 01.967	100.000
05	1962	004.828 + 00.874	066.060 + 02.451	095.200
05	1963	004.547 + 00.670	063.738 + 01.284	091.800 + 06.133
05	1964	009.905 + 01.658	066.309 + 00.662	089.400
05	1965	034.117 + 03.736	068.053 + 02.106	084.500
05	1966	002.053 + 00.291	060.729 + 01.023	082.080 + 05.205
05	1967	014.293 + 02.546	077.140 + 02.350	079.400
05	1968	017.693 + 02.555	070.564 + 01.863	076.640 + 04.957
05	1969	016.547 + 01.799	060.700 + 02.503	074.720 + 04.805
05	1970	005.293 + 00.688	063.380 + 02.496	072.120 + 04.673
05	1971	001.080 + 00.192	050.341 + 02.219	070.120 + 04.538
05	1972	001.140 + 00.258	059.340 + 02.203	068.560 + 04.369
05	1973	000.120 + 00.046	049.913 + 01.423	067.240 + 04.346
05	1974	000.380 + 00.106	081.720 + 02.098	066.600
06	1967	022.773 + 02.370	063.800 + 02.715	045.760 + 03.353
06	1968	017.270 + 02.034	058.860 + 01.488	040.960 + 03.023
06	1969	021.027 + 02.749	066.354 + 02.026	038.840 + 03.848
06	1970	013.680 + 01.397	064.437 + 01.902	039.280 + 05.709

Table 1 (continued)

Plot	Year	Egg clusters per tree ¹	Eggs per cluster ²	Living jack pine trees per unit area ³ (404.68 metres sq.)
06	1972	027.080 + 04.841	058.687 + 02.250	030.240 + 02.696
06	1973	025.760 + 04.198	063.592 + 01.965	029.480 + 03.012
06	1974	013.760 + 01.907	087.420 + 02.350	027.000 +
07	1970	000.060 + 00.034	--	092.480 + 04.177
07	1971	000.000 + 00.000	--	090.600 +
07	1972	000.000 + 00.000	--	086.000 + 03.498
07	1973	000.000 + 00.000	--	090.600 + 03.878
07	1974	000.000 + 00.000	--	081.500 +

¹ With standard error.

² No sample of less than 25 egg clusters included. For missing entries, the mean for the series (63.76) is used.

³ Samples with no variance estimates are extrapolations from Plonski's (1960) site index curves for jack pine.

reached a peak in 1965, but declined in 1966 owing to accidental drift of insecticide from an operation in a neighbouring stand. The populations rebounded to pre-spray levels in 1967, but events were complicated in the early 1970s by a massive outbreak of a pitch nodule maker, *Petrova* spp. (McLeod and Tostowaryk 1971) which caused extensive top killing and deformation in the tree crowns. Because *Petrova* is a sap-feeder, it was able to compete successfully with the sawfly for food. Survival of sawfly larvae declined dramatically in the *Petrova* outbreak years, and by 1974 sawfly populations were at a very low level.

Plot 7 — Monitoring in this 51-year-old stand was carried out from 1970 to 1974. Only in 1 year of the 5 were sawflies recorded. Casual observations in this stand from 1964 to 1971 would also indicate that sawfly populations were very low during that period.

The sharp discontinuities in the distribution of sawfly numbers may best be seen by replotting the data of figure 4 as a recruitment factor curve, i.e., $\log_{10} (N_{t+1}/N_t)$ vs. $\log_{10} (N_t)$ where N_t is the number of sawfly eggs per square metre (fig. 5).

The outlying points to the right at (a) trace the population of plot 3 which completely destroyed its food supply (table 1) and collapsed from starvation. Below this is a collection of points with a negative slope crossing the replacement line at about $\log_{10} N_t = 2$. An additional cluster of points

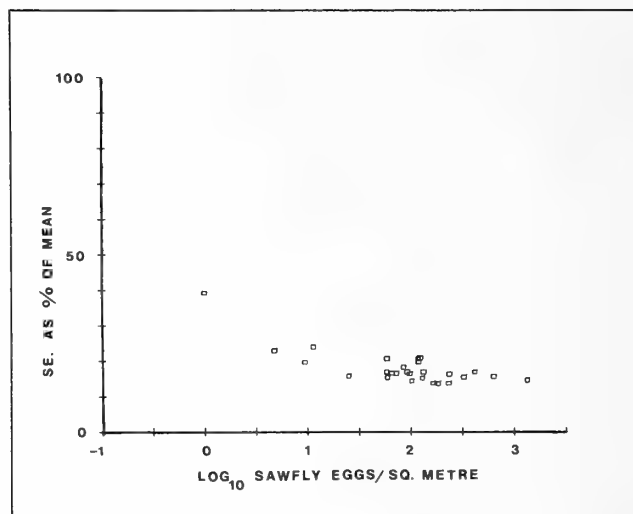


Figure 3.--Standard error of mean as function of mean for *N. swainei* eggs/sq. metre as calculated by propagation of error (see text). Only complete data sets of table 1 are used.

is found two orders of magnitude lower, crossing the replacement line just above $\log_{10} N_t = 0$. Between these two clusters are three trajectories resulting from system perturbations. At (b) is the dramatic one-generation shift from the high to low density caused by insecticide application (plots 1 and 2). At (c) is the more gradual decline to the lower density resulting from competition with an associated insect (plot 5). Finally, the clockwise circularity in time of the points in each cluster would seem to suggest oscillations resulting from lag effects.

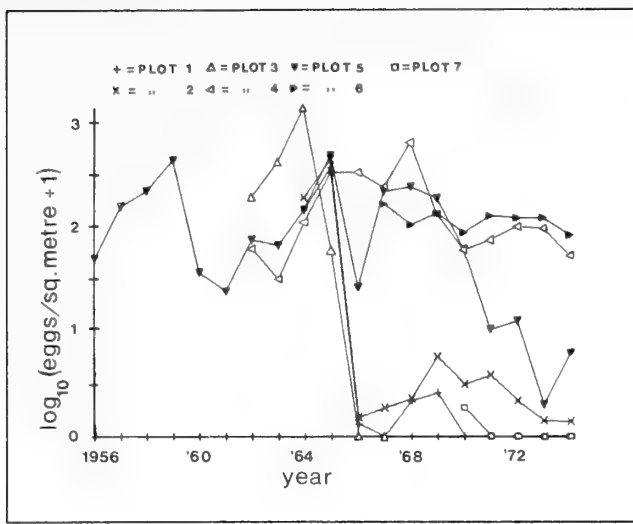


Figure 4.--Trends in *Neodiprion swainei* egg populations in seven localities in Quebec, 1956 to 1974.

I know of no statistical averaging techniques which would permit the replication either of the discontinuities, or of the trajectories following perturbation of the observed populations. Instead, I shall

presume cause, measure the effects in a simulation model, and compare the results with the observed world.

These presumed causes are:

1. competition among groups of animals at different trophic levels for a common limiting resource;
2. a "Type III" (Holling 1965) density response of a group of predators which saturates at an extremely low sawfly density: in the sawfly life system, these are insectivorous birds, feeding on larvae and adults (fig. 1);
3. a second group of predators exhibiting a Type III response saturating at high prey densities, just below the level at which food begins to be limiting to the sawfly: these are cinereus shrews (fig. 1);
4. an upper equilibrium set by foliage: this equilibrium is stable on the insect plane but conditionally unstable on the forest plane (Jones 1975, 1977; Holling *et al.* 1978), if the replacement rate of foliage is not fast enough to prevent widespread killing of trees as the sawfly reaches this level.

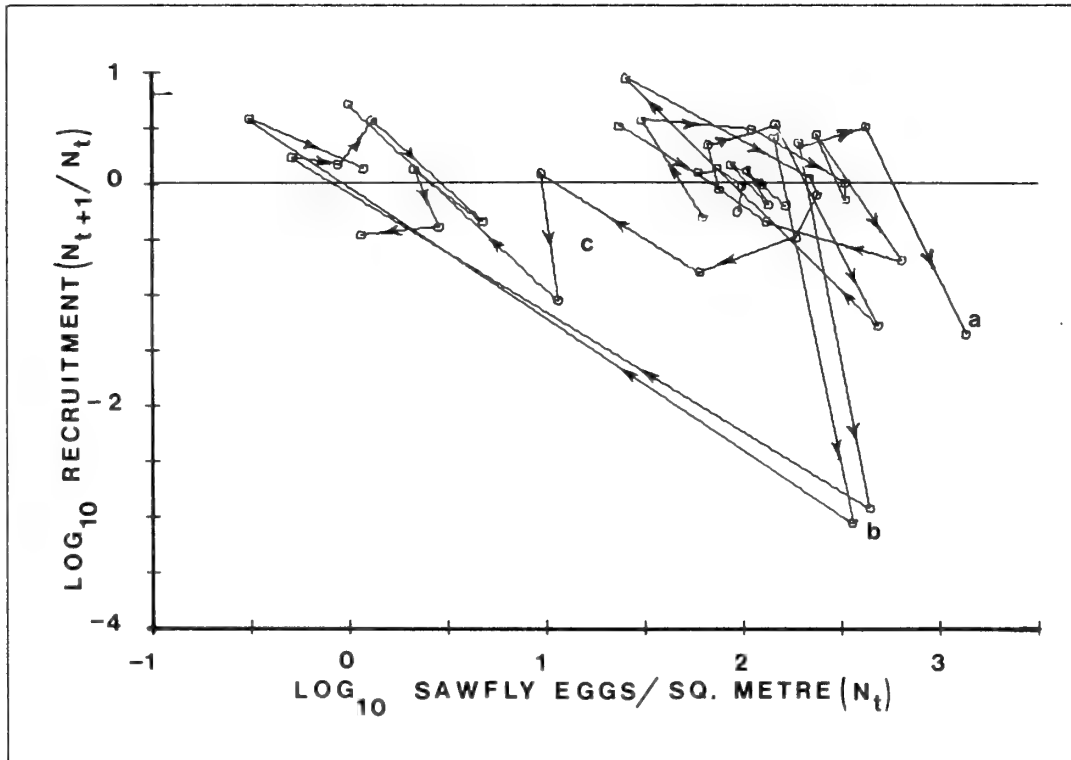


Figure 5.--Data of fig. 4 expressed as recruitment; $\log(N_{t+1}/N_t)$ vs. $\log N_t$. Arrows show direction in time.

5. system "clocks" or time constants caused by lags resulting from the effects of competition: one of these is the replacement of foliage parts following defoliation at very high densities, but a second more powerful lag is caused by the numerical response of the synchronous univoltine parasitoids (McLeod 1975a);
6. random inputs from a powerful driving variable such as weather.

With this simple set of assumptions, most of the major components in the sawfly life system (fig. 1) may be modeled. Not included, however, are forest growth, forest replacement (driven by fire), or insect dispersal. The forest model is not included because in this paper we are concerned only with events after the forests mature. Also, the very short time frame of the outbreak periods (ca. 10 years) would not suggest their dependence upon forest replacement. Similarly, sawflies, unlike spruce budworm (Morris 1963), have only one dispersal stage (adults) and they are relatively poor fliers. Dispersal would be important only in the event of forest replacement.

The schema (fig. 6) follows the life history and mortality schedules of the sawfly outlined in McLeod (1975a). The only dynamic variables are the sawfly, its larval parasitoids, and foliage replacement.

Functional responses are of the Michaelis-Menten type:

$$NA = \frac{\beta \cdot NO^n}{\alpha^n + NO^n}$$

where

- NA = number of prey attacked
- β = the saturation level of the response
- NO = the number of prey available for attack
- α = the prey density at which 1/2 saturation occurs
- n = an exponent. When n=1, the response is Type II (Holling 1965). When n>1, the response is sigmoid (Type III).

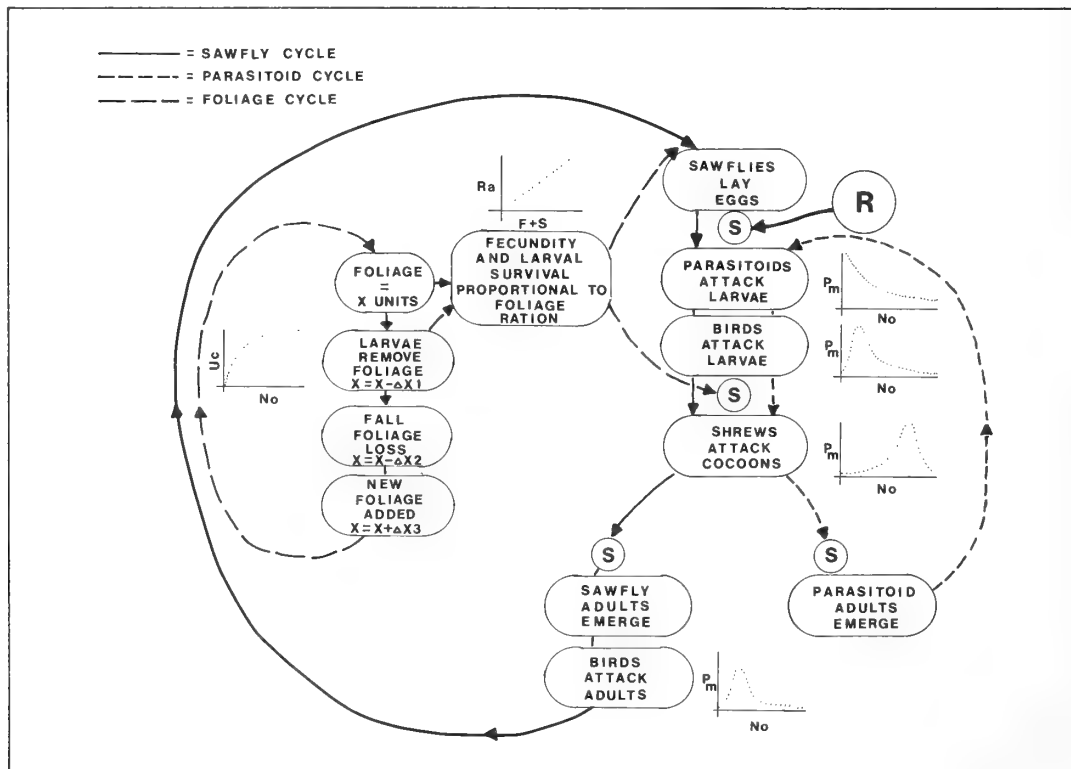


Figure 6.--Schema of *Neodiprion swainei* simulation model. The forms of the processes are shown in graphs, at each step: N_0 , number of prey available; P_m , percent mortality; U_c , units of foliage consumed; $F+S$, sawfly fecundity and larval survival; R_a , foliage ration. The circled S = a fixed survival rate, and the circled R = a log-normally distributed random variable applied to a fixed survival. (For details see Appendix.)

Competition is modeled with a negative binomial function (Griffiths and Holling 1969), where:

$$NHA = NO \cdot [1 - (1 + NA/NO \cdot K)]^{-K}$$

where. NHA = the number of prey attacked
K = the dispersion coefficient,
where $K \rightarrow \infty$ the function
becomes the Poisson, $e^{-NA/NO}$.

Weather is simulated by a log-normally distributed random variate acting on young larvae (fig. 6).

The maximum number of foliage units available to larvae is four (one for new foliage and three for old). Larvae respond functionally to the available foliage and the response is coupled with a competition equation. Larvae feed first on units 1 to 3 and will not feed on unit 4 (new foliage) unless the ration of old foliage is exhausted. Survival of larvae and fecundity of adults is directly proportional to the foliage ration. The latter is expressed as the total number of units per larva consumed versus the total required (a constant).

Details of the model are presented in Appendix I. The expressions listed, and the three initializations (sawfly egg density, parasitoid adult density, and foliage units) are all that are required to replicate the outputs in this report. The derivations of the parameters for the functional and numerical responses and the competition equations will be given in a future report.

Validation

The usefulness of a process model such as this one is not to make fine-scale year-to-year predictions of changes in insect numbers, but rather to determine what qualitative changes in populations would occur as a result of perturbations. Therefore, the appropriate statistical tests are those which compare the means and variances of the data (table 1), and the model (Appendix I) before and after perturbations (cf. fig. 7). Since changes in numbers are geometric, \log_{10} transformations have been used (table 2).

Undisturbed Populations (fig. 7A)

The data from plots 4 and 6 are used for this validation. The model's output, for 30

generations, shows approximately the same mean density, amplitude, and periodicity as the observations, and this is also supported by the statistical tests which show that the means and variances of the data and the model's output for undisturbed populations (table 2) are essentially similar.

The clockwise circling of the points around the replacement line (\log_{10} recruitment = 0) is set by three events. The functional and numerical response of shrews fixes the replacement crossover at about $\log N_t = 2$, and the 10-generation cycle is determined by the lag in the response of the larval parasitoids. Further confirmation of this is seen in plotting parasitoid progeny density and sawfly density in phase (fig. 8). Some damping is also provided by the foliage function peak populations, but by the time outbreaks have reached this level, a crash is almost inevitable in any event because of the lag in the parasitoids's response.

A Natural Perturbation (fig. 7B)

In plot 5, from 1970 to 1972, small larval survival averaged 0.2 which is less than one-half the normal rate (Appendix I). This caused a steady decline in numbers, and even when small larval survival returned to high levels in 1972, populations continued to drop and were trapped in the lower domain of attraction. This was simulated in the model by setting the larval survival to 0.15 for three consecutive years, and this provided the same effect as the observations (table 2). Even when larval survival was set back to normal after 3 years, the populations were sufficiently close to the lower stability domain to fall into its zone of attraction.

Insecticides

Here also, the model's output is essentially similar to observations (table 2). Given a very strong negative perturbation, populations are shifted in only one generation to the lower stability domain and remain locked there for several generations.

I conclude that the model faithfully mimics much of the richness of qualitative population behaviours in the real world system including the periodicity and amplitude of oscillations and the shifts between stability domains made under a variety of perturbations.

Chemical insecticides have come under heavy criticism in recent years because of potentially harmful environmental impacts. However, the results of this study would indicate that chemicals may not just be a necessary evil to be used when all else fails,

Clearly, the success of insecticide control against *Neodiprion swainei* was as much dependent on the existence of a lower stability domain as on susceptibility to the poison itself.

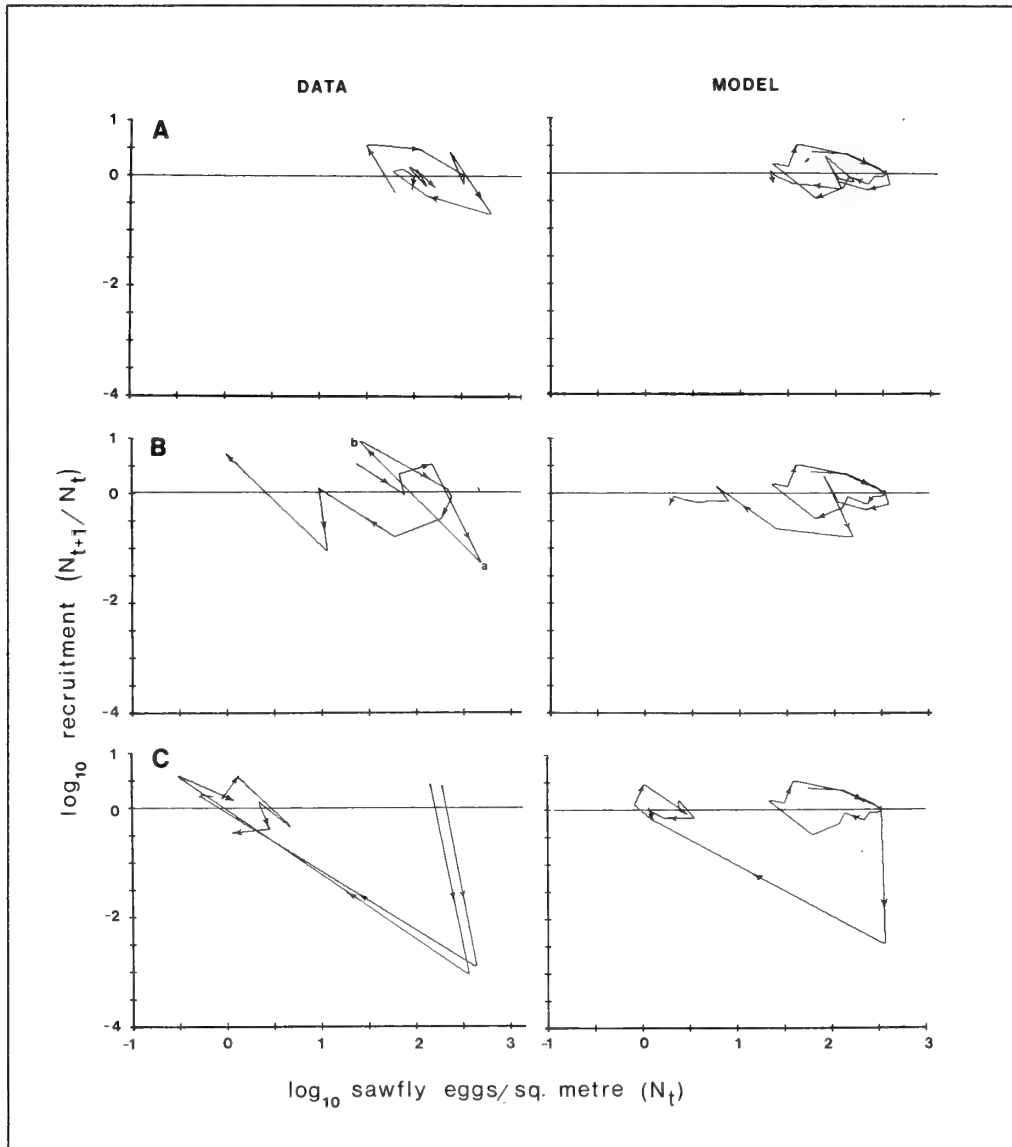


Figure 7.--Comparison of observed recruitment for *Neodiprion swainei* (left) with simulation model (right). Model runs are for 30 years. Sawfly egg populations are initialized at 55/sq. metre; parasitoid adults at 0.03/sq. metre; trees have full complement of foliage at initialization; standard deviation of log-normally distributed random driving variable = 0.17. Undisturbed populations at upper equilibrium (plots 4 and 6) (A). A shift from upper to lower equilibrium under natural stress (competition for food by an associated insect) (B); in the model, for years 21 to 23 inclusive, small larval survival was set at 0.15 ("normal" = 0.45. Sprayed plots (1 and 2) (C); in the model, "spray" was applied at year 18, and simulated with small larval survival rate of 0.005. Arrows show direction in time.

Table 2.--Statistical comparison of output of the simulation model (Appendix), expressed as \log_{10} sawfly eggs/sq.m., with the data of table 1

	N	Model $\bar{x} + sd^1$	N	Data ₁ $\bar{x} + sd^1$	Differences between model and data
1. Undisturbed populations (fig. 7A)	30	2.0128 + 0.4067	21	2.0654 + 0.3008	N.S.
2. Natural disturbance prior to perturbation (fig. 4B)	21	2.136. + 0.3722	9	2.0318 + 0.4495	N.S.
3. Natural disturbance following perturbation (fig. 7B)	9	0.8306 + 0.6133	5	0.9033 + 0.6422	N.S.
4. Insecticide application pre-spray (fig. 7C)	19	2.1549 + 0.3786	4	2.4083 + 0.2298	N.S.
5. Insecticide application post-spray (fig. 7C)	11	0.1679 + 0.2509	11	0.0608 + 0.3618	N.S.

Differences between

1 and 2	N.S	N.S
1 and 4	N.S	N.S
2 and 4	N.S	N.S
1 and 3	***	***
2 and 3	***	***
1 and 5	***	***
4 and 5	***	***

¹ All variances are homogeneous.

Figure 9 shows from the model what might have happened had there been no lower equilibrium. Numbers drop to low levels in the years following spraying, but recovery is rapid, and the risk that sawfly populations would overshoot food resources in the release phase is high. Some suggestion of this is also given by the observations in plot 5 following insecticide drift in that area in 1965 (fig. 7B). The populations dropped to low levels in 1966 [cf. the point (a)] but not sufficiently to be attracted to the lower stability domain.

The result was a dramatic recovery of populations to pre-spray levels in the year following. However, the existence of the lower stability domain has furnished an unexpected benefit to the manager, since only one application of insecticide is required to maintain pest populations well below economic levels, for several generations following application. The benefits reaped are low environmental impact and high rate of return on the initial investment.

Are discontinuous stabilities the rule rather than the exception in ecological sys-

tems? If so, it might be useful to reconsider the trade-offs between single-shot heavy applications of insecticides and the temporary ecological disruption they cause, versus lighter application rates and the potential long-term consequences of repeated applications.

However, if the distance between stability domains is great, for example as in the eastern spruce budworm (Holling *et al.* 1977), then when the insect is in outbreak conditions, no reasonable amount of insecticide would suffice to lower the populations to endemic levels. The best that can be done during an outbreak is to try to save foliage until outbreaks subside, and this usually means repeated applications with all the attendant risks.

A better control policy may be to apply treatments when the pests are still trapped in a lower stability region, but in "threat" stage, potentially reaping the same benefits as the sawfly example cited in this report. Indeed, this new way of looking at insect ecosystems points to a better way of "ounce of prevention" pest management.

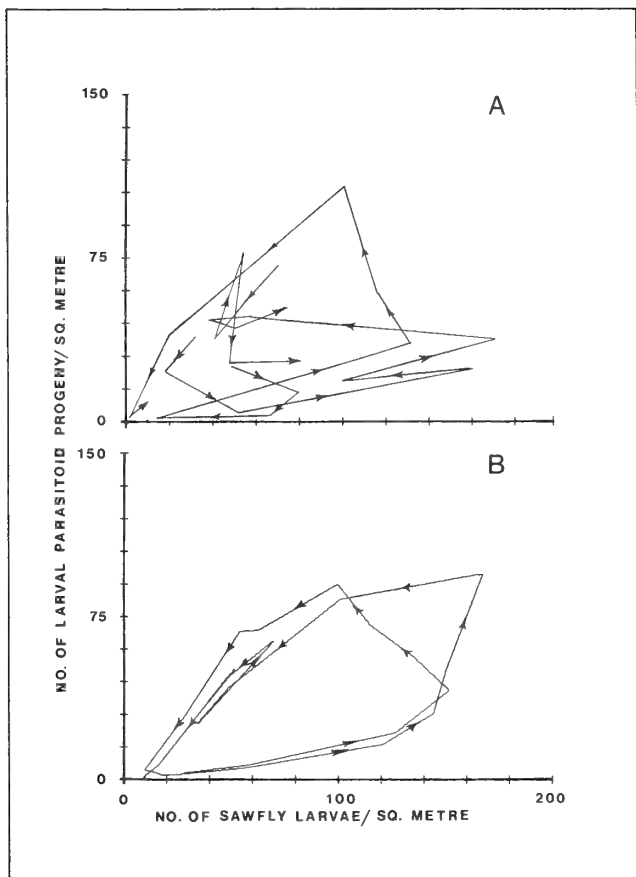


Figure 8.--Phase plots showing response of parasitoids to changes in numbers of *Neodiprion swainei* large larvae per sq. metre. Data (plots 4, 5, and 6) (A). Model (oscillating at upper equilibrium) (B). These parasitoids are responsible for the cycling around the stability domains seen in figure 7. Arrows show direction in time.

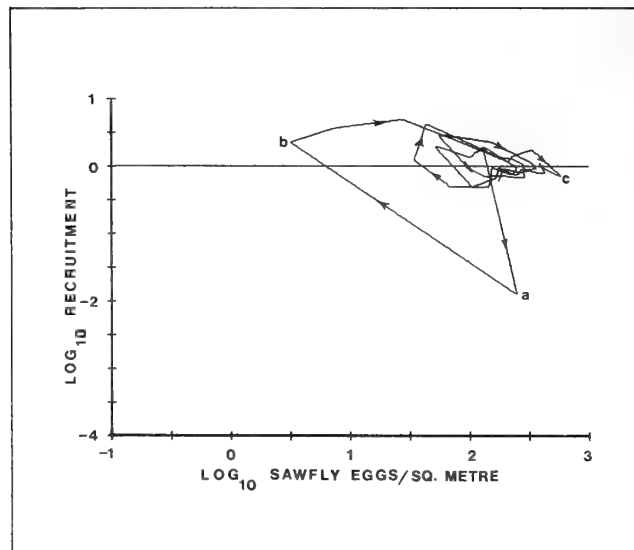


Figure 9.--Sawfly recruitment in model under same conditions as fig. 7C, except that bird predation functions are removed. With no lower stability domain, populations are depressed only one year (b) following "spray" application (a). A rapid return to the upper equilibrium occurs over a few years, and the system overshoots at (c) before returning to normal. Severe defoliation and some tree mortality would result. Arrows show direction.

Appendix--Details of *Neodiprion swainei* simulation model

Initialization:	sawfly eggs/sq. metre	= 55 (EGG)
	parasitoid adults/sq. metre	= 0.03 (PARAD)
	foliage	= 4 units { YFOL(4) = 1 }
	standard deviation of log-normally distributed random variate	= 0.17 (RAND), (variate initialized at SEED = 333)
Start		EGG = 55
Fixed survival to larvae and log-normal random function		LARV = EGG* 0.45+RAND
Foliage function:		UPERL = 0.0041
	UPERL is the mean number of foliage units consumed per larva	
	Set up the first three units to be defoliated	ZFOL = YFOL(1)+YFOL(2)+YFOL(3)

Appendix (Continued)

Larvae compete for units of foliage and defoliation assigned equally to each of three units

$$\begin{aligned} \text{COMP} &= 1 - e^{-(\text{UPERL} * \text{LARV} / \text{ZFOL})} \\ \text{OLDF} &= \text{ZFOL} * \text{COMP} \\ \text{YFOL}(1) &= \text{YFOL}(1) - \{ \text{OLDF} * \text{YFOL}(1) / \text{ZFOL} \} \\ \text{YFOL}(2) &= \text{YFOL}(2) - \{ \text{OLDF} * \text{YFOL}(2) / \text{ZFOL} \} \\ \text{YFOL}(3) &= \text{YFOL}(3) - \{ \text{OLDF} * \text{YFOL}(3) / \text{ZFOL} \} \end{aligned}$$

Remaining requirements are competed for on current foliage

$$\begin{aligned} \text{UNITS} &= \text{OLDF} / \text{LARV} \\ \text{COMP} &= 1 - e^{-\{ (\text{UPERL} - \text{UNITS}) * \text{LARV} / \text{YFOL}(4) \}} \\ \text{NEWF} &= \text{YFOL}(4) * \text{COMP} \\ \text{YFOL}(4) &= \text{YFOL}(4) - \text{NEWF} \end{aligned}$$

Calculate the foliage ration available to each larva

$$\text{RATN} = (\text{OLDF} / \text{LARV} + \text{NEWF} / \text{LARV}) / \text{UPERL}$$

Drop the first year of foliage (normal fall loss) and add one unit of foliage the following spring

$$\begin{aligned} \text{YFOL}(1) &= \text{YFOL}(2) \\ \text{YFOL}(2) &= \text{YFOL}(3) \\ \text{YFOL}(3) &= \text{YFOL}(4) \\ \text{YFOL}(4) &= 1 \end{aligned}$$

Disc equation for functional response of larval parasitoids

$$\text{NATT} = \text{PARAD} * .235 * 20 * \text{LARV} / \{ 1 + (.235 * .041 * \text{LARV}) \}$$

Competition function for parasitism

$$\text{PCOMP} = \{ 1 * (\text{NATT} / \text{LARV} * 1.68) \}^{-1.68}$$

Birds prey on larvae with Type III functional response

$$\text{NATT} = 20 * .098 (\text{LARV})^{2.5} / \{ (.91)^{2.5} + (\text{LARV})^{2.5} \}$$

Bird attacks on larvae cycled through a competition function

$$\text{BLCOMP} = 1 + (\text{NATT} / \text{LARV} * 1.5)^{-1.5}$$

Survival to cocoon stage following removal by birds, a fixed mortality, and a reduction proportional to foliage ration

$$\text{COC} = \text{LARV} * \text{BLCOMP} * .38 * \text{RATN}$$

Shrew functional response (Type III)

$$\text{NATT} = 115 * 300 * \text{COC}^2 / 55^2 + \text{COC}^2$$

Shrew numerical response (Type III)

$$\text{NSHR} = (27 * \text{COC}^2 / 75^2 * \text{COC}^2) + 9$$

Combined shrew response and conversion from hectares to sq. metres

$$\text{NATT} = (\text{NATT} * \text{NSHR}) / 10^4$$

Survival from shrew predation

$$\text{SHCOMP} = 1 - (\text{NATT} / \text{COC})$$

Survival to adults following shrew predation, emergence of parasitoids, and a fixed survival

$$\text{ADULT} = \text{COC} * \text{SHCOMP} * \text{PCOMP} * .33$$

Functional response of birds to sawfly adults

$$\text{NATT} = 20 * .018 * (\text{ADULT})^{2.25} / \{ (.3)^{2.25} + (\text{ADULT})^{2.25} \}$$

Competition equation for birds

$$\text{BACOMP} = \{ 1 + (\text{NATT} / \text{ADULT} * 1.5) \}^{-1.5}$$

Removal by birds, reduction for sex ratio, proportion of fecundity realized, reduction for foliage ration and multiplied by potential fecundity to yield eggs of following generation

$$\text{EGG} = \text{ADULT} * \text{BACOMP} * .66 * .72 * \text{RATN} * 120$$

Influx of eggs to prevent extinction

IF(EGG.EQ.0) EGG = EGG+.00001

Emerging parasitoids, and fixed parasitoid survival, yields parasitoid adults of following generation

PARAD = ADULT*(1-PCOMP)*.041

An influx of parasitoid adults to prevent extinction

IF(PARAD.EQ.0) PARAD = PARAD+.001

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Quantitative Evaluation of Pest Management Options:
The Spruce Budworm Case Study

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G. Baskerville, and R. M. Peterman

Introduction

The boreal forests of North America have, for centuries, experienced periodic outbreaks of a defoliating insect called the spruce budworm (*Choristoneura fumiferana*). In any one outbreak cycle, a large proportion of the mature softwood forest in affected areas can die, with major consequences to the economy and employment of regions like New Brunswick, Canada, which are highly dependent on the forest industry. An extensive insecticide spraying programme initiated in New Brunswick in 1952 has succeeded in minimizing tree mortality, but at the price of maintaining incipient outbreak conditions over an area considerably more extensive than in the past. The present management approach is, therefore, particularly sensitive to unexpected shifts in economic, social, and regulatory constraints, and to unanticipated behaviour of the forest ecosystem.

Most major environmental problems in the world today are characterized by similar basic ingredients: high variability in space and time, large scale, and a troubled management history. Because of their enormous complexity, there has been little concerted effort to apply system analysis techniques to the coordinated development of effective

descriptions of, and prescriptions for, such problems. The budworm-forest system seemed to present an admirable focus for a case study with two objectives. The first, of course, was to attempt to develop sets of alternative policies appropriate for the specific problem. But the more significant purpose was to see just how far we could stretch the state of the art capabilities in ecology, modelling, optimization, policy design, and evaluation to apply them to complex ecosystem management problems.

Three principal issues in any resource environmental problem challenge existing techniques. The resources that provide the food, fibre, and recreational opportunities for society are integral parts of ecosystems characterized by complex interrelationships of many species among each other and with the land, water, and climate in which they live. The interactions of these systems are highly non-linear and have a significant spatial component. Events in any one point in space, just as at any moment of time, can affect events at other points in space and time. The resulting high order of dimensionality becomes all the more significant as these ecological systems couple with complex social and economic ones.

The second prime challenge is that we have only partial knowledge of the variables and relationships governing the systems. A large body of theoretical and experimental analysis and data has led to an identification of the general form and kind of functional relations existing between organisms. But only occasionally is there a rich body of data specific to any one situation. To develop an analysis which implicitly or explicitly presumes sufficient knowledge is, therefore, to guarantee management policies that become more the source of the problem than the source of the solution. In a particularly challenging way, present ecological management situations require concepts and techniques which cope creatively with the uncertainties and unknowns that in fact prevade most of our major social,

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economic, and environmental problems.

The third and final challenge reflects the previous two: How can we design policies that achieve specific social objectives and yet are still "robust"? Policies which, once set in play, produce intelligently linked ecological, social, and economic systems that can absorb the unexpected events and unknowns that will inevitably appear. These "unexpecteds" might be the one-in-a-thousand year drought that perversely occurs this year; the appearance or disappearance of key species; the emergence of new economic and regulatory constraints; or the shift of societal objectives. We must learn to design in a way which shifts our emphasis away from minimizing the probability of failure, towards minimizing the cost of those failures which will inevitably occur.

What follows is a summary of certain elements of the spruce budworm case study. We can only hope to provide the reader here with a brief synopsis of the research; a full discussion of the study is contained in a forthcoming book (Yorque *et al.* 1978).

The Descriptive Analysis

The descriptive analysis of the budworm/forest system is aimed to produce a well-

tested simulation model that could be used as a laboratory world to aid in the design and evaluation of alternative policies. The key requirement of that laboratory world is that it capture the essential qualitative behaviour of the budworm/forest ecosystem in both space and time. Extensive data concerning forest-pest and economic interrelations had been collected over the past 30 years by Environment Canada as one of the earliest interdisciplinary efforts in the field of renewable resource management. There are many missing elements, but this is an inevitability rather than a drawback. If systems analysis is to be applied successfully to the management of ecological systems, it must be able to cope with unknowns.

The essential qualitative behaviour in time has been identified through an analysis of tree ring studies (Blais 1968). At least five outbreaks have been detected since 1770, (fig. 1), each lasting 7 to 16 years, with a 34- to 72-year period between them. During the inter-outbreak periods, the budworm is present in barely detectable densities which, when appropriate conditions occur, can increase explosively over four orders of magnitude during a 3- to 4-year period.

The distinctive pattern in time is paralleled by one in space. The historical outbreaks typically initiated in one to three or four local areas of Eastern Canada and from those centres spread and contaminated progres-

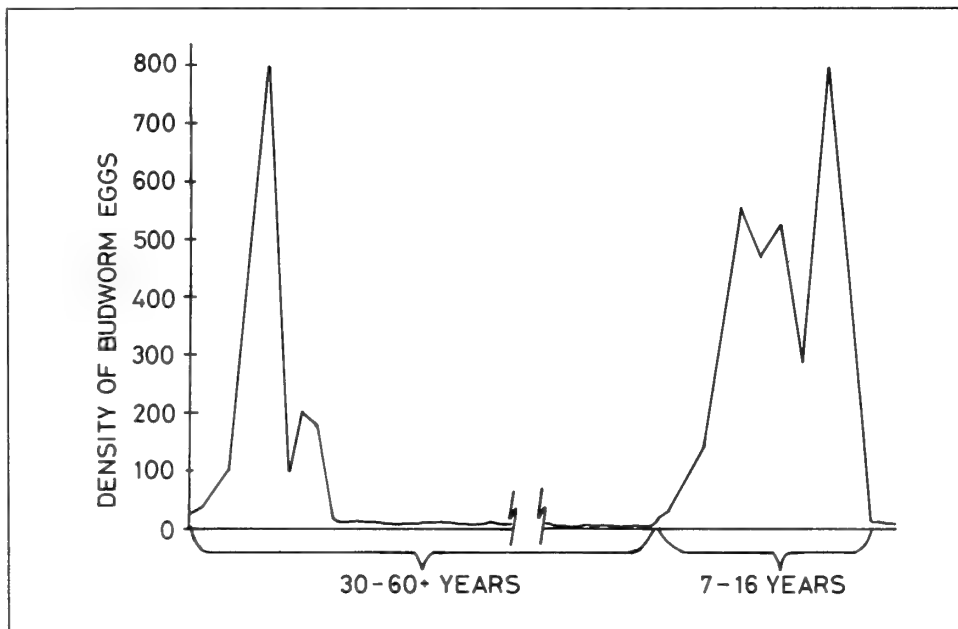


Figure 1.--The pattern in time. Representative historical pattern of spruce budworm outbreak. There have been at least five major outbreaks since 1770. Budworm numbers are per 10 square feet of branch area.

sively larger areas. Collapse of the outbreaks occurred in the original centres of infestation in conjunction with mortality of the trees, and similarly spread to the area infested at later times. The resulting high degree of spatial heterogeneity in the forest age and species composition is closely coupled to the "contamination" features caused by the high dispersal properties of this insect.

The essential first step in the dynamic description of this system is a parsimonious bounding of the problem in terms of prime variables, space and time. The process of bounding the problem from the very start of the analysis is a key activity. Everything else in the analysis flows from these decisions, and they profoundly influence the final form and relevance of the policies. The key requirement in bounding the problem in space, time, and variables is to ruthlessly simplify while still retaining the essential properties of behaviour and needs for management.

Bounding Time

Because of the pattern of outbreaks shown in figure 1, the minimum time horizon required is that which can contain two outbreaks -- that is 150 to 200 years. In order to capture the dynamics of this system, it is essential to have a time resolution of one year with seasonal events implicitly represented.

Bounding in Space

As in many pest species, the budworm disperses over long distances. The modal distance of dispersal is about 25 miles from one site, but dispersal distances of several hundred miles have also been recorded. It was thought essential to have a minimum total area based on at least twice this modal distance, leading to a minimum modelled region of 14,000 to 15,000 square miles. The area chosen in this study was a 17,000 square mile area containing much of the Province of New Brunswick (fig. 2). But even events in this size of area are profoundly affected by contagion from outside it. It was therefore necessary to add a buffer zone of approximately 75 miles width around the area in order to compensate for edge effects. The behaviour of this system is as highly heterogeneous in space as it is in time, and because of the contagion problem, spatial disaggregation is essential. There is high variation in the spatial distri-

bution of the primary tree species, of harvesting activities and of recreational potential, in part as a consequence of the historical interplay between the forest and the budworm. The 25-mile modal dispersal distance also suggests a minimum resolution of about one-fifth to about one-tenth of that distance. Hence, the overall area is divided into 265 distinct subregions each approximately 6 by 9 miles (fig. 3).

Bounding Variables

An ecosystem of this extent has many thousands of species and potential variables. Our understanding of the dominant budworm/forest dynamics is sufficiently detailed, however, that the system's relevant behaviour can be captured through the interrelations among five species, each of which represents a key role in determining the major dynamics of the forest ecosystem and its resulting diversity. These key variables are summarized in figure 4.

The principal tree species are birch, spruce, and balsam fir. In the absence of budworm and its associated natural enemies, balsam fir tends to out-compete spruce and birch, and so would tend to produce a monoculture of balsam. Budworm, however, shifts that competitive edge since balsam fir is most susceptible to damage, spruce less so, and birch not at all. Thus, there is a dynamic rhythm, with balsam fir having the advantage between outbreaks and spruce and birch during outbreaks. The result is a diverse species mix.

As noted earlier, between outbreaks, the budworm is rare but not extinct. Its numbers are then controlled by natural enemies such as insectivorous birds and parasites (see Morris *et al.* 1963). But a key feature of this control is that there exists an upper threshold of budworm numbers which, once exceeded, allows the budworm to "escape" predation and multiply unchecked. There is, in other words, a distinct but limited stability region at low budworm densities (Yorke *et al.* 1978).

In addition to tree species and natural enemies, there is a key stochastic driving variable, weather, which affects survival of the budworm and can flip the system out of the low density stability region if forest conditions are appropriate. Outbreaks cannot occur unless the forest has sufficiently recovered from the previous outbreak to provide adequate

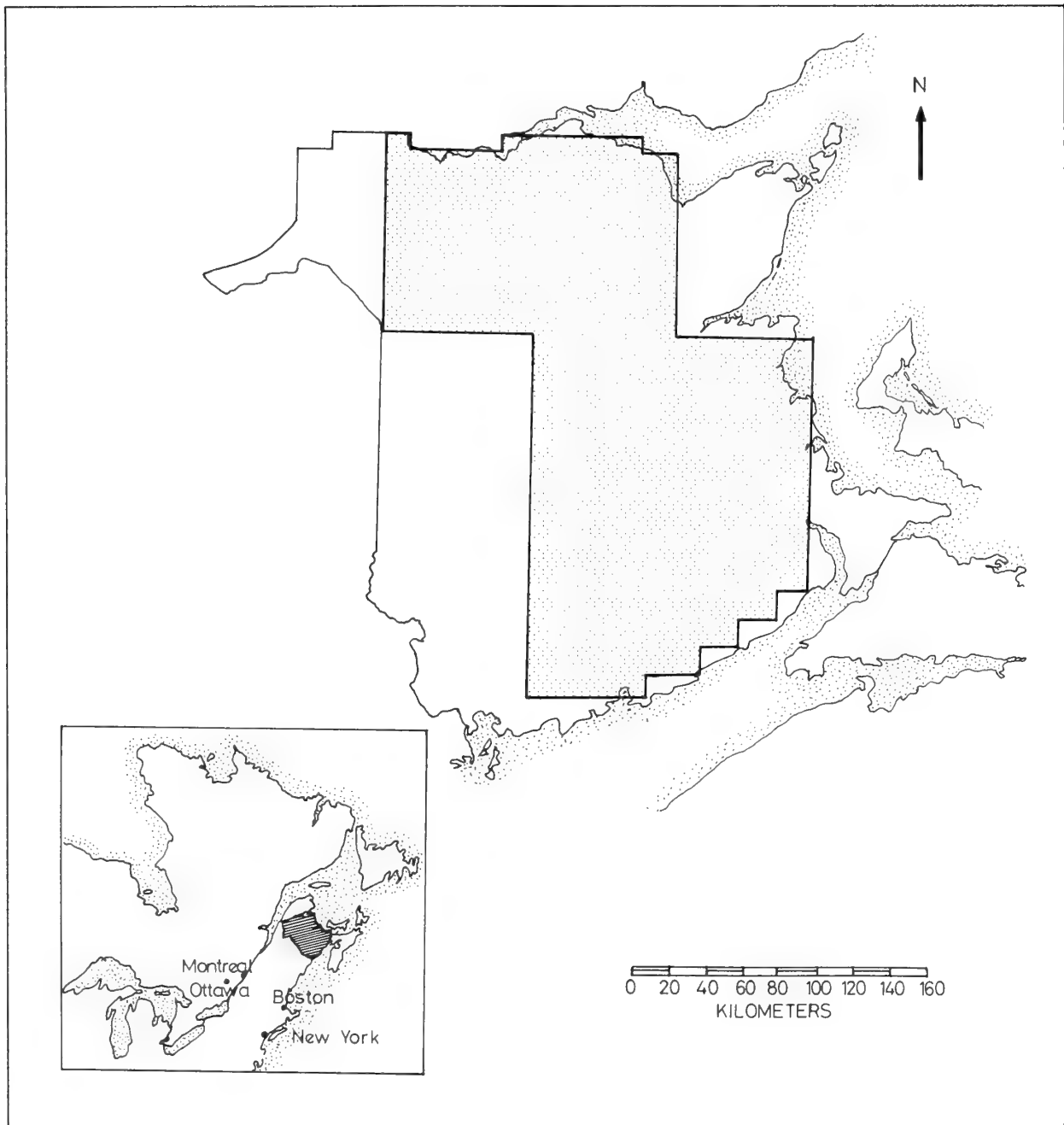


Figure 2.--Study area within the Province of New Brunswick used in the current study. The hatched area includes the primary forested regions of New Brunswick.

food. Even with the food conditions met, however, the budworm remains at low densities under control by natural enemies until the weather shifts to successive years with warm dry summers. Such conditions allow larvae to develop so rapidly that densities above the escape threshold are achieved. An outbreak is then inevitable, irrespective of weather.

In summary, the decisions on bounding the problem are as follows:

- | | |
|------------------------------------|---|
| Time horizon | -- 150-200 years |
| Time resolution | -- 1 year with seasonal causation |
| Spatial area | -- 17,000 square miles |
| Spatial resolution | -- 265, 6 x 9 mile sub-regions |
| Key variables to capture behaviour | -- ideally, three tree species, budworm, natural enemies and weather. |

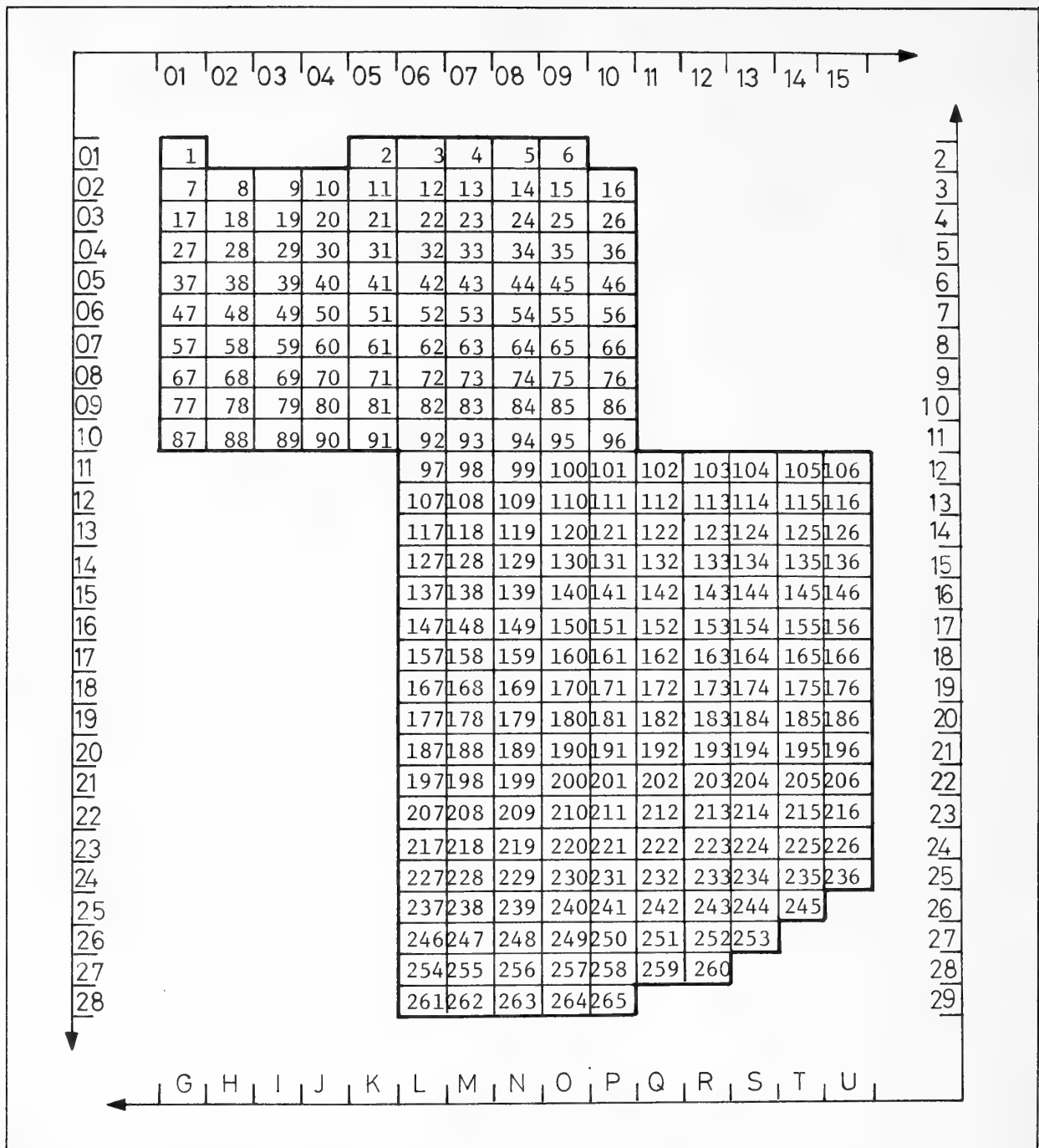


Figure 3.--This figure shows the numbering and indexing system for the 265 subregions, or "sites" in the study area.

This bounding of the problem immediately determines the number of state variables, which, in turn, affect the decisions about subsequent analytic steps such as optimization. Even though the previous steps of bounding seem to have led to a highly simplified representation, the number of state variables generated is still enormous. Table 1 summarizes, for this ideal condition, the

minimum number of state variables necessary to represent the essential behaviour of the system in space and time. In any one subregion, 107 state variables are required, but of course, for the whole 265 subregions, a total of 107 x 265 or 28,355 state variables are required. Thus even this drastic simplification accomplished through the bounding exercise leaves an impossible number of state variables, thus

demanding further simplification. It would, of course, be quite possible to develop a simulation model with this number of state variables. This would be expensive and time consuming to run and debug, but it would be possible. Our key goal, however, is to provide a useable and well tested model for exploring behaviour and policy alternates. With such a high dimensionality, the model would become nearly as incomprehensible as the

real world, and the opportunities for systematic exploration would be greatly reduced.

As a consequence, a systematic series of further compressions and tests was made to determine whether the number of state variables could be significantly reduced. This led to four prime variables: tree density, foliage conditions, budworm density, and weather. In the full model, the tree density actually had to be represented by 75 state variables associated with tree age, but techniques were developed to collapse these into one for descriptive purposes. The effects of all other variables can be incorporated implicitly so that this ultimate compression requires essentially four state variables per site or 1060 for the region. When policy explorations were done with the simple single site model, "optimal" policies were than tested in the full regional model to ensure that the compression process was realistic.

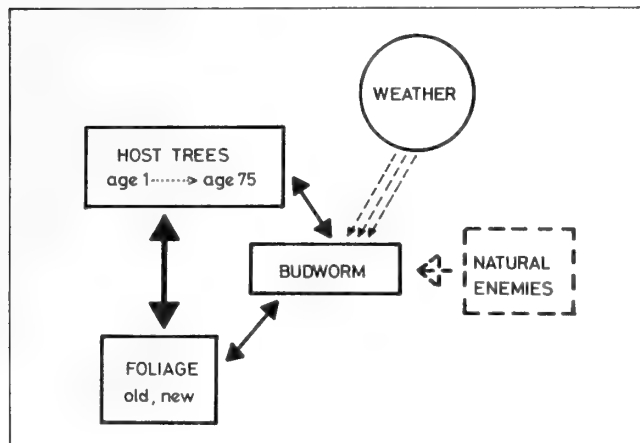


Figure 4.--The key roles or variables and their interrelations in the natural ecosystem. The principal tree species (birch, spruce and balsam fir) have a dynamic interaction of their own. This interaction is altered by the presence of budworm which consumes some spruce but primarily balsam. The budworm is, in turn, affected by a complex of natural enemies and a stochastic weather variable.

Table 1.--The state variables emerging from the bounding of the problem

Ideal Number of State Variables	
In one subregion	
Birch	1
Spruce by age	30
Balsam fir by age	70
Budworm	1
Natural enemies	1
Weather	1
Tree stress	1) retains memory
Foliage new	1
Foliage old	1
Number of state variables per subregion	107
Total number of state variables in all 265 subregions	107 x 265 = 28,355

The Model

The basic form of the model structure is shown in figure 5. Budworm reproduction and survival, forest response, and control policies are independent for each of the 265 sites. Once each year, dispersal occurs among the sites, and the process is then repeated for the next simulated year. The budworm and forest response models were developed from the extensive set of data collected by Environment Canada over the past 30 years. Many of the component processes, such as growth and reproduction, have been examined in extensive detail by Morris *et al.* (1963) using multivariate statistical procedures. But there are three critical processes that are not clearly understood at present and for which there is, at best, qualitative information. These three areas of semi-knowns are the effect of natural enemies at low densities of the insect, the detailed response of trees to defoliation, and the specifics of dispersal. Since this problem of grappling effectively with substantive unknowns is central to any successful analysis of ecological problems, considerable effort was spent in developing a formal procedure to cope with such uncertainties. Moreover, these three particular areas of uncertainty are typical of many situations. Rarely, for example, is there much detailed information about events when the number of organisms is very small. Nor is there often much knowledge concerning very slow processes such as those involved in tree responses. Finally, dispersal occurs over such large areas that only the very recent application of

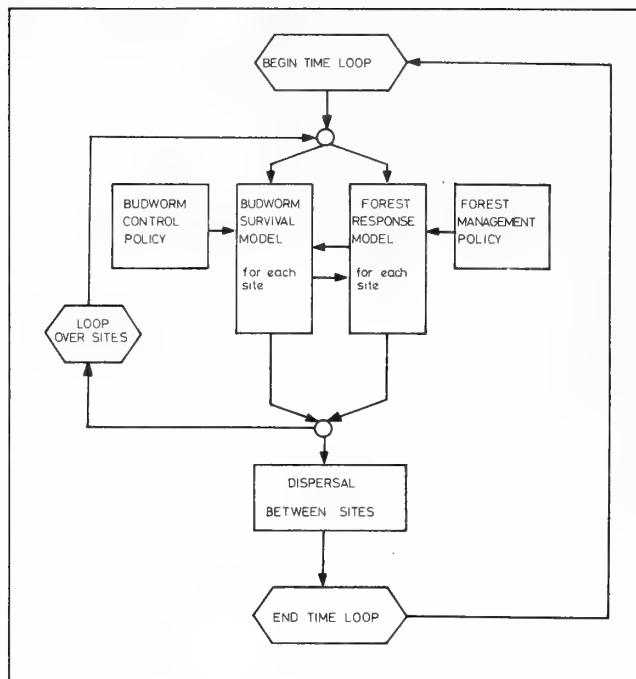


Figure 5.--The basic model structure for the budworm/forest simulation model.

radar technology has made it possible to define and quantify the form and magnitude of spatial contagion. And yet, we know each of these three sources of uncertainty to be critical in determining aspects of renewable resource systems behaviour which have been particularly troublesome in past efforts of environmental management.

The ecological literature contains a particularly rich body of experimental and theoretical analyses of key ecological processes. These have led to the identification of classes of interactions, each characterized by a specific family of mathematical equations. For example, predators display a set of responses to prey or host species which fall into nine primary classes. Not only are each of these classes defined by a specific family of functional relations, but the biological attributes for each class have also been sufficiently well identified that quite qualitative information usually makes it possible to assign a specific example to the appropriate general class.

This work provides a theoretical framework allowing us to mobilize the existing information, however sparse, in a way which lets us proceed in a series of steps to gradually define a narrower and narrower range of possible relations. Having identified in this manner the classes of responses characterizing specific situations, it remains

necessary to parameterize them. Even in the worst of circumstances, information usually exists to permit rough specifications of the parameters, leading to the definition of a maximum possible range for each response class.

The final step is to cycle these possible relationships through the full simulation model in order to define a "feasible range" of forms which results in retaining the known qualitative behaviour of the system. At that point informed judgment can informally select a "standard" relationship for use. Alternatively, an organized application of decision theory can assign subjective probabilities and so generate a range of possible outcomes.

This procedure was applied to the predation process mentioned above (Yorque *et al.* 1978). But the key point of this exercise is to directly face the reality of unknowns and to recognize that an organized approach in dealing with them can not only provide reasonable solutions that will allow the policy design process to proceed, but, at the same time, can provide very clear and specific priorities for future research.

A dynamic descriptive model of the sort described here is useless for prescription unless it presents opportunities for meaningful management intervention by policy actions. There are two main classes of policy action possible -- one relating to control of the budworm and the other to management of the forest. These are structured in broad terms allowing for the exploration of not only insecticide control of budworm but for biological and other methods of control as well. Similarly, the forest management policy can include specific actions of cutting by age in different regions of the forest and also, at least implicitly, a variety of silvicultural and tree breeding actions. Although the model is structured to accommodate a wide range of possible actions, for the purpose of this case study, attention was largely directed towards budworm control using insecticides or bacterial agents and forest management using different techniques of scheduling cutting in space and time and by tree age.

Model Testing

Validation of an ecological model is always a difficult problem. In this example, a statistically rigorous validation would require detailed historical information on all the state variables over a large spatial area and covering a very long period of time -- at

least 70 to 150 years. Only in that way could the full dynamic interplay of the system over time and space be adequately tested. The budworm case is rare in that such data are in fact available for a 30-year period, but that is scarcely long enough to instill a profound confidence in the model. Our present validation approach has, therefore, been to combine a quantitative comparison of state variable values over the period for which detailed historical data are available, with a qualitative comparison of gross behavioural properties (mean outbreak densities and variances, length of inter- and intra-outbreak periods, and so on) for the longer term. Some sense of this latter exercise can be drawn from figure 6A. This figure shows a series of computer drawn maps generated by the simulation model showing on the vertical axis the density of budworm eggs over an 84-year period. It covers portions of two outbreak sequences, and the essential pattern of these predictions has been confirmed by historical data from New Brunswick and elsewhere in eastern Canada.

Another type of analysis which increased our confidence in the model's prediction capabilities was the inclusion of different forest, weather, and insect disperser conditions which represented conditions in other Canadian provinces. The model correctly predicted the observed frequency and duration of outbreaks in these other provinces, thereby suggesting that no major processes had been omitted (see Chapter 7 of Holling *et al.* 1978).

In summary, the descriptive analysis led to the development of a dynamic simulation model that could describe the behaviour of the forest/pest ecosystem in space and time, with opportunities for intervention with a variety of management acts. It provides, therefore, a laboratory world in which the consequences of a variety of alternative policies can be explored and constitutes the essential base for the prescriptive analysis.

The Prescriptive Analysis

The goal of the prescriptive analysis is to provide a management tool which can aid in policy design and evaluation. There are three parts to the analysis as we implemented it. The first was the definition of a strategic range of management objectives; the second, the application of optimization techniques to develop policy rules for each objective, and the third, the development of a framework to broadly evaluate the consequences of each policy in terms of a wide range of potential management goals.

Strategic Range of Objectives

The uncertainties and unknowns in describing an ecological system are trivial compared to the ambiguities in defining societal objectives. The objectives that seem so clear at any moment can shift dramatically, as testified to by the recent concern for environmental issues. Moreover, as has been discovered by the water resource planners in particular, even the best of policy analyses can founder on unrecognized or hidden public objectives. Since social objectives are hidden, ambiguous, conflicting, and otherwise indefinite, the analyses rarely can accommodate them satisfactorily. Hence, they become uncomfortable, intrusive, and divisive issues of confrontation. In response to this essential ambiguity of objectives, we felt it essential to identify a strategic range of objectives containing a systematic spectrum of plausible and not-so-plausible management goals. Any specific example drawn from that spectrum was initially considered only as a touchstone and in no sense a realistic or desired objective. Again, our aim was to provide a tool for articulating and exploring alternatives, not a predictor of prepackaged social goals. The strategic range, as we conceive it, covers at one extreme objectives that attempt to achieve long term profit maximization for the forest industry and minimize probabilities of failure. At the other extreme, and equally unrealistic, the objectives seek more to retain the dynamic variability of the system in ways less sensitive to ecological surprise or changes in social systems that are resilient, or robust; that work with the dynamic rhythm of the system rather than against it. If the first extreme represents the goal of a fail-safe world, the latter represents one which is safe in failure.

Five strategic touchstones of this kind were defined as follows:

1. unconstrained profit maximization;
2. constrained profit maximization, where the maximum processing capacity of the existing logging industry sets constraints;
3. recreation maximization, acting as an additional constraint on (2) above;
4. budworm minimization, replacing the historical spraying policy with alternate methods of forest management and budworm control; and
5. variability transformation, operating independently of (2) above, in which the goal is to transform the high temporal variability, which causes a boom and a bust situation for employment and the

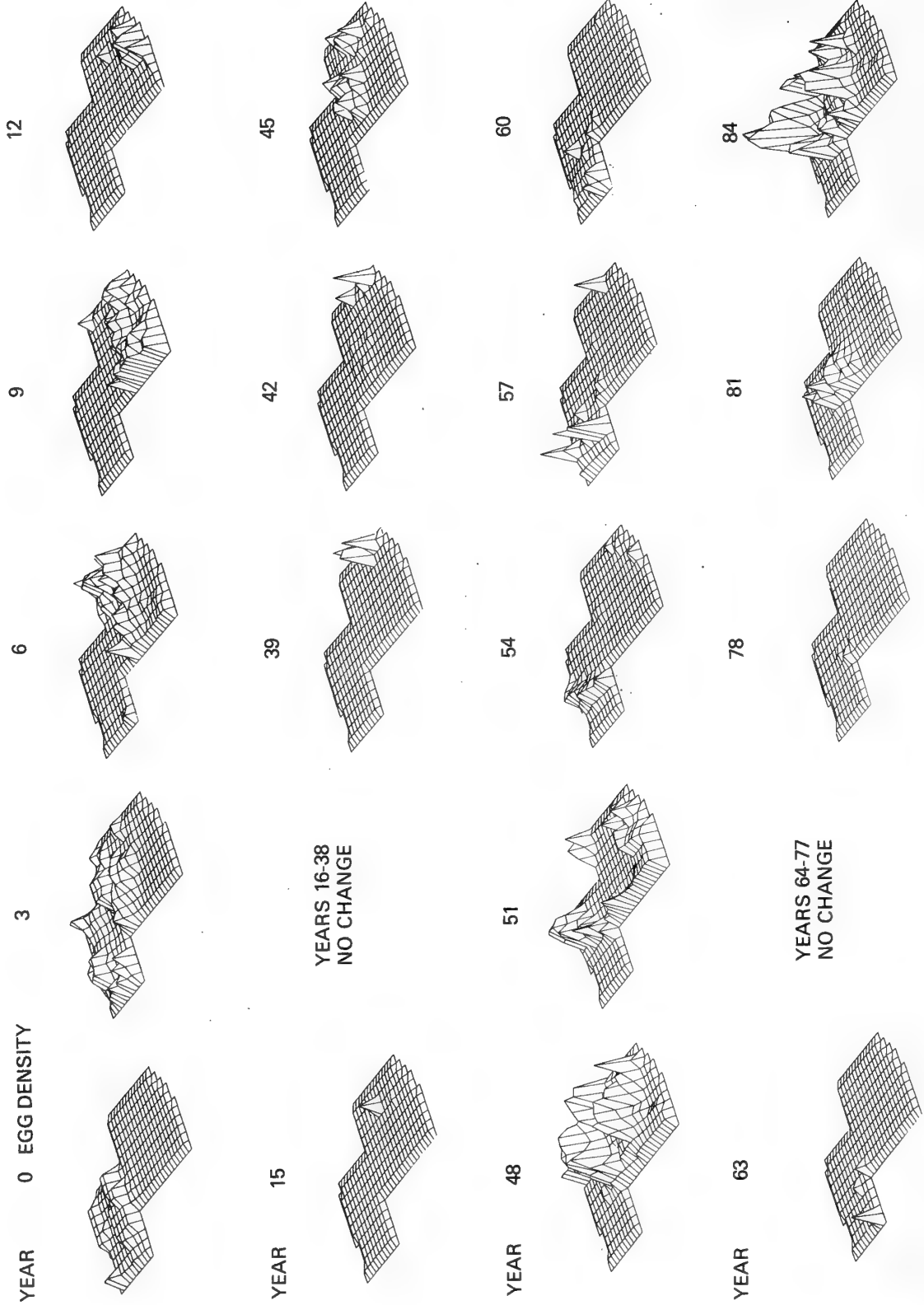


Figure 6A. ---Computer simulation maps of budworm egg density -- (no management). Redrawn, with permission, from Clark *et al.* (1978). All rights reserved.

forest industry, to spatial variability. The goal in this extreme is to develop a forest ecosystem in which the budworm can be used as a forest manager and the essential dynamic interplay of natural forces is retained.

In addition, of course, two additional policies are explored -- one of no management and one of the historical management. This produces a total strategic array of seven alternate objectives that, after evaluation and comparison, can be modified, combined, and refined as starting points for a policy design dialogue with managers and specific interest groups.

Optimization

Given a range of objectives, the next step is clearly to specify ways of combining available management actions in sets of policy rules appropriate for their realization. Simulation gaming, at an early stage, is a useful exercise for heuristically exploring the possible consequences of different management acts. Even after more formal optimization procedures have suggested specific rules, such gaming can still be a rich environment for dialogue. But the immense variety of different ways of combining acts in space and time demands more structured procedures as well. Figure 6B is an example of a gaming simulation run.

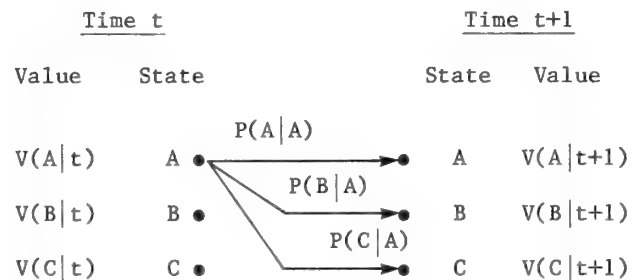
The approach we have taken is to regard the simulator as a means of bringing the real world into the laboratory. The various policies (whether obtained by common sense, or by common practice or through the use of an "optimizer") can always be compared by making a sufficient number of runs on the simulator. An analyst weak on analytic skills, poorly trained in the formulation of models, poorly informed about algorithms for solving classes of models, or unfamiliar with software availability may well opt to run many cases on the simulator to see if local improvements in a proposed policy are possible. Most simulation efforts unfortunately end up this way. Unfortunate because the high cost of using simulators to test many cases usually exhausts the patience and funds of sponsors to support development of an optimizer. If these funds had been used instead to develop a simplified model, then the process of determining an optimal policy for the simplified model could serve as a "brain" for the simulator and would have resulted in significantly better policies being found.

Generally speaking, there are two types of analytic models that have had many successful applications: (1) "Linear programming," and (2) "dynamic programming" models.

The first, the linear programming model, is characterized mathematically by a system of linear inequalities. Many kinds of nonlinear relations can be practically approximated by such systems which can be both dynamic and stochastic. Software is available for solving such systems at reasonable costs even when they involve thousands of inequalities and variables. But linear programming was not appropriate here because of the highly nonlinear nature of the ecological system.

The second, the dynamic programming model, is characterized by a dynamic system that moves from any given state in time to the next without being affected by the past history of how it arrived at its given state. Many practical models can be cast in this form. In practice, however, applications are narrowly limited to those whose "state space" may be approximated by a small number of variables. In our research, however, we have pursued an alternate possibility -- one which allows the state space to be multidimensional and continuous in certain components. We were able to do this by finding a practical way to approximate the "pay off" for each state if one follows henceforth an optimal policy.

For the budworm optimizer, we used a mathematical model closely related to the dynamic program -- the so called *Markov Process*. At each point in time t , the system is in some state, A, B, C... If in state A, it will move to state A or B or C, ..., at time $t+1$ with probabilities $P(A|A)$, $P(B|A)$, $P(C|A)$, ...; [$P(C|A)$ is read as probability of going to state C, given that you are in state A now]. Similarly, if in state B it will move to A or B or C at time $t+1$ with probabilities $P(A|B)$, $P(B|B)$, and $P(C|B)$,...etc.



In our application, these probabilities can be changed at a price by engaging in certain alternative actions. The problem is to find the best choice of these alternative actions.

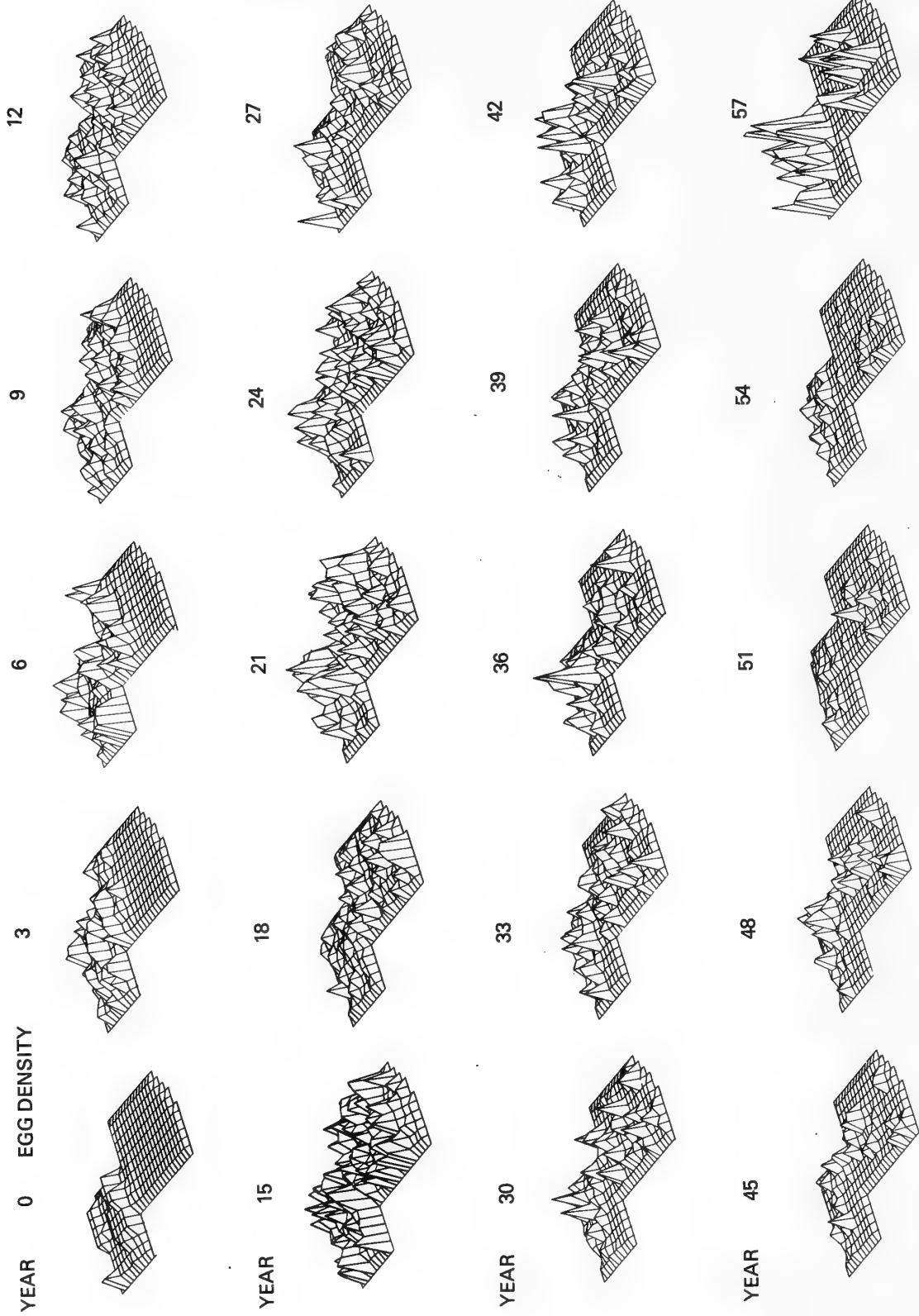


Figure 6B.--An example of gaming simulation in which a spraying procedure, similar to that used historically, produces a sustained semi-outbreak situation. Redrawn, with permission, from Clark *et al.* (1978). All rights reserved.

This is easy to do if we know the value $V(A|t+1)$, $V(B|t+1)$, ... of being in various states at time $t+1$. Thus the expected value $V(A|t)$ is given by

$$V(A|t) = P(A|A) \cdot \{V(A|t+1) - C_{AA}\} \\ + P(B|A) \cdot \{V(B|t+1) - C_{AB}\} \\ + P(C|A) \cdot \{V(C|t+1) - C_{AC}\} \dots$$

where C_{AB} , for example, is the cost (revenue, if negative) of transitioning from A to B in time period t . If there are alternative actions in period t which can affect these probabilities, then the action that yields the maximum value of $V(A|t)$ is chosen. The procedure is thus a backward induction to time $t = 0$ but requires (in order to get it started) the knowledge of $V(A,t)$, $V(B,t)$, $V(C,t)$ for some time $t = T$ in the future.

As noted, a Markov type model was the one used for the budworm study. The key idea employed to develop this analytic model was to view the *single* tree (or an even-aged stand) as an entity which changes state from year to year -- its state being defined by its age, stress, and the number of budworm it hosts (Winkler, 1975). The tree, depending on the weather and whether or not it is sprayed or cut, will (with certain probabilities) become one year older with certain stresses and egg densities or reverts to age zero and is replanted. If it were not for the spread from one timber stand to another of budworm eggs by the adult moth, this model has the merit that all other relations can be used with little or no simplification or change. This leaves open the question of how to approximate the effect of egg contamination. Several approaches have been posed and are dealt with elsewhere (Holling and Dantzig 1976). But acute simplification is the role in dynamic programming applications, and we shall show how we have presently elected to live with this one after outlining the existing model and its solution.

For the simplified model, we wish to find for every state (tree age, stress, and egg density) the optimal policy.

One way to determine optimal policy is to begin with a guess V_0 as to the entire discounted future value of a tree starting at age zero including the value of all its future harvesting and replanting (to time infinity) when we always carry out an optimal policy in the future with regard to the tree and its replantings. A tree planted a year from now has present value of $0.95 V_0$ for its time stress from 1 year to infinity where 5 percent (say) is the discounted factor (without inflation). If for the moment we accept our

guess V_0 , we are in a position to evaluate the present value of all other states. One begins by noting that as far as harvesting the merchantable volume of the tree now (or in the future), it does not pay to allow a tree to become older than 60 years (say). If so, then the optimal policy is to cut it down and its present value $V_{60} = V_0 + L_{60}$ where L_{60} is the value of the 60-year-old tree (less any cost for replanting it). To obtain the V_{59} of the 59-year tree (which is in some state of stress and egg infestation) and, at the same time, to obtain the optimal policies, we compute: (1) cutting it down, $V_0 + L_{59}$; (2) leaving it alone, $0.95\{pV_{60} + (1-p)V_0\}$, where p is the probability of the tree living; and (3) spraying, $-S + 0.95\{\bar{p}V_{60} + (1-\bar{p})V_0\}$, where S is the cost of spraying and \bar{p} is the probability of the tree living after it is sprayed. The policy which yields the highest value is selected as optimal. Note that the effect of random weather factors is part of the calculations (i.e., weather affects the probabilities of dying or the probabilities of moving from one state to another) so that values (and optimal policies) of various states can be determined backwards from the highest age 60 down to age 0. If it turns out that our guess V_0 checks with the value V_0 obtained by the backward calculations, we accept it -- if not, then we revise our guess up or down until it does check.

This procedure defines, therefore, an optimal way to apply the variety of management acts for a specific objective in terms of the values of the key state variables. These policy rules may be represented in the form of policy tables such as those shown in figure 7. For any age of tree, foliage condition and density of insects the manager can either do nothing, spray (and the spray can be at different intensities and concentrations), or harvest. The advantage of such policy tables is that they are clear, unambiguous, and can be easily applied by a forest manager attempting to manage a stand in isolation from the rest of the regional forest system.

But to achieve these "optimal" rules required gross simplifications due to the limitations of available optimization techniques. Two major simplifying assumptions were required. The first concerned a simplified expression of the objective function, and the second required that dispersal between spatial areas was unimportant. It was only in this way that the high dimensionality of the problem could be simplified to the point where dynamic programming could be successfully applied. Similarly, gross simplifications will be required in most problems involving dynamic management of resource and environmental systems.

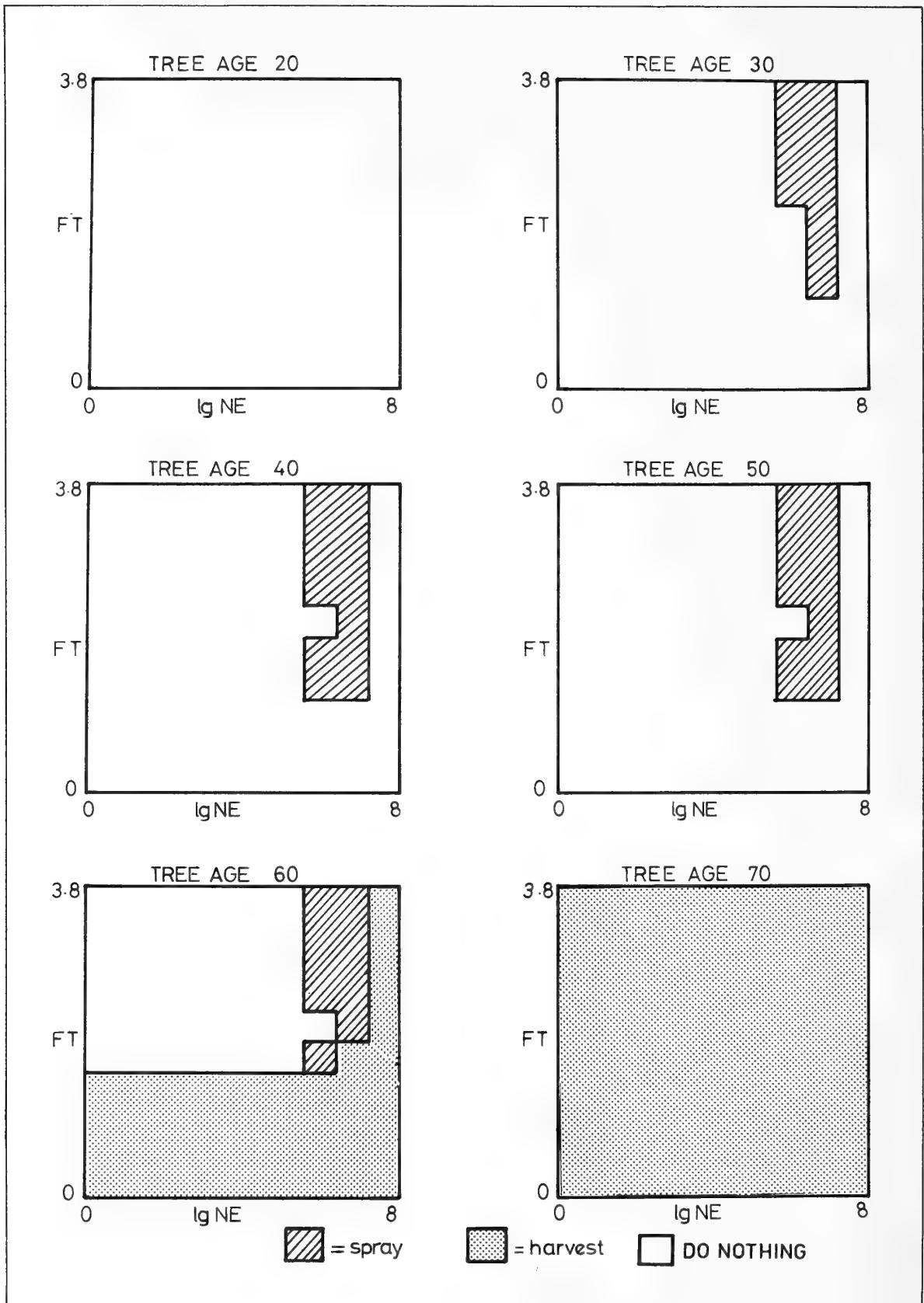


Figure 7.--Policy tables for representative ages (price = \$55/cunit; discount rate = 5 percent). F_T is a measure of foliage density and lg NE is \log_{10} of eggs/10 acres.

Dynamic programming is a particularly powerful and valuable tool for use in ecosystem management studies. But unless really substantial advances are made in its ability to handle certain classes of high dimensionality, it will properly remain a special-use "sub-optimizer" methodology only. For the foreseeable future, we will have to learn to make the most (without making too much!) of that.

Sub-optimal or partial optimal solutions have a useful role to play, however. The key to their constructive utilization is an ability to cycle such simplified policies through the full simulation model with all its complexity. By using a variety of indicators, each of these policies can be assessed in terms of a possible drift of solution from some broader societal and environmental goal. When this is detected then ad hoc, heuristic modifications of the policies can be employed to produce more desirable behaviour.

This process, again, should be in the form of dialogue with both managers and interest groups. As we said earlier, the optimization model was designed to provide a "brain" for the simulator. But that "brain" is a childish thing, and for its proper functioning, it requires the guidance that can only be provided by those that make policy and those that endure it.

Evaluation

A program of policy exploration and evaluation using a simulator requires the development of a rich array of social, economic, and environmental indicators, and a framework for their use and interpretation. The manager must be able to converse with the model in a critical and flexible manner if the latter is to have any legitimate use as a policy design tool. A system of indicators was, therefore, designed to serve as the common, comprehensible language in which that conversation could take place. The grammar and syntax rules which give structure to the manager's dialogue with the model are derived from the discipline of operations research and, more particularly, decision analysis.

The central difficulty in applying traditional decision analysis approaches to the budworm-forest management problem has been the essentially dynamic nature of both the system itself and the majority of possible policies for its control. The "present state" description of the system tells us only a little about future states, and the essence of

a good management policy is precisely the ability to adapt quickly and successfully to the inevitable future state surprises as they arise. We are really more interested in what the forest is doing than what it is at a given moment, and the standard paraphernalia of a discipline still mightily concerned with relatively complacent marbled urns has predictably been unable to give us quite the help we need.

Our ad hoc solution to the problem of specifying objectives for a time changing system has been to present the decisionmaker with full time series descriptions of the forest's behaviour, without regard to the policies employed to generate that behaviour. In principle, the choice problem simply becomes one of ranking time streams rather than state descriptions of the managed system. But the full panoply of time stream indicators associated with any simple management policy is exceedingly complex. To enable consistent rankings of alternatives, we must first simplify, and simplify both drastically and meaningfully.

The first step in the process is straightforward. Each individual manager is asked to review the list of indicators, strike those of no or minor relevance to the determination of his time stream preferences, retain the rest, and add or alter where necessary. A representative list of one decisionmaker's "things I am interested in" is shown in table 2.

A little bit of additional simplification can be done rather easily. These indicators are listed by intuitive groups of like "kind". It turns out that the decisionmaker's expressed tradeoffs among indicators within such groups are often independent of the values taken by indicators outside the group (a sort of preferential independence). As one put it: "I can add apples and apples without caring too much about oranges." In addition, within-group tradeoffs were usually expressed as "noncompensatory" or threshold phenomena in which a given indicator became important only when it took a value outside a wide "normal" range. These convenient simplifications made it possible to reduce most of the table 2 groups to single, aggregate indicators in a relatively unambiguous and intuitively plausible manner. An example is shown in figure 8. Following similar procedures, one manager reduced his initial long list of indicators to only three: one for economic effects (including logging, spraying, and operating costs); one for recreational value (including accessibility factors, forest composition, logging and insect damage, and so on); and one for social issues (essentially the level of labour

force displacement due to forest destruction by budworm).

Table 2 -- Preliminary "grouped" list of relevant indicators

-
- A) Economic
1. "Profit" to logging industry
 2. Cost of insecticide spraying
 3. Cost of other control measures
- B) Forest Appearance
4. Age class diversity
 5. Proportion of trees in "mature" classes
 6. Proportion of trees severely defoliated
 7. Proportion of trees dead
 8. Proportion of area logged
- C) Social
9. "Unemployment"; prop. of mill capacity not filled
- D) Forest Potential
10. Amount of merchantable wood present
 11. Amount of merchantable wood harvested
- E) Ecological
12. Average concentration of insecticide in sprayed areas
-

Having completed the initial indicator selection and aggregation, we possess a reasonably concise way of describing any given pattern of system behaviour. The task remains, however, of systematically, meaningfully, and unambiguously ranking alternative sets of time streams such as those shown in figure 9. And most regrettably, this seems to present a problem wholly beyond the capacity of present theory and methodology in decision analysis. Consider for a moment the difficulties.

Time lies at the heart of all our problems here. If we wish to assign a single ranking value to a given set of indicator time streams, we must ultimately compress indicator values across time. The first inclination is to take variously weighted time averages of the indicators; means, discounted sums, and so forth. But any such time averaging scheme implies an explicit attitude of intertemporal tradeoffs through which we are willing to

relate the future to the present. It is debatable whether standard "1 to 15 percent" discounting arguments can be defensibly applied to even purely financial matters. Their appropriateness outside the world of capital investment is highly suspect, to say the least. And despite the large volume of writing on "social rates of discount," little of practical import has yet been said on this matter either. It would seem that our society has yet to agree upon a fixed rate at which it is willing to discount its posterity into insignificance. And whatever it may be, the proper solution to the discounting problem certainly does not involve convincing them to do so.

Even if the overall time averaging problem could be resolved, however, we are left with the problem of assigning appropriate ranking weights to different temporal patterns of an indicator. Surely an unemployment rate time stream averaging 10 percent and based on alternating years of full employment and 20 percent unemployment deserves a different ranking from one which holds a static 10 percent year after year. Potentially meaningful properties of time stream behaviour are almost certainly captured in correlation and runs statistics as well as variance estimates. As with the averaging problem, the issue is not whether we can perform requisite calculations -- which are trivial -- but how we could make the results meaningful to the manager -- which is not.

One potentially useful compromise approach to the time problem has been to compress indicators across kind but not time, resulting in a single aggregated value function time trace (fig. 9). The key here is conditionally to assume temporal independence of indicator tradeoff values, in essence, pretending that the relative weighting attached to various indicators in a given year is independent of their values in neighboring years. With this assumption made, intra-temporal, inter-indicator tradeoffs are evaluated using a standard multi-attribute, revealed preference approach, and an overall value function calculated. This function is applied independently to each year's separate indicator values, generating the aggregate value time stream shown in figure 9. In our work, we have permitted no discounting of the component indicators or final value stream because of the ambiguities inherent in aggregating across differentially discounted indicators.

The manager has, at this point, reduced his ranking problem to one of comparing a single aggregate value stream for each pattern of system behaviour in question. By visually

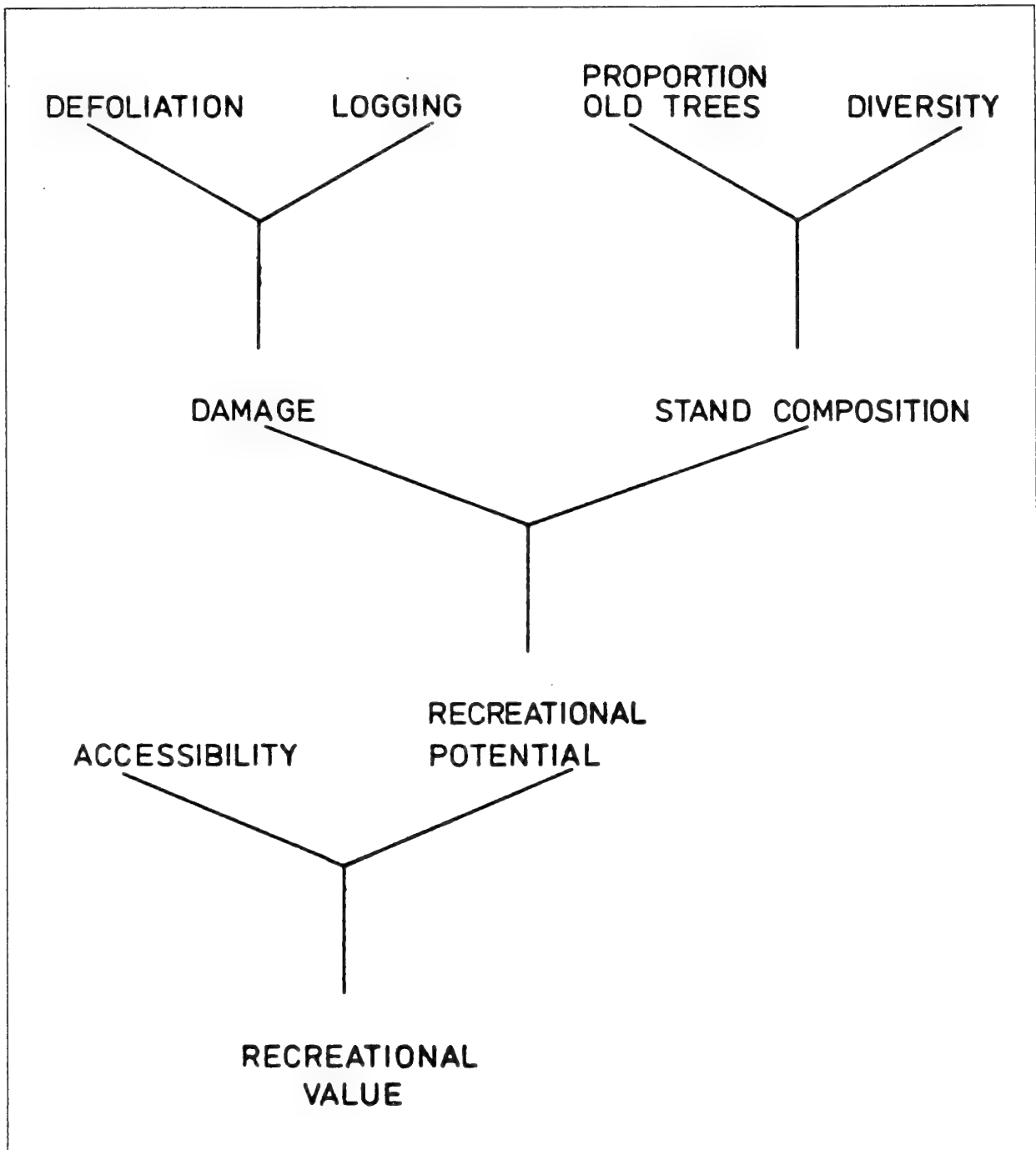


Figure 8.--Steps in aggregating four basic variables into a recreational indicator.

pairing these value streams with their component indicator streams, the decisionmaker may be able to interpret the former consistently and to evolve a stable ranking pattern. The pairing also serves to show, through the component indicators, which portions of the value stream are most likely to be sensitive to the temporal independence assumption. We have no methodology to cope with this sensitivity, but the "flag" at least serves to

temper our interpretation of the aggregate value stream with skepticism.

Other works have examined alternative ways of comparing indicator time streams which result from different policy options (Bell 1977; Peterman 1977) and have explored a wide variety of management actions and objectives (Holling *et al.* 1978).

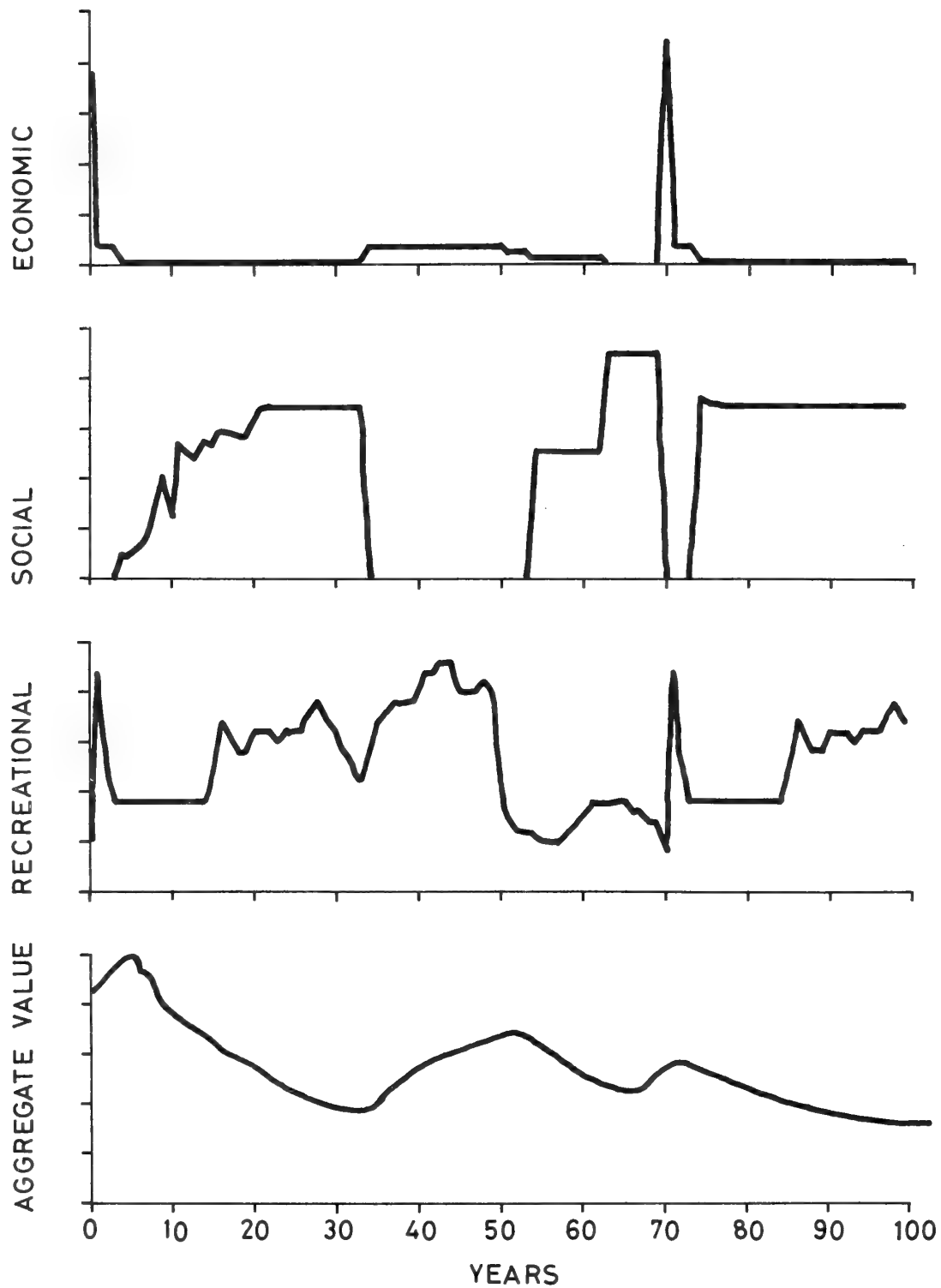


Figure 9.--An example of time traces of three selected indicators and their aggregate.

What Has Been Done

The intent of this case study was to see just how far one could proceed in combining the best of ecology, modelling, policy design, policy evaluation, and decision theory, toward a realistic and characteristic problem of ecosystem management. The key ingredient of this analysis was the development of a rigorous, parsimonious, and well-tested simulation model that explicitly addressed issues of unknowns and uncertainties. It provided the laboratory world for the development and exploration of alternate policies. The process led to optimization, where the limitations of existing techniques required an evaluation of "sub-optimal" policies through the simulation model. This process of evaluation, in turn, generated the need for a rich variety of social, economic, and environmental indicators that could be used to judge the consequences of alternate policies.

Although it has not been mentioned, it additionally became essential to develop an alternate array of indicators, explicitly designed to handle the uncertainties or unknowns. These are necessary because ecosystems and, for that matter, social systems, are generally multi-equilibria ones in which each equilibrium is bounded by a stability region. Very little information can usually be mobilized to concretely and specifically establish where those boundaries lie, or how the stability regions may contract with the application of management activities. There is, however, growing evidence from fisheries, forest, and other ecological systems which suggests that these domains of stability do contract with no obvious indications until collapse occurs. Hence, three classes of "resilience indicators" were also developed -- one set measuring the unused environmental capital that would provide the alternate options required in the event of an unexpected event, one set relating to measurements of the stability boundaries, and one set concerning the resilience of benefits. The latter are generated by explicitly simulating specific kinds of policy failure and monitoring the stream of benefits thereafter.

The final key piece that linked the whole range of techniques was an explicit effort to generate a strategic range of objectives as first-cut management alternates. This range was designed to cover both non-resilient and resilient objectives with the intent of providing a rich menu for comparison

and subsequent modification.

But so far, we have emphasized mainly the techniques used, saying very little of the process by which they were developed and employed in the research program. And yet, a crucial element of this exercise has been the inter-disciplinary and inter-institutional character of the operation. From the start, the Maritimes Forest Research Centre, Department of the Environment, Fredericton, was involved in every stage of the project. Much of the economic and ecological analysis was performed at the MFRC Laboratory in close conjunction with other members of the team. The Institute of Resource Ecology, University of British Columbia, provided the expertise in systems ecology and mathematics. The whole activity was given focus and a disciplinary breadth at the International Institute of Applied Systems Analysis (IIASA), Vienna. The final group of collaborators involved ecologists, systems mathematicians, and operations researchers, covering a wide spectrum of talents. Despite that interdisciplinary breadth and the several thousand miles between the three key participating institutions, the degree of cooperation and communication was truly remarkable, in large part due to the initial fostering and flexible interactive environment of the International Institute of Applied Systems Analysis.

What Is Missing

If the test of this study is whether critical systems analysis can provide a more effective approach to ecosystem management problems than past approaches, the answer is yes. At the very least, a quite specific list of research priorities can be defined, critically focused on management needs, and leading to a more effective expenditure of available funds. Similarly, the exploratory policies generated, although needing further modification as the effort leads to implementation, suggest management routes to greater benefits and robustness at considerably less cost.

But if the test is whether this range of techniques and the new ones added are adequate for the problems at hand, then the answer is no. Several major issues are quite unresolved. One of the most important concerns the difficulties of meaningfully aggregating indicators across kind, time, and space so that rational preferences can be expressed among alternate futures. The use of present discounting procedures to handle intertemporal tradeoffs is clearly totally inadequate, the

more so because it makes the problem deceptively tractable. We know of no meaningful and effective way to make this time compression. Similarly, fundamental problems in the effective application of optimization techniques have already been discussed.

Beyond the technical inadequacies, however, there are more important elements totally missing from the full process of policy design. When we compared the steps taken in the present case study with others that were developing simultaneously at IIASA, a total set of analytic steps began to emerge

which would cover the full range of activities required in effective policy design. These are shown in table 3 and in figure 10. The budworm case study concentrated on the steps contained in the heavily outlined region of the table. Our implementation phase is just starting, and it will encounter major issues of practical concern relating to availability of an infrastructure of roads, logging logistics, and capital availability. That effort will need to develop additional tactical and more detailed simulation models and optimization routines, and must proceed in close interaction with those agencies and

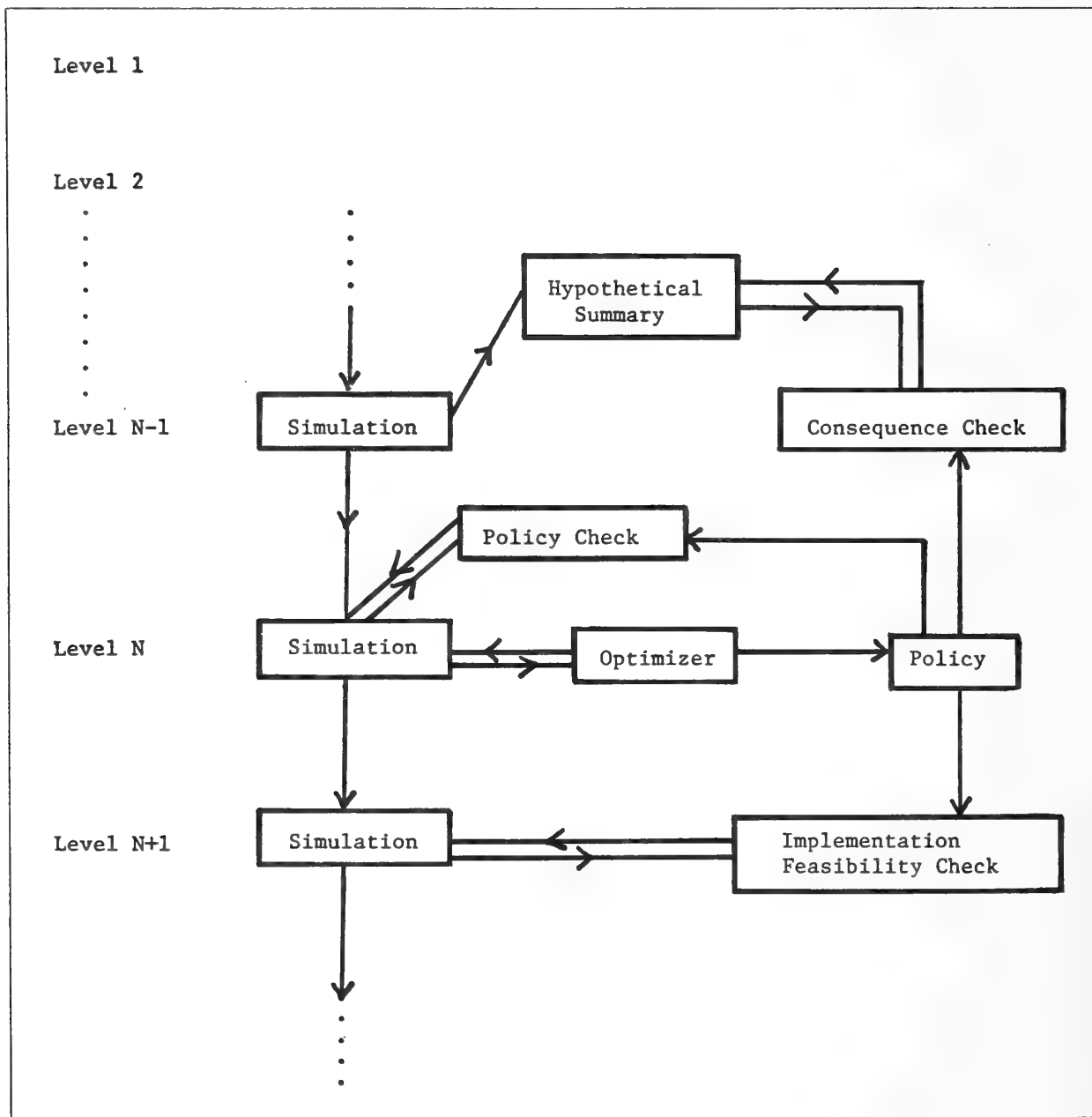


Figure 10.--Flow chart for policy determination.

Table 3.--The full policy design process

Analytic step	Systems level	Function	Technique	Purpose
Hypothetical overview (embedding)	N-1	Consequence check	-	To assess larger societal consequences of local policies.
Detailed dynamic description	N	System description	Simulation model with full spatial disaggregation	To describe, dynamically, the local system with enough confidence in its reality to be treated as reality.
Policy prescription	N	Policy design	Strategic range of objectives; optimization using simplified simulation model	To develop policy rules which are <u>only</u> state dependent, <u>using</u> simplifying assumptions.
Policy evaluation	N	Policy check	Cycling policies through full model; generating indicators (social, economic, recreational, environmental and resilience); decision analysis	To evaluate broader consequences and feasibility of policy rules within the local system.
Policy implementation	N+1	Implementation feasibility check	-	To develop detailed operational rules for implementing policy

industries actually responsible for management. The step of implementation is one which very few exercises of systems analysis have successfully accomplished, and certainly there are few major examples in the environmental field, outside of water resources work, which have involved effective implementation. That will be the challenge and acid test for the budworm programme over the next few years.

An equally important missing element in our programme has been the embedding of whatever policies are developed within the larger socioeconomic reality of New Brunswick and of Canada. Typically, relatively little effort is expended in specifically addressing these questions of social embedding. And yet, it is essential to develop some general overview of the broadest consequences of local policies. A promising lead has been provided by the energy case study at IIASA, which has argued that it should be possible to develop some simplified alternate societal models that in no sense pretend to be accurate representations of reality, but rather provide a framework or "mythology" to interpret the consequence as one person's view of the world.

But in its final analysis, those societal consequences must be explored by those who must make the management decisions, and those who must endure them.

The effective exploration of societal consequences is dependent upon communication, and communication in its broadest sense. That, too, is an area of neglect in this and nearly all other efforts. If we were to devote 5 percent of the ingenuity we now spend on analysis to innovative and effective ways of communication, the payoff in terms of improved management would be outstanding. The questions at issue is how information concerning such a complex system can be presented in forms that are clear, understandable, and usable; usable in a way that the perceptions and experience of the non-experts can be brought to bear on the analysis in a full and effective manner.

One final point needs re-emphasis. Past efforts in resource management have been essentially trial and error approaches to coping with the unknown. And, indeed, that is the way our society has advanced since the industrial revolution. Existing information

is mobilized to suggest a trial, and if an error is detected, then that provides additional information to modify subsequent trials. But we are now at the point where the intensity and extensiveness of our trials generate errors that are potentially larger than our society can afford. Trial and error seems increasingly to be a dangerous method for coping with the unknown. We need a new strategy to deal with ignorance. The concept of systems resilience provides at least a hint of a direction to proceed, focusing, as it does, not on the prediction of future surprises, but on designing systems that have the internal resilience to absorb those surprises when they inevitably appear.

Unless we can integrate into our design activities some such approach for dealing explicitly with the unknown, unless we honestly and effectively address the larger issues of social embedding and meaningful communication, all that we applied systems analysts can do is promise larger disasters, achieved faster, and in a more pretentious and disciplined manner.

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Integrated Management of Pine Weevil (*Hylobius abietis* L.) Populations in Sweden

Hubertus H. Eidmann¹

Introduction

Foresters have always known that insects are part of our forests just as much as trees, flowers, and birds. Sometimes one species will cause losses, and it is not always a result of natural events. Often we cause the conditions for insect damage by our manner of utilizing natural resources.

This knowledge and the steady increase of our understanding of ecological relationships gives us the key to managing forests in such a way that we can avoid damage at least from some of the potentially noxious insect species. Therefore, the concept of integrated management of forests and their insect populations has aroused worldwide interest. In simple words, this concept of integrated management means the combined use of all suitable methods to get highest productivity with the least damage to the natural environment. This, of course, is not new, as it has always been the essence of sound forest protection. However, much of our growing ecological knowledge is new, as is the widely and strongly felt necessity to preserve our natural resources.

There are not many standard methods of forest protection. The ecosystems are so diversified and the correlations so complicated, that usually every case needs special attention and consideration. There was, however, in the past, one generally accepted standard method: the protection of seedlings against the pine weevil *Hylobius abietis* by insecticide treatment. The use of insecticides against this old world species, a close relative to the North American pales weevil, *Hylobius pales* Herbst, had become a routine matter and was considered to be so effective that sometimes other basic precautions were neglected. This can be traced down even to the handling of seedlings and planting procedures.

I do not believe that such a development is unique to Europe or Sweden or to the pine weevil. However, for several reasons, pine weevil damage increased gradually, the situation in many reforestation projects was rather unsatisfactory, while at the same time, a growing concern about the routine use of insecticides called for alternative methods.

Research has not found any spectacular new method of seedling protection. What we have found is a considerable fund of knowledge, both old and new, which can be put together in a comprehensive and diversified approach to the problem. This may be called integrated management. It is an example which has parallels in North America. Therefore, it may be of interest also for North American foresters.

Cause of Losses

The pine weevil *H. abietis* (fig. 1) has a wide distribution over the coniferous forest region of the old world. In those parts of the region where clearcutting and reforestation by planting are practiced, the adult weevils cause heavy damage by feeding on young seedlings.

Recent studies in Sweden have arrived at rather good estimates of the losses caused by the pine weevils. In 1975, about 1200 reforestation sites planted the same year were investigated. Already in this first year, 20 percent of the plants not protected by insecticides had been killed by the weevils in southern and central Sweden. We know from this and earlier studies that the seedlings in this part of the country run a high risk of attack during the first 3 years after clearcutting (Hägström 1976; Nordic Forest Entomologists Research Group 1970/71; Eidmann 1974a).

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The economic loss of the plants alone is estimated at present to be at least 10 million American dollars per year. The total loss

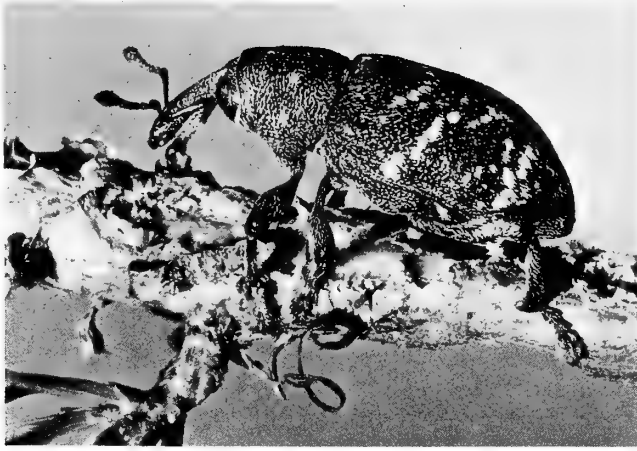


Figure 1.--*H. abietis* feeding on pine seedling.

including the cost for replanting and other measures, as well as the value of the growth loss, amounts in Sweden to more than 25 million American dollars annually.

The pine weevils belong to the large group of forest insects which may be termed "requisite-governed," because their population dynamics to a large extent is governed by requisites which tend to occur in limited quantity. *H. abietis* develops in stumps and in roots of dying and dead conifer trees. The occurrence of this trophic requisite influences abundance, fecundity, and dispersal of the weevils. Active dispersal and recognition of the breeding sites are highly important for the survival of the species.

The adult pine weevils have a long life -- in our experiments, up to 4 years -- and feed mainly on the bark of conifers. If conifer seedlings are present in the breeding areas, they are attacked and often killed by the weevils. The feeding weevils may belong to the parent generation or to the new generation that had developed in the stumps and roots for one or more years previously (fig. 2). The generation period is 2 to 5 years depending on climate (Bejer-Petersen *et al.* 1962). The heaviest damage occurs in regions where a 2-year generation period predominates (Häggström 1976; Nordic Forest Entomologists Research Group 1970/71; Eidmann 1974a). This is related to developmental time, reproduction, and the strong dependence of feeding on temperature (Eidmann 1974b).

The temporal coincidence of breeding material and seedlings is the cause of damage. Such a coincidence is not common in natural forests, but is generally the case in modern



Figure 2.--Pine root with larval galleries and entrance to pupal chamber of *H. abietis*.

forestry where clearcutting and planting are practiced (fig. 3). Thus, as is the case with a number of requisite-governed forest insects, the economic losses caused by pine weevils are a consequence of silvicultural practices. This suggests several ways of avoiding or reducing losses.

Elements of Management

Different methods can be integrated to effectively reduce damage caused by *H. abietis*. This integrated management is aimed at keeping losses at a tolerable level and not at total protection or at eradication of the weevils. The details of this management will differ according to climatic regions and local conditions.

The following elements can -- at least theoretically -- be integrated into a management system: 1) Avoid coincidence, 2) disrupt orientation, 3) prevent breeding, 4) reduce weevil abundance, and 5) protect seedlings.

Avoidance of Coincidence

The temporal coincidence of suitable breeding material and seedlings is most easily avoided by natural reforestation or direct seeding. These methods, however, usually result in a prolonged rotation and cannot be generally practiced because: 1) genetic manipulation is not possible; 2) soils with heavy vegetation, very dry conditions, and frost heaving damage decrease stocking levels; and 3) for natural regeneration, irregular seed production may permit less desirable species to occupy the site.

Another possibility is a fallow period. Depending on the weevils' generation period,

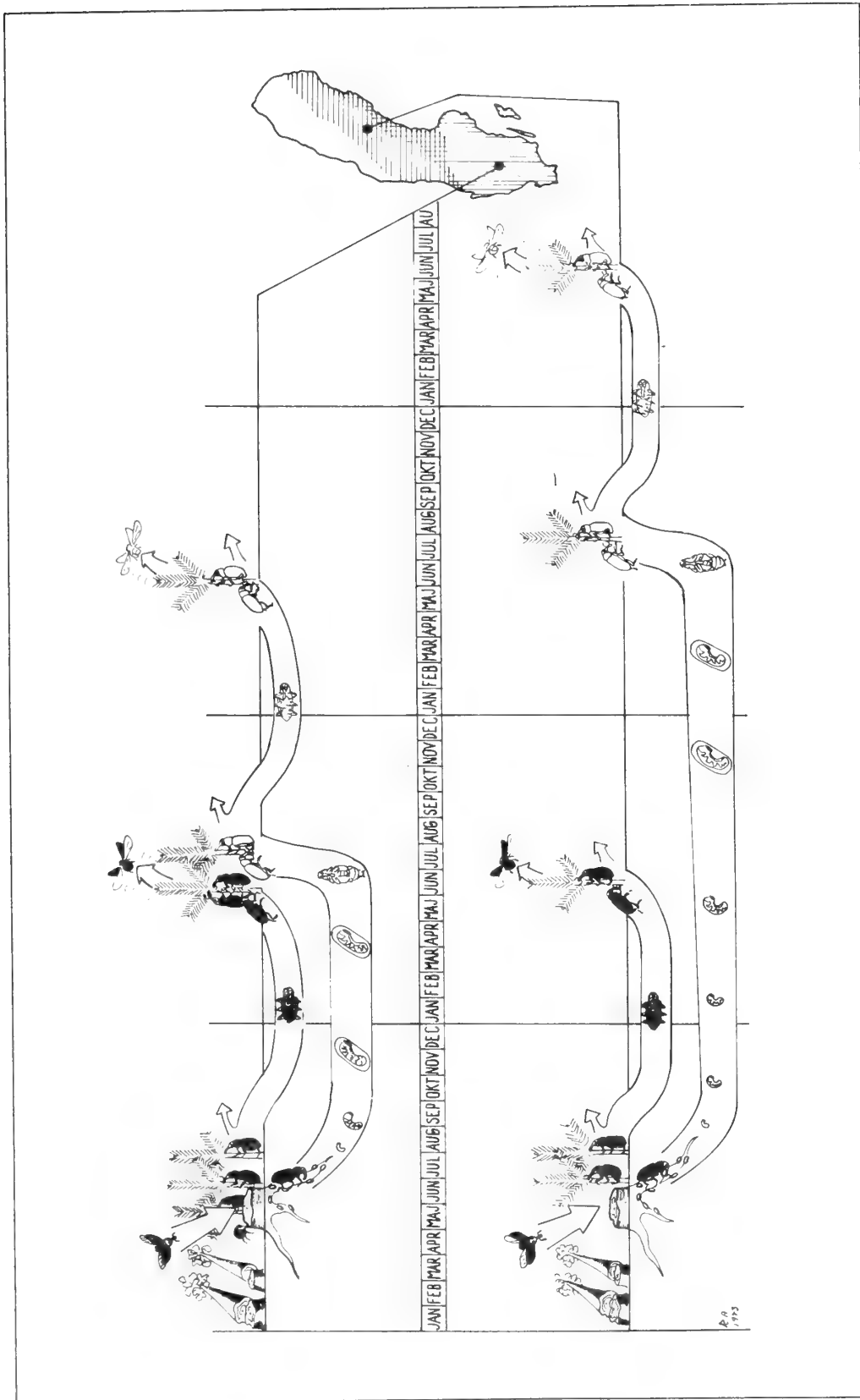


Figure 3.--Development and feeding periods of *H. abietis* in Sweden. Black: parent generation. Light: new generation.

this must be two or more years. The disadvantages of a fallow period are growth of forest weeds and the loss of production by prolonging the rotation. Fallow periods are practiced in regions and on sites where these disadvantages are not serious, especially where growth of forest weeds is not an obstacle to reforestation.

Newly clearcut areas attract weevils. In 2-year or older clearcut areas and depending on climate, the new generation of weevils will be released. Therefore, the close proximity of sites with young seedlings to areas attracting or releasing weevils should be avoided.

One possibility to do this is to divide forest districts into management areas. One year's cuttings are concentrated into one management area while the following year's cuttings are made in another, more distant, management area. This does not, of course, advocate large clearcut sites. This method may have another important advantage. The new generation weevils must find new breeding sites, *i.e.*, fresh stumps and roots. Olfactory orientation plays an important role in the location of breeding material. Large distances between development areas and new breeding sites make it more difficult for the weevils to find suitable breeding sites and may result in lower reproduction. The same may be important for the reproduction of bark beetles.

The timing of clearcutting may affect the orientation of weevils (and bark beetles). The slash from late summer and early autumn cuttings loses much of its attractiveness through dessication before the flight period next season. Therefore, such late cuttings should be favored.

Disruption of Orientation

The orientation of weevils can be influenced in other ways. It seems possible to disrupt orientation to breeding sites or to seedlings by the use of attractants or anti-attractants. Disruption of the olfactory orientation of insects is an interesting field of research and engages scientists in many countries. To date, however, there are no practical results to indicate the usefulness of this method to disrupt pine weevil orientation.

This also holds true for the use of repellents or feeding deterrents for the protection of seedlings. Both types of

substances could -- in different ways -- disrupt orientation. As a rule, seedlings need protection against pine weevils for more than one growing season. Therefore, olfactory repellents do not appear promising unless an effective slow release formulation could be developed.

It is unlikely that sexual attraction in *H. abietis* can be disrupted to prevent reproduction, because the weevils are long-lived, have many opportunities and many places to meet, and mate often. The possibility that all of these situations could be covered seems very small.

Prevention of Breeding

Prevention of breeding in stumps and roots would be a very good method to lower populations. However, the weevils cannot be kept away from breeding material for a long enough period. It is not possible to lure them permanently to other places, and there are no effective repellents or feeding deterrents (*i.e.* disrupt orientation). Nor does it help to debark or poison stumps. Sooner or later, the weevils will find the roots and breed in them.

However, when stumps and roots are taken out of the soil, the weevils cannot breed. This possibility has become promising in Sweden and Finland as the prospect of a negative balance of raw material for the pulp industries has induced the development of harvesting systems for the utilization of stumps and roots. According to our preliminary results, the breeding material on a site can be reduced by about 80 percent with the existing machines. A thorough utilization of stumps and roots in clearcutting areas of a region, leaving reproduction to torn roots, small stumps, and stumps in thinnings, would reduce the weevil population to one-third or a half of their numbers (Eidmann 1976a). This harvesting method would reduce damage to new seedlings.

Reduction of Weevil Abundance

There are several methods to reduce the numbers of pine weevils directly. The effectiveness of these methods has been discussed repeatedly, and a sound skepticism should be advocated. Considering the tens of thousands of pine weevils invading and breeding in clearcut areas, it will not be very effective

to trap or kill some hundreds of thousands. Biological control is one possibility to reduce numbers, but unfortunately, no such method has been developed. At present, the known natural enemies and diseases cannot be used effectively for this purpose.

Trapping methods using natural substrates with or without the addition of insecticides may reduce weevil abundance. However, in our experience, these methods are rather expensive and give satisfactory protection only when very little naturally attractive material is present on the site (Eidmann 1976b). This situation may change when highly attractive substances are developed. In any case, the effect of trapping methods on natural enemies and the associated fauna would have to be studied carefully.

In some countries, insecticides are spread all over the reforestation site, on plants as well as soil to reduce weevil populations and to protect seedlings. While this method is ecologically unsound and should not be used, the spot treatment of individual seedlings in the plantation may be advantageous in certain situations, e.g., plantations adjacent to new clearcuts. This method and the preplanting treatment of seedlings with insecticides also reduce insect numbers, but the intent is to protect seedlings (see below).

Protection of Seedlings

The protection of seedlings from serious damage is one of the best approaches to control of *H. abietis*. The weevils can live on other food than seedlings without causing economic losses. Therefore, it may be quite sufficient to protect the seedlings and not attempt to reduce population size. This is not quite a reality at present as no known method gives sufficient protection against very high numbers of weevils.

Silvicultural Protection

In any insect management scheme, the silvicultural possibilities should be given greatest attention. A sufficient number of seedlings per unit area in excess of expected survival should be planted. From the start, the seedlings should be given good growing conditions. Careful handling of the plants and careful planting seem unnecessary to mention, but much can be improved in this

respect. Good site preparation may include soil scarification. Our recent experience has shown that pine weevil damage may be reduced on the average to one-half if the seedlings are planted in mineral soil and are free from surrounding vegetation (Häggström 1976; Lekander and Söderström 1969; Österström and Anderson 1975).

Vigorous and resistant plants should be used. In many cases, that means relatively large, transplanted seedlings. Also small rooted plants may give good results. Although they are easily killed, they often escape attack. The choice of plants depends on local conditions. We have found that spruce seedlings are more resistant to pine weevil attack than pine seedlings (Eidmann 1969). *H. abietis* seems to have a slight preference for pine.

Physical Protection

Many ways to give seedlings physical or chemical protection against pine weevil feeding have been tried, some with success. For more than 100 years, coating (sand, clay, lime, glues, resins, tar, plastics, etc.) and casings for physical protection have been tested. The treatments either harmed seedlings or were difficult and expensive, or protection was unsatisfactory. No method for practical use has been developed.

Chemical Protection

The possible use of repellents and feeding deterrents for chemical protection of seedlings has been mentioned in connection with methods to influence the weevils' orientation.

During more than two decades, chemical protection of seedlings by insecticides has been one of the most important methods in all countries, where the pine weevils cause great losses. Usually the seedlings are given a protective coating of insecticide by dipping before planting or by spraying in spray tunnels or in the nursery bed. In some locations, seedlings are sprayed individually in the stands.

The preplanting treatment has several advantages: it is effective, cheap, ecologically selective, it can be done under centralized, controlled conditions, practically no insecticide waste contaminates nature, and it

protects also against other species -- e.g., other weevils (*Strophosomus* spp.), Scolytidae (*Hylastes* spp.), and Hymenoptera (*Acantholyda* spp.).

The insecticides suitable for this treatment should fulfill several criteria, among which effectiveness for at least one growing season and safety for human health and nature are especially important. The most used substances are DDT, and, in recent years, lindane and some other compounds.

Since 1975, no substance is registered in Sweden for protection of seedlings against pine weevils. In the years before the ban, only DDT was used. Every ounce was recorded and therefore we have exact figures of DDT consumption (Skogsstyrelsen, undated, unpublished reports). The mean gross consumption in the nurseries per seedling was about 40 mg. This corresponds to about 70 g/ha (varying with plant size and plant number). On 15-cm sections of 4-year-old spruce transplants recently dipped, the coating contained 3 to 7 mg of insecticide (Eidmann 1976b).

There has been doubt that a protective treatment before planting could be effective for more than one growing season. After many years of tests in all parts of Sweden, this effectiveness in the second year has been established. In one of these studies, the reduction of seedling loss by pine weevils was on the average for all study sites in Sweden as follows:

	DDT	lindane WP
First growing season	77 percent	94 percent
Second growing season	83 percent	90 percent

Another figure has practical importance, i.e. the estimated need for restocking blanks or for total replanting. This may be expressed as the number of sites with plant mortality caused by *H. abietis* during the first 2 years that exceeded one third of the seedlings. Results of an unpublished Nordic study (Nordic Forest Entomologists Research Group 1970/71) on a large number of sites show that DDT-dipping reduced the need of restocking by about 75 percent in Sweden.

In the search for new means of protection of seedlings, many compounds have been tested. Our tests comprised laboratory experiments, tests in field cages, and open field tests. In recent years, more than 50 substances were studied (Eidmann 1975).

Most insecticides were unsuitable because of unsatisfactory toxicity or persistence or

for other reasons, such as high mammalian toxicity. To date, no method using systemic insecticides has been developed. More than a dozen tested carbamates were unsatisfactory, and the only one with good effect -- carbofuran -- cannot be used because of its high toxicity. Some organophosphorous compounds gave good protection during one growing season. Dursban seems to have the best effect of these substances. The possible use of the latest biodegradable DDT-analogues and synthetic pyrethroids has not been sufficiently studied.

Presently, the protective effect of DDT and lindane is not equaled or surpassed by any acceptable substance. This does not, however, mean that new compounds or methods for safe and effective chemical protection of seedlings cannot be found.

Example of Integrated Management

It has been pointed out that the details of management will differ according to climatic regions and local conditions. However, an example may illustrate how this can be realized in practice.

We assume the following situation: a forest located in southern Sweden where the generation period of *H. abietis* is 2 years. Heavy attack may be expected during three growing seasons following clearcutting. The rotation period of forests is 80 to 100 years. Species composition is mixed Norway spruce and Scots pine with some birch and other deciduous trees. After clearcutting, forests weeds, dominated by raspberry, rose bay (*Chamaenerion angustifolium*), and bracken (*Pteridium aquilinum*), are expected to predominate. As rabbits are absent, management does not have to take into account damage by this species.

The integrated management comprises the following:

Clearcutting: In a year when no other clearcut area less than 3 years old is in close vicinity. Time of cutting is August-October. Where possible, stumps and roots are harvested, preferably earlier than May 15.

(Long distance to recently clearcut areas may reduce extent of weevil invasion. Autumn cutting reduces attractiveness of slash to weevils in the next year. Harvesting of stumps reduces reproduction and possibly attractiveness of site. However stump removal must occur prior to the flight period.)

Site preparation: Soil scarification in the year following clearcutting. A sufficient number of spots and an adequate area of mineral soil per spot must be provided for planting.

(Seedlings in mineral soil have better growing conditions and generally are less damaged by weevils than seedlings planted in humus and vegetation.)

Plants: Vigorous 3-to-4 year old transplanted seedlings and utilizing Norway spruce for parts of the site suitable for this species.

(Vigorous and large seedlings do not die very easily from weevil feeding activity. Spruce resists attack better than pine.)

Chemical treatment: Centralized treatment before planting by dipping or spraying of seedlings, using DDT, lindane, or other suitable insecticide.

(Protective treatment results in considerable reduction of plant mortality caused by feeding of H. abietis and other insects.)

Planting: In autumn of first or spring of second growing season after clearcutting. Careful handling of seedlings and careful planting in mineral soil. Plant about 2,500 seedlings per hectare.

(This time of planting avoids first year's attack by pine weevils and still permits the seedlings to escape early competition from forest weeds. Careful handling and planting gives the seedlings a good start and a chance to survive damage by H. abietis, Hylastes sp., and drought. The high number of seedlings planted allows for some mortality.)

This example uses only methods which are at our disposal presently. Management affects not only seedlings and pine weevils, but also other organisms, e.g. bark beetles.

Conclusion

This survey of possibilities to protect reforestations against pine weevils shows that integrated measures well adapted to actual conditions can reduce losses considerably. We need not rely on chemical protection only. Integrated management utilizing silvicultural measures and physical or chemical protection can keep *H. abietis* populations and their resultant damage at an acceptable level. However, before this can happen, greater

efforts in research, extension of information, planning, and supervision will be necessary. Only then can we accept the pine weevils as ordinary members of the forest ecosystems and as the fascinating insects that they are.

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The Concept of Impact in Integrated Pest Management /

Ronald W. Stark¹

Introduction

In its present state of semantic evolution, impact has as many definitions as there are categories of forest users. Concept is a general notion and, while also of personal conception, such a discussion permits broader latitude and less precision. However, I cannot resist including one elegant definition (I did not, alas, record the source):

"A perturbation of a dynamic human resource ecosystem that is a system in constant adaptation to new environmental conditions."

It is only within the past decade or two that we have had to concern ourselves seriously with accounting for the ecological and economic effects of our attempts to regulate insect populations. This somewhat forced state of accountability has paralleled growing ecological awareness and from it have emerged the concepts of integrated control and integrated pest management, both of which incorporate the principles that suppressive tactics should be ecologically compatible with the environment and that treatment be "necessary," *i.e.*, that treatment is justified (Stern *et al* 1959; Stark and Smith 1969). The necessity for treatment has been justified, almost exclusively to date, on economic grounds, and "economic threshold" is now almost a household phrase (Stern 1966; Headley 1972). However, there are, when economic justification cannot be proven, many other justifications for suppression of real or imagined "pests."

A significant event concerning recognition of true impact in forest protection in America was the U.S. Forest Service Marana Park conference on impact in 1972. The conclusion reached was that we did not have adequate systems for measuring or predicting the impact of any organism or factor capable of affecting forest growth. Nor did we have sufficient understanding of the concept of

impact in a resource management framework. It was, and is, generally agreed that the first step in any protection program is the determination of the true impact of the organism under consideration before it is labelled a "pest" warranting regulation.

The unpublished report of the Marana Park conference ascribes two components to impact: "(1) Ecological -- the cumulative net effects of insects and diseases on the ecological parameters of forest stands or other land management units containing trees, and (2) socio-economic -- the effects that alter value judgments and/or decision criteria established by management objectives." Correctly, impact is described as a "dynamic variable, as a function both of changes effected in forest stand condition and of criteria established for particular management objectives." However, the only ecological effects described are the negative ones created by the insects and the socio-economic parameters are restricted to the insects' role in "management activities for specified forest resources." No mention is made of the impact of regulation. The role played by insects, diseases, and other injurious agents and factors in the forest ecosystem must be viewed in a broader context than temporal activities and resources -- in short, in a total ecological context. Further, the actions taken by man in response to their presence must be considered.

Agreement can never be achieved between the various factions involved in forest production on the meaning of impact until we reach agreement on the term "pest." "Pest" is an anthropocentric concept which can be applied to anything in the plant or animal kingdom, not excluding *Homo sapiens*. Although most of those involved recognize that not all phytophagous insects are pestiferous nor all pestiferous phytophagous insects are constantly so, we continue to refer to most of them as "pests." The fact that "pest" is a term coined to describe a personal relationship emphasizes the importance of development of the meaning of impact. Perhaps we should renounce the term "Integrated Pest Management" in favor of "Integrated Forest Protection." This would imply protection

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against all organisms and factors affecting the forest negatively -- both ecologically and economically.

Our concept of impact and even more so, our definition, cannot escape anthropocentricity. Three books cover the entire range of possibilities of our view of impact from two extremes to a somewhat central position. These are Rachel Carson's "Silent Spring," Jamie Whitten's "That We May Live," and Robert Rudd's "Pesticides in the Living Landscape." They cover impact from the basic ecological viewpoint to the very fabric of the American way of life. In my attempt to provide an abstract, I have chosen to consider three major categories of impact: ecological, economic, and axiological. They are not mutually exclusive.

Ecological Impact

Although phytophagous insects are capable of causing severe economic damage, it should be recognized that they are common elements of most terrestrial ecosystems (Mattson and Addy 1975). Normal insect grazing usually does not impair primary production, indeed, it may accelerate growth. Outbreaks do occur, probably most commonly in relatively unproductive forest ecosystems already under stress by natural factors or because of technological coercion (Schimitschek 1964). There is evidence that after outbreaks have subsided, the residual vegetation is more productive than the vegetation growing before the outbreak (Mattson and Addy 1975). Some of the ecological effects of insect activity include: Increased light penetration, reduced competition among plants, altering plant species composition, increasing rate of nutrient leaching, increasing fall of nutrient-rich litter, stimulating redistribution of nutrients, altering water reception and distribution, and stimulating activity of decomposer organisms. The ecological effects (impacts?) may be reflected in events immediately observable for forest managers, e.g., increased water yield (Bethlany 1974; Clary *et al.* 1974) and improved wildlife and domestic forage. The effects of these may be viewed as positive or negative depending on 'management objectives', but they are ecological effects largely ignored in our current concept of impact. We are most familiar with the 'ecological effects' cited in the Marana Park report, *viz.* "discolor foliage, defoliate, stunt and deform, cause internal defects and kill trees (or parts thereof) and other

vegetation." What must be remembered continuously in our stewardship of forests is that insects and plants are evolving, competing, interdependent systems. Because they have evolved for eons, the balance between the systems is often very fine and easily, unwittingly and unrecognizably seriously altered by our actions. Man's abuse of the environment stems largely from our view that man is somehow separate and distinct from the natural environment (Kimmins 1972). The successful management of any complex production system must of necessity be based upon a thorough knowledge of the natural laws controlling that system. To do otherwise (as we have seen throughout recorded history) is to court disaster. In evaluating impact therefore, one must take into account the long-term ecological impact, both of the forest insect, disease or other influence, and our reaction to them. Instead of viewing today's activity as the final result, we must place that activity in an appropriate time sequence. In forests, unlike agricultural systems, time is generally on our side. What is left after an insect mass fluctuation, or what transpires later in a forest utilized by insects, may be more important and to our advantage (or at least not to our disadvantage) than the current event. For example, a long-term analysis of spruce beetle outbreaks in the western United States showed that control and salvage methods used were contrary to objectives for perpetuating the timber resource (Schmid and Hinds 1974). Although few such examples are documented (because we have rarely truly evaluated our "control methods") many pine stands are probably improved by activities of *Dendroctonus* species (Klein *et al.* 1972). One technique for such long-term evaluation of impact, suggested at least 7 years ago, was to adapt the life table technique to follow events in forest stands (Waters 1969). To the best of my knowledge, this idea has not been widely accepted.

It is widely acknowledged that if we are to be successful in managing our forests to reduce the negative impacts of phytophagous or injurious agents, we must have a thorough knowledge of the population dynamics of the organism, the stand dynamics of its host(s), and the interaction of the two within their shared ecosystem (Geier 1966; Stern *op cit*; Addy *et al.* 1971; Kimmins 1972; Franz 1973; Mattson and Addy 1975; N.A.S. 1976). It is a sad commentary on our research administration to view the paucity of support for such basic research. Only with such fundamental knowledge can we assess the effects of insect population fluctuations properly.

An overwhelming majority of literature on impact has been in this area with probably the least results, given that excessive attention. My reason for this personal, provocative, and perhaps inflammatory remark derives from two statements with which I concur:

"Most of the current available information on agricultural and other losses attributable to insects is at best a compilation of estimates which may or may not deserve the title of "Educated Guesses." How long can entomology tolerate such a condition and still survive?" (Decker 1955); and

"Economists have not been telling you the whole truth. We have largely ignored the price effects of pest control. We have totally ignored, in Pollyana fashion, the fact that trees do not really live happily ever after, after pest control treatment" (Flora 1967).

These statements were written 21 years and 9 years ago, respectively, and are still largely true today. The paper by Leuschner (1976) hopefully indicates that we are entering an era of economic honesty where all facts relative to economic impact, the positive as well as the negative effects, total costs, etc., are entering into the equation from which the decisionmaker will decide whether the probable end justifies the means rather than compiling educated guesses to justify the action already decided upon or concluded.

The concept of economic impact seems deceptively simple. It is the effect of phytophagous insects, diseases and other injurious agencies upon the monetary receipts from the production of goods and services from forest lands. Since the production of goods from our forests is fundamental to our national economy, it is understandable that any threat, real, possible, or imagined, evokes an immediate response from those responsible for the continuance of production. Crying "Wolf" in order to effect a decision to control is one means of protecting our continued resources (Johnson 1972). It is the apparent simplicity of the concept which has led to multiple confrontations between various segments of society. The economists ignore ecology and esthetics; the ecologists ignore economic reality.

The useful sub-concept of economic impact which has almost become a household phrase is "economic threshold." I call it a concept because it is constantly being redefined:

"The density at which control measures

should be determined to prevent an increasing pest [why not insect?] population from reaching the economic injury level" (Stern, *et al.* 1959). The economic injury level is defined as the lowest population density that will cause economic damage. Most subsequent authors ignored this subtle distinction.

"The level at which the loss caused by a pest [why not insect?] just exceeds in value the cost of the control measures available" (Geier and Clark 1961). "The critical level of damage above which damages will not be tolerated" (Beirne 1966). "A pest [why not insect?] has reached the economic threshold when the population is large enough to cause damage valued at the cost of practical control" (Clark 1970). "The population that produces incremental damage equal to the cost of preventing that damage" (Headley 1972).

This concept was derived by agricultural scientists and is still largely utilized solely by them. The pioneers in this area pointed out that even in the relatively simple agrarian systems "the economic injury level (and presumably also the threshold) can vary depending upon the crop, season, area, and desire of man" (Stern *et al.* 1959). Consider then the variations possible in the infinitely more complex forest system.

Examined in greater depth, the concept of economic impact becomes as complex as that of the ecological impact, partly because they are to some extent inextricably joined with one another and also with what I have called "Axiological Impact," and partly because there is a hierarchical stratification of effect. For example, the loss of a few million units of timber privately owned in Boundary County, Idaho means little to the national economy. It is a fraction of a percent of the total, and will probably be replaced in due time. However, it is of somewhat greater significance to the State of Idaho, of very great significance to Boundary County, and catastrophic to the owner. These descriptions would change if the land were *not* privately owned, were not commercially accessible, or were in lands classified as wilderness or primitive.

The parameters embodied in the concept of economic impact include:

1. The ownership or user group. The value of trees varies in urban forestry, natural and wilderness areas, public and private recreation areas, and commercial forests (Campbell 1972).
2. Vagaries of the market place. As with any commodity, the value of forest

products varies according to economic "laws" little understood even by economists. Commodity "gluts," such as may be created by an insect outbreak or wind-storm, temporarily affect values.

3. Regulatory and tax laws. Natural disasters, such as outbreaks, have been taken into account in federal and State laws, some of which may be of positive economic benefit.
4. Company and agency objectives and flexibility. "Losses" from an outbreak may be staggering if that outbreak destroys the current crop requiring total alteration of plans, or minimal if it occurs in a "reserve" area not contemplated for use in the immediate future.
5. Effects on the residual unit under management. Productivity of the remainder may be increased, offsetting some of the "loss," or conditions may be created causing high replacement costs, site preparation costs, susceptibility to other injurious conditions, etc., or other benefits may accrue such as improved hunting, fishing, etc.
6. Actuarial considerations. Investments, actual dollar investments or those represented by the inherited forest, must be discounted over time. This applies not only to effect of the event, outbreak or whatever, but also to the costs of the actions taken as a result of the event.
7. Costs of contemplated action. The total costs of protection strategies including their effects, if predictable and measurable, should be included. I am sure there are others, but in this somewhat superficial treatment, I have attempted to restrict my thoughts to the economic impact of injurious agents on the production of goods and services divorcing it from the axiological impacts. This removes from the vocabulary the now almost meaningless phrase "socio-economic" impact.

Axiological Impact

"Axiology is that branch of philosophy dealing with matters of value as in morals, esthetics and metaphysics" (Day 1976). I believe there is some merit in incorporating this definition of impact in our lexicon, as

it provides a convenient receptacle for those imponderables which we cannot fit into ecology or measure in dollars. Protection against such injurious agents as "pesticides," "herbicides," "nematicides," etc., has of late been attacked and defended on political, moral, and emotional grounds (Doutt and Smith 1969; Peterson 1976). While having little effect on ecologists or economists, such arguments are of considerable significance, often paramount, to public officials and even boards of companies. Decisions to implement control measures are frequently made on the basis of rhetoric prompted by sometimes mysterious, sometimes obvious, motivation.

Emotion over esthetics often transcends fact, and terms such as destruction, devastation, and decimation creep into our vocabulary (Klein *et al.* 1972). The subconscious attitude shared by entomologists involved in forest protection causes us to transmit to the lay public (non-entomologists) a negative, if not fearful, attitude towards phytophagous insects by repeatedly referring to them as pests (Gonzalez 1970). By our lack of knowledge, we support the general belief that pest populations are unpredictable and may increase to catastrophic levels at any moment. Anyone who attempts to argue restraint in retaliating against these "pests" may be subject to public abuse from many sources. On the other hand, anyone who proposes a technological approach to an ecological problem may receive abuse from the ecological camp -- as Day (1976) put it -- "ecosystems are always fragile" (actually and fortunately, most are very resilient). My current favorite example of one form of axiological impact is derived from the 1972-74 controversy over whether or not the Environmental Protection Agency would permit the use of DDT to treat a Douglas-fir tussock moth outbreak in the northwestern United States. At the time of the article, from which these quotes were taken, the EPA, then headed by William D. Ruckelshaus, had rejected the application by the U.S. Forest Service, for limited use of DDT.

"In making that decision, the fledging EPA earned a place in history. The question is, will William D. Ruckelshaus be remembered as a naive bureaucrat whose political expediency was responsible for the continuation of an epidemic that destroyed thousands of acres of forest land? Or will he be remembered as the man who saved the nation from the use of a dreaded chemical?" (Patterson 1973). From this and others in the same colloquium, I found "hero," "armchair tyrant," "symbols of government stupidity," "utter devastation," "shall we stop this holocaust with proven DDT

or choose total destruction of the forest environment?" and "this great forest disaster." Such is the stuff with which axiological impact is concerned. A permit to use DDT was eventually granted.

Within the realm of axiology is the inherent faith of *Homo sapiens* in traditional methods and precepts. The most elegant ecological or economic model describing the respective impacts may have little effect on changing existing methods for the idea of the forest practitioner may be far more difficult to change than the direction of the insect population change (Vogt 1948). Behind nearly every human act lies an "emotion" that sets the act going; behind that emotion lies a "thought" or an "idea." If we are to make peace with impact that peace must begin in our minds; we must seek and consider many new ideas and we must reconsider many old ones. The spiritual ethic that many people, including those not directly involved with forestry, feel for the forest makes this lasting peace extremely difficult to obtain.

On a more mundane plane, we can include under axiological impact those public reactions which are measurable but difficult, if not impossible, to quantify in monetary terms. In urban or heavily used recreation areas, there is little outcry when it is proposed to control mosquitoes, hornets, black flies, or chiggers. The cries of the ecologically minded public are submerged by the sighs of relief of those who like to recreate in comfort.

In short, axiological impact may include those effects for which we can only exercise value judgments as determined by the majority, the most influential, or those in positions of authority.

Conclusion

I have attempted to outline the concept of impact in pest management hopefully applicable to all organisms capable of achieving pest status but with particular reference to forest insects. I conceive impact of potentially injurious agencies in three categories inextricably linked -- ecological, economical, and axiological. The first two are measurable and quantifiable; consequences can be weighed against material benefits; the third is difficult to measure and quantify in material terms.

The person or agency responsible for decisionmaking is required to consider all impacts before deciding to let natural events

run their course or to take action to prevent or limit them. The consequences of either course can be serious. Scientists and economists have largely neglected the essential first step in forest protection, determining the consequences of counteracting that event. Our estimation of impact to date has been grossly superficial and self-serving -- and we have usually ignored the most important aspect of the problem -- the ecology of the forest ecosystem. Economic and axiological effects wax and wane with the Gross National Product and beliefs of the moment; the cycle of forest growth is hopefully infinite. We must learn more about the effects of natural fluctuations of organisms on our forests, we must better understand the natural growth and cycles of our forest, we must learn more about the effects on the forest ecosystem of our utilization of the forest and attempts to counteract natural biological events. Beside the potential effect man's actions may have on the forest ecosystem, other impacts pale into insignificance.

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IV. BIOLOGICAL CONTROL OF FOREST INSECTS

Some Recent Approaches to the Biological Control of Forest Insect Pests in Japan

Keiji Kanamitsu¹

Japan has not imported any foreign parasites and predators in the conventional method of biological control against forest insect pests. One reason may be that most Japanese forest entomologists consider it important that the indigenous natural enemies should be evaluated better. Since so-called natural control is apparently taking place everywhere in the forest, and many insect populations have been kept naturally at fairly low levels, this approach seems wise. Such was the case of the Japanese chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu² (Torii 1959). The native parasites, which had been previously feeding upon the other gall making insects in the forest, gradually switched to the chestnut gall wasp, and finally suppressed the pest population in about 10 years. This example of natural biological control stimulated many Japanese forest entomologists to open their eyes to the importance of native parasites.

Discussion

Artificial Propagation of Indigenous Parasites

Yamaguchi (1973) studied a fir aphid, *Cinara todocola* Inouye,³ and its native parasite, *Pauesia momicola* Watanabe & Takada,⁴ in Hokkaido. He reared this parasite in the laboratory and released it into a field cage in

which a host tree had been heavily infested by the aphid. After parasitization, the cage was taken away, and the parasite could soon propagate on the neighboring trees. The high percentage of parasitism did not last long, but it was a useful technique for pest control, since the aphid only affects trees in a very young plantation.

Local Transport of Parasites

Since it is not very unusual that two neighboring forests have different fauna and abundance of parasites and other natural enemies, it should be useful to transport promising natural enemies from one place to another. Kuranaga and Morimoto (1969) transferred two species of parasites of the pine shoot moth *Evetria cristata* Walsingham⁵ into a different pine plantation where the parasites were scarce, and recorded 70 percent parasitism in the third year. Miura (1961) conducted an interesting study of promoting an indigenous parasite in Shimane Prefecture where *Platygaster* sp.⁶ was a known native parasite of the pine gall midge *Thecodiplosis japonensis* Uchida et Inouye. He noticed that the parasite was more abundant in pine woods containing grasses and shrubs. In his experiment, the dense pine forest was first thinned so that grasses and shrubs could grow naturally, and then *Platygaster* sp. reared in his laboratory was released. The percentage of parasitism increased from 14 to 80 percent in 3 years, and the affected trees soon recovered their growth.

¹ Tokyo University Forest, Seto, Aichi-ken, Japan

² Hymenoptera: Cynipidae.

³ Homoptera: Lachnidae.

⁴ Hymenoptera: Aphidiidae.

⁵ Lepidoptera: Olethreutidae.

⁶ Hymenoptera: Platygastridae.

⁷ Diptera: Cecidomyiidae.

Dendrolimus spectabilis Butler⁸ is a pest on Japanese pines. The eggs are laid on pine needles in July and August. Kokubo (1963, 1975) noticed that the egg parasites were always more abundant in late season, as they could quickly increase their populations. One of the egg parasites is *Trichogramma dendrolimusi* Matsumura⁹ which is easily reared in the laboratory. The egg of the well-known Japanese silkworm *Bombyx mori* L.¹⁰ can be used as an alternate host, and be released in the field in May and June when the natural host eggs are scarce. Thus, it is possible to augment the initial population density of this egg parasite, so that they can be ready to attack the eggs of *D. spectabilis* appearing in the field in July. Unfertilized eggs of the pest, *D. spectabilis*, are considered to be more useful for this purpose, since they are available for some other egg parasites as well. Field release of actually living insect pests for biocontrol purposes requires caution, as it carries with it the danger of increasing the pest population. However, at times it seems worth trying. The insect pest together with its parasite are transferred to some other place so that the parasite can establish itself quickly in the new environment in the presence of the host pest. A detailed study on the biology of the pest and its natural enemies will open a way to this approach.

Long-Term Evaluation of Pest Control

Forestry is a long-term enterprise of at least 50 years in Japan, and any artificial pest control should be evaluated over that length of time. Fairly heavy damage at one time is often interpreted as being almost negligible in the long run. The needed control in forestry is usually slight in comparison with agricultural crops and orchards. Often it is not necessary to achieve a complete control of forest insect pests. Sometimes, very good control of the insect pest is eventually not good for the forest.

⁸ Lepidoptera: Lasiocampidae.

⁹ Hymenoptera: Trichogrammatidae.

¹⁰ Lepidoptera: Bombycidae.

* English translation by present author.

In the Tokyo University Forest in Seto, some experimental studies of silvicultural treatment have been carried on. One is a mosaic patterned regeneration, in which some small-size plantations of different tree species of different ages are scattered over naturally growing deciduous woods. The size of one plantation has been set about 0.1 to 0.2 ha. A detailed investigation for shoot boring insects and their natural enemies was undertaken in some pine plantations in such mosaic patterned woodlands. It was noted that the population fluctuation of the pine shoot moth was kept far lower there than in wide open plantations (Kanamitsu, unpublished data). Another example is a linear plantation in natural woodland. The width of each line is fixed about twice the height of the naturally growing trees. These types of silvicultural arrangement maintain control by natural enemies, and seem to be the best solutions to the forest insect pest problem.

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Operational Use of *Bacillus thuringiensis* against the Spruce Budworm [1, 2]

W. A. Smirnov¹

Since 1967, the spruce and fir forests in the Province of Quebec have been severely attacked by the spruce budworm, (*Choristoneura fumiferana* Clemens).² In 1976, some 82 million acres were infested. Although chemical insecticides were primarily used in trying to minimize damage caused by the insect, every effort was made to find alternative methods of control. The Insect Pathology Unit of the Laurentian Forest Research Centre has been involved in research on the use of *Bacillus thuringiensis* (*B.t.*) against the spruce budworm since the early 1960s (Smirnov 1963), and new studies were initiated in 1969. Results of the early studies showed that parasporal endotoxin produced by *B.t.* played only a minor role in spruce budworm mortality, and that larval mortality is mostly the result of a typical septicemia (Smirnov 1963, 1965). Septicemia does not begin until the organism has penetrated the gut wall and entered the hemolymph (Smirnov 1971). It was suggested that destroying the chitinous lining of the gut lumen would permit better contact of ingested spores with cells of the gut wall and facilitate penetration. Traces of the enzyme chitinase, which hydrolyzes chitin, were added to *B.t.* preparations administered to spruce budworm larvae. Thus the disease was accelerated and the mortality rate increased even at temperatures in the normally critical range 14-18°C (Smirnov 1971).

On the basis of these promising results and to determine with certainty the possibilities for using *B.t.* operationally for the control of spruce budworm, several field tests were conducted from 1971-1976 using different combinations of aircraft, formulations, and rates of application. The following discussion reports results of experimental and oper-

ational field dispersions of *B.t.* against the spruce budworm.

Results

The first field tests were made in 1971. A small Stearman aircraft, 100 gallon U.S. capacity, equipped with Micronair^R spray heads, was used for spraying. Two 100-acre forest blocks were used; one was sprayed with the *B.t.*-chitinase formulation, and the other with *B.t.* without chitinase.

The formulation per acre was composed of:

0.5 gal. Thuricide HPC^R
0.5 gal. Polyglycol 400^R
1/20 gal. Nu-Film Bt^R sticker
1 gal. water
5.5 mg of chitinase (test block only)

The rate of spraying was 7.8 International Units (I.U.)/acre in 2 gal. of final spray (Smirnov *et al.* 1973a).

The results of these field tests showed the feasibility of using *B.t.* treatments for the control of spruce budworm and for the protection of host trees, and that the formulation with chitinase resulted in higher larval mortality and foliage protection, thus confirming the results of laboratory tests. Corrected larval mortality (Abbott 1925) in the block was 55 percent with moderate foliage protection while in the block treated with *B.t.*-chitinase corrected mortality was 78 percent with good foliage protection.

However, the small Stearman aircraft was not satisfactory for *B.t.* treatment over large areas. So plans were made in 1972 to conduct semi-operational treatments with the type of aircraft and spray systems used at that time for spraying chemical insecticides. Therefore, three TBM Avenger aircraft (625 gal. capacity) equipped with booms and nozzles were used for spraying *B.t.* over 10,000 acres in

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² Lepidoptera: Tortricidae.

1972 with the *B.t.*-chitinase formulation used in 1971. Where deposit was 0.4 gal./acre and over, corrected larval mortality was 77 percent and defoliation 53 percent. In untreated areas, these figures were 48 percent and 88 percent respectively (Smirnoff *et al.* 1973b). This confirmed, for the first time, the feasibility of using *B.t.* in operational treatments against the spruce budworm. However, the high rate of evaporation of the water-based formulation and the large amount of material required, 2 gal./acre, which necessarily affected treatment costs, suggested the need for a more compact and low-volume formulation.

During the winter of 1972-73, every effort was made for development of a concentrate and low-volume formulation. A formulation composed of: 0.25 gal. *B.t.* concentrate, 0.25 gal. 70 percent sorbitol solution, 1/1600 Chevron sticker, and 5.5 mg chitinase was laboratory tested and recommended for field tests in 1973. This formulation permitted dispersion of 6.8 I.U./acre in only 0.5 gal. of final spray, thus reducing cost of material and application and making *B.t.* treatments more realistic over vast areas.

In the summer of 1973, the proposed formulation was tested on 300 acres of forest with a TBM Avenger and a larger aircraft, the twin-engine CL-215, 1800 gallon capacity. Larval mortality of 75 percent was sufficient, but little foliage protection was observed because of the poor condition of the stand prior to treatment (Smirnoff *et al.* 1974). For this reason, and to check the new formulation on an operational level, the formulation was tested on a 10,000-acre area by means of the CL-215 and DC-6B aircraft, 3500-gallon capacity. Unfortunately, the aircraft used were calibrated for oil-based chemical insecticide formulations; consequently, deposit with the *B.t.* formulation was lower than expected and unevenly distributed. The maximum number of *B.t.* colonies/cm² was 19 out of an expected 50, and the maximum volume deposited was 17 oz. on an emitted volume of 48 oz., both obtained with the DC-6B aircraft. Nevertheless, in areas of higher deposit, corrected larval mortality was 78 percent, which is good, and defoliation was 46 percent, which is also acceptable (Smirnoff *et al.* 1976).

The main conclusion of this operation was that *B.t.* can be used operationally and successfully for the control of the spruce budworm provided that proper aircraft calibration is made. Therefore, during the winter of 1974-75, calibration tests with several formulations were carried out in Southern California. As a result, additional water was added to our sorbitol-based formulation which became: 50 parts *B.t.* concentrate, 30 parts

70 percent sorbitol solution, 20 parts water, and the usual Chevron sticker and chitinase.

In 1975, this formulation and two water-based formulations were used operationally on 250,000 acres of forest. In general, with proper timing of application, the formulations with sorbitol suppressed the population levels to acceptable limits and foliage protection was good. However, results were also affected by improper aircraft calibration, and, in some areas, only 1/10 of the emitted volume was found at ground level. Nevertheless, analysis of the various parameters leads to following conclusions:

1. Formulations with water as a carrier cannot be recommended because of high evaporation during application. Formulations with sorbitol are more efficient.

2. Timing of the spray application is very important and necessary for foliage protection. When treatment is applied too early, shoots do not present a surface sufficient to retain enough spray. When applied too late, the insect has time to destroy the young shoots which compromised foliage protection. In a large scale operation, timing is one of the most critical factors for insect control.

3. Low deposit has been the principal weakness in the operation, and emphasizes the need for an improved aircraft calibration.

4. With formulations containing sorbitol and with deposits closer to normal, the insect population affects foliage protection as follows:

- a) At population levels close to 30 to 35 larvae per 18-in. branch tip, foliage protection is good.

- b) When population levels exceed 2 to 3 times the known limits for *B.t.*, there is no foliage protection but the stems and next year's buds are unaffected and a limited degree of effectiveness of *B.t.* is indicated even under such critical and unusual conditions.

- c) When the population is 100 to 160 larvae per 18-in. branch tip, *B.t.* is ineffective, and even the partially opened shoots that show no damage prior to treatment are destroyed within a few hours.

To determine whether the uneven distribution of *B.t.* resulted from improper aircraft calibration, a small test was made in 1976

using a Sikorsky helicopter, the same *B.t.* formulation used in 1975, and the same rate of application, i.e., 0.5 gal./acre. Deposit was 35 *B.t.* colonies/cm², 19.8 droplets/cm² and 45.4 oz/acre² which was closed to the 50 *B.t.* colonies/cm² and 64 oz/acre recommended. Results were proportionally good with 81 percent corrected larval mortality and 72 percent foliage protection throughout the territory.

These results clarify much of the present controversy over *B.t.* When deposit is sufficient and when larval populations are within the recommended limits for *B.t.*, foliage protection resulting from *B.t.* treatments exceeds accepted levels of success. The critical and urgent aspect of the problem lies in the development of spray systems.

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Biological Control Prospects of an Egg Parasite, *Telenomus alsophilae* Viereck

G. F. Fedde, V. H. Fedde, and A. T. Drooz¹

For many years, the egg parasite *Telenomus alsophilae* Viereck (fig. 1) was regarded primarily in terms of its role in the effective control of its principal host, the fall cankerworm, *Alsophila pomataria* (Harris). Until recently, no one knew the extent of its capabilities or seriously considered using it for biological control purposes. In 1964, however, attitudes toward *T. alsophilae* changed in the wake of one of the most destructive outbreaks caused by the elm spanworm, *Ennomos subsignarius* (Hübner), in eastern North America (Ciesla 1963, Drooz 1964). Ironically, the telenomid responsible for the dramatic collapse of that infestation eventually proved to be a species different from *T. alsophilae* (Drooz *et al.* 1976, Muesebeck 1978).

Today, one can be optimistic about the prospects of *T. alsophilae* for biological control, largely because it is easy to rear under controlled conditions. No elaborate equipment is needed, nor are special precautions necessary to maintain continuous generations throughout the year. Initially, our goal was to develop a rearing system that would free us from dependence on naturally parasitized material to keep our colonies going. We were also eager to find out more about the parasite's basic biology, particularly those aspects that would improve rearing efficiency.

Host Rearing

Rearing *T. alsophilae* successfully depends primarily upon providing suitable

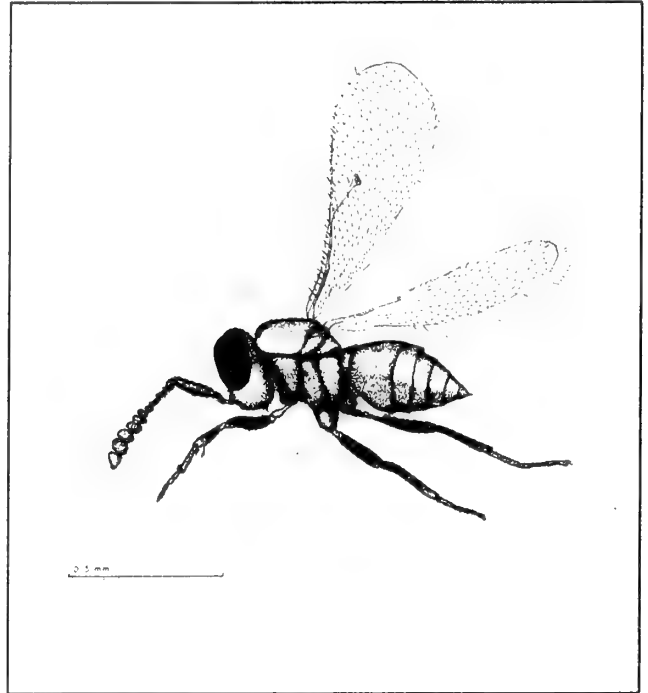


Figure 1.--*Telenomus alsophilae* adult female.

laboratory hosts on demand. When the cankerworm proved to be a recalcitrant host, other alternatives were investigated. In this regard, Maltby *et al.* (1973) discussed advantages of turning to substitutes that ordinarily may not be parasitized in nature. Screening various lepidopteran hosts established that *T. alsophilae* can reproduce in eggs of at least 12 geometrids and two noctuids (Fedde 1977).

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The host we selected was *Eutrapela clemataria* (J.E. Smith), a widely distributed species in eastern North America and a general feeder for which more than 40 food plants have been recorded (Prentice 1963). Using the artificial medium developed by V.H. Fedde (1974), successive generations were reared at the rate of one every 1-1/2 months for 2 years. Larvae up to 32 hours old fed inside inverted 32-dram, plastic condiment cups, each containing diet previously dispensed to a level of 1-1/2 cm.

Usually, we began with four to six individuals per cup and progressively reduced that number during later stadia until all containers held only one larva each. When larvae were midway through development, we positioned a toothpick diagonally in each cup to facilitate transferring insects to new diet and to provide a convenient perch for feeding. Just before pupation, the insects were isolated in 5-cm cubical plastic boxes where they spun loose cocoons in the tissue paper provided for that purpose. After pupae were sexed according to the guidelines established by Mosher (1917), emerging moths were mated in large paper bags and the eggs removed several times daily.

All rearings were conducted under 16-hour daily illumination and ambient temperatures of 21 to 30°C. Under these regimes, the entire process was completed in 30 to 45 days. In a typical rearing, we handled 600 insects of which 80 percent survived from hatch to emergence. Up to 1000 viable eggs were recovered from individual masses.

Parasite Rearing

Surprisingly, the selection of parasite stocks to initiate rearings requires almost as much care as finding a suitable host. In the laboratory, wild populations from different geographical sources vary not only in their ovipositional response but also in fundamental behavior. Thus, parasites bred from cankerworm eggs collected in Fauquier Co., Virginia, aggressively attack both host and non-host eggs. In either case, females always use their ovipositor to mark eggs they have just parasitized. In contrast, their counterparts from Maine parasitize only cankerworm eggs and do so without marking them.

Parasites from the Virginia "strain" attacked eggs of *E. clemataria* in all stages

of embryogenesis up to and including hatch (Fedde 1977). However, only eggs parasitized during the first 2 days after deposition produced yields better than 92 percent. When eggs were incubated at 22°C and 76 percent RH, the first parasites emerged in 25 days. Based on a representative sample of 32 masses, survival under these conditions averaged 94.1 percent \pm 5.4.

Newly emerged parasites were transferred immediately to 3-1/2 dram vials capped with lids having a central opening for ventilation and fitted with a piece of organdy cloth between the lid and the vial. Once inside the vials, the adults were fed a 40 percent aqueous honey solution administered with a hypodermic syringe to thinly sectioned discs of dental cotton.

Initial feeding of the parasites is the single most important step in the rearing process. Unless parasites are fed as soon as possible, mortality begins within 24 hours of emergence and may exceed 75 percent. An additional feeding 1 week later is usually all that is necessary for routine rearings.

During most of the year, parasites can be kept openly on laboratory counters. In winter, when there was less moisture in the air, we transferred the vials to glass desiccators where salt solutions (NaCl) maintained RH at 75 to 76 percent. Anytime between 1 and 40 days after emergence, eggs were introduced in the cages for oviposition and the cycle was repeated.

Biological Considerations

Given the brief time fresh host eggs remain receptive to parasitism, rearing efficiency would be seriously impaired were it not for one overriding factor: the eggs can be stored. To determine how long, eggs refrigerated at 8°C were exposed to five mated females at 3- to 4-day intervals. These trials were replicated one to three times in such a way that all eggs in a given series originated from the same mass. Under these conditions, an average number of eggs which ranged from 68.3 to 203.0 were exposed to parasites for 3- to 4-day intervals over a period of nearly 2 months. The results revealed that eggs treated this way were susceptible to parasitism to some degree for at least 53 days (fig. 2). Parasite survival in eggs stored up to 37 days exceeded 85 percent.

A prime concern also was to determine the best numerical combination of parasites and hosts to insure efficient productivity. We particularly wanted to know how behavior patterns associated with parasite density might affect oviposition. Initially, the egg-laying capacity of individual females was investigated during 24 hours of exposure. When 26 egg masses varying in size from 71 to 135 eggs were submitted to females averaging 26 days old, the mean number parasitized was 61.3 ± 14.6 per female. The high recorded was 87 for a 21-day-old female.

T. alsophilae evidently retains its ability to reproduce at high levels for considerable lengths of time. When the above tests were repeated using 4-month-old females exposed to 12 egg masses, the mean number parasitized per female was 43.6 ± 15.3 , with a high of 64 by a 128-day-old female. In this test, 95.8 percent ± 3.3 of the new parasites emerged successfully.

Despite the impressive reproductive capacity of individual females, uncertainty remained about the effect interactions between parasites would have when more than one female was present. Accordingly, 10-14

eggs were glued to each of 12 cards and exposed to six female parasites per card. Parasite responses were observed continuously until 25 minutes after all eggs were parasitized.

The important facts to emerge were (table 1): (1) Some eggs were attacked repeatedly, even though unparasitized eggs were still available; (2) some parasites failed to attack any eggs; and (3) one parasite eventually emerged from each egg in all cards no matter how many times the egg was attacked. We already suspected the latter was true because we observed that the number of offspring emerging from a fixed number of eggs was the same whether a few females were used at the start or many. Consequently, excessive numbers produce no added gain in efficiency. At the other extreme, too small a number can result in underparasitism because not all females oviposit when exposed to host eggs. As a practical matter, we found that five females usually are sufficient to parasitize 90 percent or more of the eggs in masses of up to 120 eggs each. Nevertheless, when even larger numbers of eggs were submitted, we found that a ratio of increase of at least 39 progeny to one parent is possible.

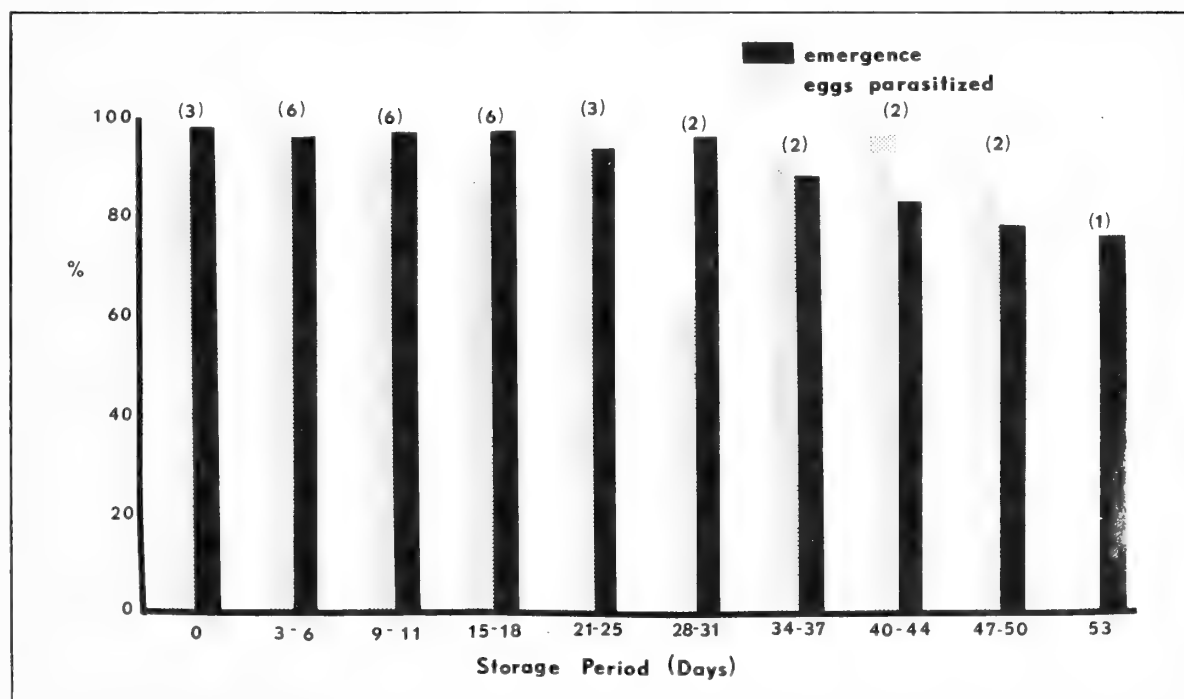


Figure 2.--Parasitism and emergence success of *Telenomus alsophilae* Viereck on eggs of *Eutrapela clemataria* (J.E. Smith) exposed for 3-4 days following storage at 8°C and 75 percent RH. Numbers in parentheses represent total observations.

Table 1.--Oviposition behavior of *Telenomus alsophilae* Viereck following exposure of mated females to eggs of *Eurypela clemataria* (J. E. Smith) (replicated 12X, 6 females/10-14 eggs)

Observation period	No. ♀♀ attacking eggs ¹	Time till all eggs attacked (min.)	No. eggs attacked 1X	No. eggs attacked >1X	Maximum attacks on 1 egg
Till all eggs parasitized	2.3±1.2	25.8±8.8	7.7±2.5	3.3±1.8	3
25 min. after all eggs parasitized	4.3±0.5	-	4.1±2.7	6.8±2.5	5
t between categories	5.48**		3.44**	3.94**	

Observation period	Total eggs	Percent parasitism	Percent emergence
Post oviposition	133	100.0	100.0

¹ No. at beginning and end of observation period. **P>.01

Conclusions

With refinements, the methods outlined above could be developed into a mass rearing capability that is both efficient and economical. Bustillo and Drooz (1977) already have hinted at the enormous potential of *T. alsophilae* as a biological control agent if its use is expanded to other pests. Although its first major success in this capacity was outside North America, there is no reason why native insects should not also be considered as prospective targets.

Lambdina pellucidaria (Grote and Robinson), a periodic defoliator of southern pines (Yates and Ebel 1972), is readily parasitized by *T. alsophilae* in the laboratory. The genus *Lambdina* also contains at least two more important conifer pests, the hemlock looper, *L. fiscellaria* (Guenée), which feeds primarily on hemlock and balsam fir, and *L. athasaria* (Walker), which feeds on hemlock (Schaffner 1949). Further screening of forest geometrids, and possibly noctuids as well, might bring to light additional prospects. More than anything else, what is needed now is to get out of the laboratory and into the field.

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213
Insect Parasites as Regulators of the Gypsy Moth Population at Hawk Mountain, Pennsylvania (27)

R. C. Hedlund and G. W. Angalet^{1 2}

The privately-owned Hawk Mountain Sanctuary and adjacent State game lands in the Blue Mountains of Pennsylvania (Berks and Schuylkill Counties) first became infested by the gypsy moth, *Lymantria dispar* (L), in the early 1960's. By 1968, damage to the trees was severe and the area was sprayed with insecticide. In the absence of insecticide applications in subsequent years, the gypsy moth population quickly rebounded, causing total defoliation in 1972. At that time, the gypsy moth was decimated by a nuclear polyhedrosis virus, and since then, no significant tree damage by this pest has occurred.

Efforts to control the gypsy moth in the USA by introducing its insect enemies were begun in 1901, and are described in detail by Howard and Fiske (1911), Crossman and Webber (1924), and Burgess and Crossman (1929). An additional importation effort by the Department of Agriculture is currently in progress, and involves exploration in both Europe (including parts of the Middle East and North Africa) and Asia.

Ten species of introduced gypsy moth parasites are established in the United States (Hoy 1976). In addition, an introduced coleopterous predator, *Calosoma sycophanta* (L), is also well established (Burgess and Collins 1915).

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² We wish to thank Mr. Alex Nagy of the Hawk Mountain Sanctuary and Mr. Stephen C. Mace of the Pennsylvania Game Commission for allowing us access to the study locations. We also acknowledge the Systematic Entomology Laboratory, ARS, USDA, for taxonomic assistance. Appreciation is extended to Michael King, Michael McDowell, Stephen Spence, Joseph Tropp, and Timothy White for technical assistance.

This study was initiated in 1974 and continued through 1976 to determine the role of introduced entomophagous parasites in regulating the post-outbreak populations of gypsy moth at Hawk Mountain, Pa.

Materials and Methods

The gypsy moth population was sampled at three sites on Hawk Mountain. Egg parasitism was determined by collecting egg masses from each site during the winter or early spring. These were dehaired in the laboratory and examined microscopically. The numbers of parasitized and unparasitized eggs/mass were recorded.

Larvae were collected weekly from each site beginning about 2 weeks after hatch. The collection points were varied, with larvae being taken from leaves, bark, and the ground as randomly as possible. Burlap bands were placed around 20 trees in each site to aid in the collection of late instars. Larvae were taken from the burlap only when the desired number (100/site) could not be found otherwise. The collected larvae were kept in an insectary in 16-oz. paper containers (10 larvae/cup) and fed artificial diet either similar to that described by Leonard and Doane (1966) or which had been purchased from Bio-ServeTM Inc. Each cup was checked at least every 2 days and dead larvae and emerged parasites removed. All dead larvae were dissected to see if they were parasitized.

Pupal collections were made when pupation occurred, and a second collection made a week later. Each pupa was placed individually in a 1-oz. plastic cup and kept at room temperature (23°C). These were checked daily for parasite emergence. All pupae which did not yield a parasite or adult gypsy moth were dissected to see if parasites were present.

Identifications of the parasites were made using comparison specimens and/or keys supplied by taxonomists of the Systematic

Entomology Laboratory (SEL). Difficult specimens were sent to the SEL.

Results and Discussions

Five of the 10 established species of introduced parasites were found to be of significance at Hawk Mountain. These were *Ooencyrtus kuvanae* (Howard), an egg parasite; *Apanteles melanoscelus* (Ratzeburg), a parasite of small larvae; and *Blepharipa pratensis* (Meigen), *Parasetigena silvestris* (Robineau-Desvoidy), and *Compsilura concinnata* (Meigen), all parasites of large larvae. Two other introduced parasites, *Phobocampe disparis* Viereck and *Brachymeria intermedia* (Nees), were also recovered in small numbers during this study.

In the spring of 1974, a total of 73 egg masses were examined. The \bar{x} number of eggs/mass was 355 and the \bar{x} parasitism by *O. kuvanae* was 35.6 percent. In 1975, 21 egg masses were examined (\bar{x} eggs/mass = 412) and found to have a \bar{x} parasitism of 36.5 percent. Examination of 65 egg masses in 1976 showed a \bar{x} 442 egg/mass and a \bar{x}

parasitism of 31.2 percent. *O. kuvanae* is a small parasite and cannot reach the bottom layers of eggs in the mass (Howard and Fiske 1911). Thus, \bar{x} percent parasitism shown probably represents the maximum possible in egg masses of this size. Weseloh (1972) reported an average egg parasitism of 34 percent. The egg stage of the gypsy moth contains the greatest number of individuals. *O. kuvanae* attacks more than a third of these individuals, and is thus no doubt responsible for the death of more individual gypsy moths than any other parasite species.

Parasitism rates of the larvae by *A. melanoscelus* are shown in figure 1. Nearly 35 percent of the young larvae collected in mid-May 1974 have been attacked. Larvae collected during the following 4 weeks were also frequently parasitized. During the subsequent 2 years however, parasitism by this braconid peaked at about 7 percent. This parasite is very abundant in Europe (Crossman 1922) and has been reported to be quite effective in the U.S. (Reardon *et al.* 1973). Barbosa *et al.* (1975) found *A. melanoscelus* to be the third most dominant parasite recovered from two study sites in Massachusetts, but the actual numbers were small compared to the most frequently recovered parasite, *C. concinnata*.

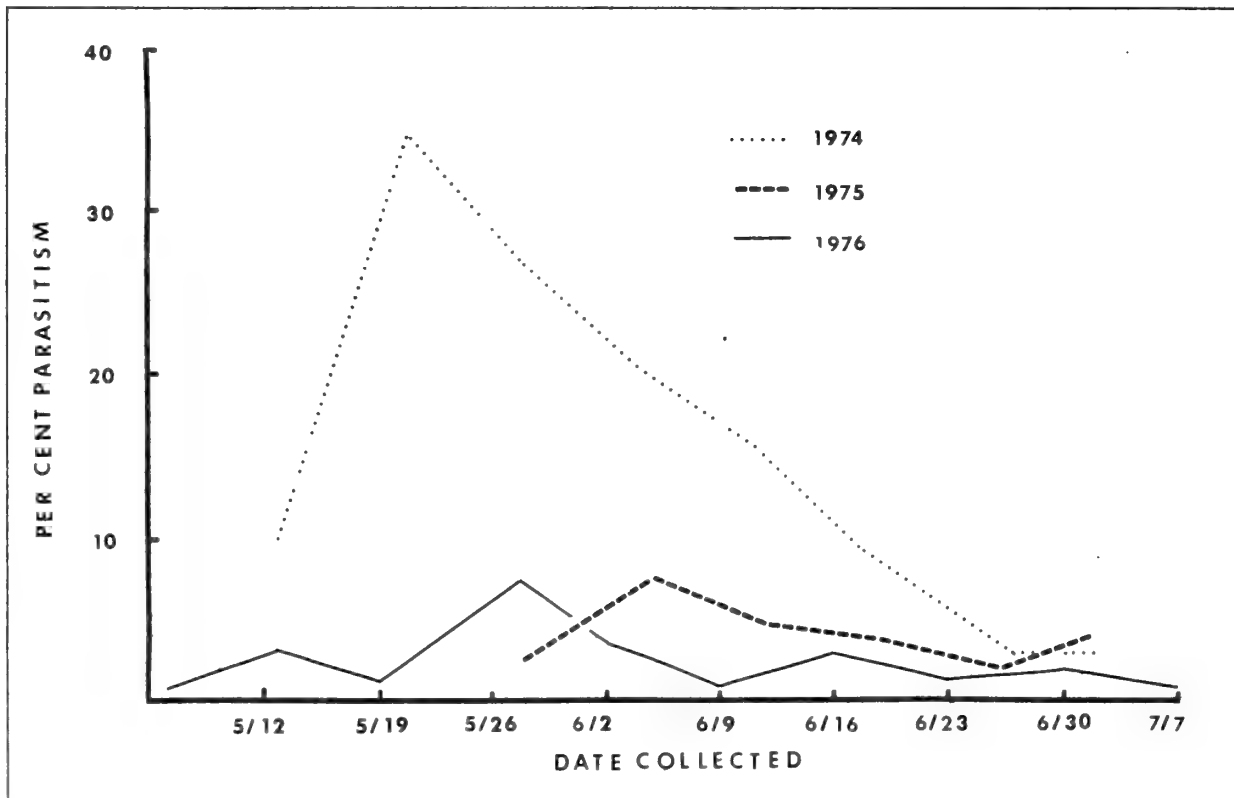


Figure 1.--Percent parasitism of gypsy moth larvae at Hawk Mountain by *Apanteles melanoscelus* in 1974, 1975, and 1976.

We do not know the reason for the decline of *A. melanoscelus* at Hawk Mountain. The collapse of the gypsy moth population in 1972 resulted in few gypsy moth larvae in 1973, and even fewer parasites, which no doubt severely curtailed the hyperparasites which plague *A. melanoscelus*. The lag time required for the hyperparasite population to recover may have allowed the high population of *A. melanoscelus* to appear in 1974.

The effectiveness of *A. melanoscelus* may be dependent on the stage of the host population cycle. Grimble (1976) released *A. melanoscelus* in large numbers in an attempt to reduce a rapidly increasing gypsy moth population. He found parasitism of larvae, both before and after releases, to be less than 2 percent. However, in the year following a gypsy moth population collapse in the release areas, the *A. melanoscelus* parasitized up to 20 percent of the larvae. The host population was then in a post-collapse stage somewhat equivalent to that at Hawk Mountain in 1974.

Parasitism by *C. concinnata* experienced a declining trend similar to that of *A. melanoscelus* (fig. 2). In 1974, it was the most abundant parasite of large larvae recovered. In mid-June, parasitism by this tachinid peaked at 44 percent. It was also the most abundant parasite found in the study by Barbosa *et al* (1975). An early evaluation of *C. concinnata* (Culver 1919) concluded that it was the most important tachinid parasite brought into the U.S. for combating the gypsy and brown-tail moths. Again, we do not know the reason for the decline of this parasite, but in 1976, out of 3398 larvae and pupae collected at Hawk Mountain, only four were parasitized by *C. concinnata*.

Parasitism by *P. silvestris* (fig. 3) and *B. pratensis* (fig. 4) was high during all 3 years of the study. These two tachinids were responsible for nearly all larval parasitism in 1975 and 1976 with *P. silvestris* being somewhat more abundant, parasitizing over 40 percent of the larvae and pupae collected

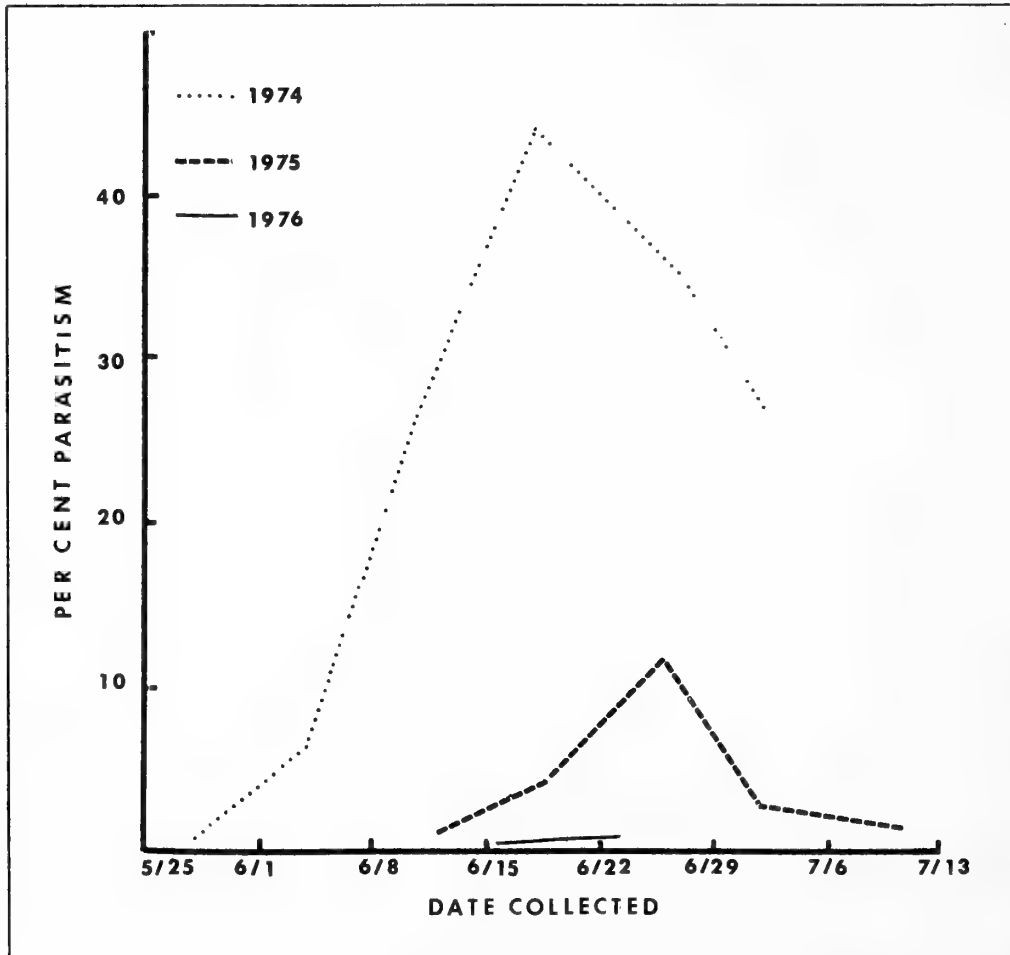


Figure 2.--Percent parasitism of gypsy moth larvae at Hawk Mountain by *Compsilura concinnata* in 1974, 1975, and 1976.

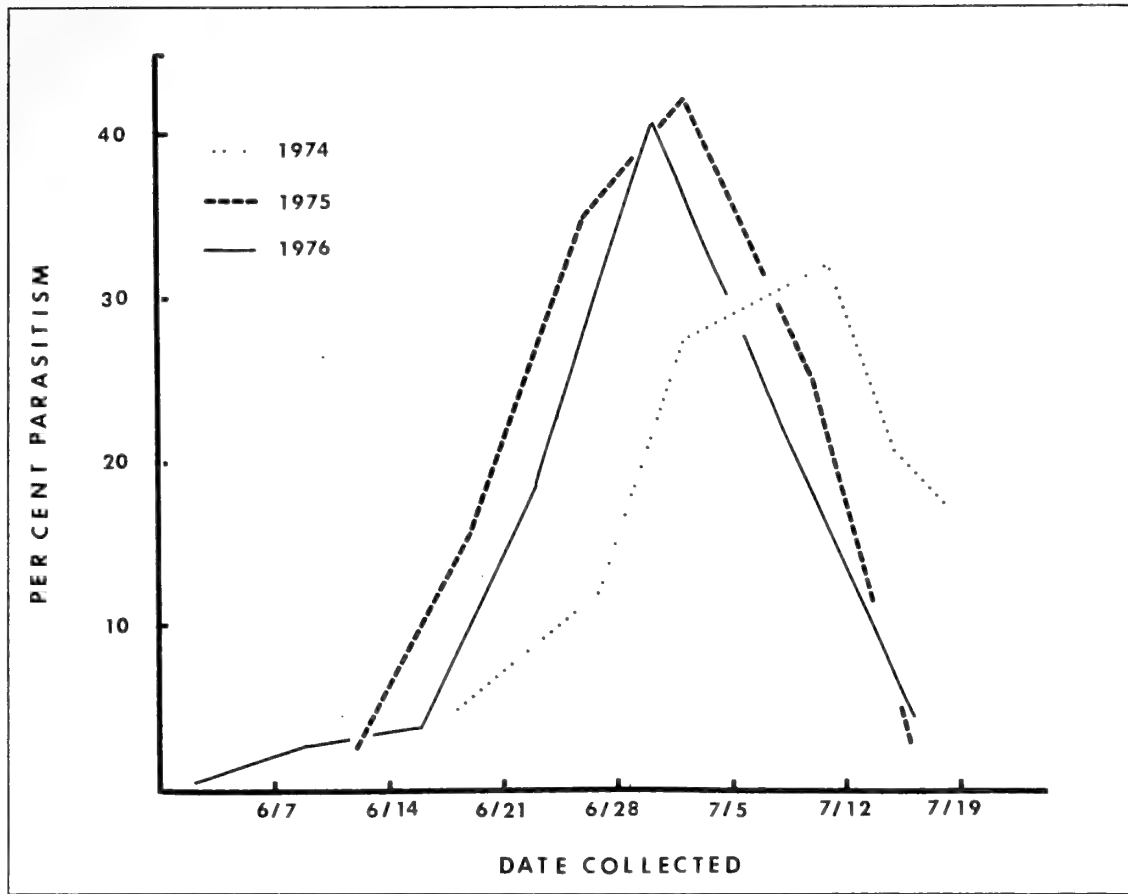


Figure 3.--Percent parasitism of gypsy moth larvae at Hawk Mountain by *Parasetigena silvestris* in 1974, 1975, and 1976.

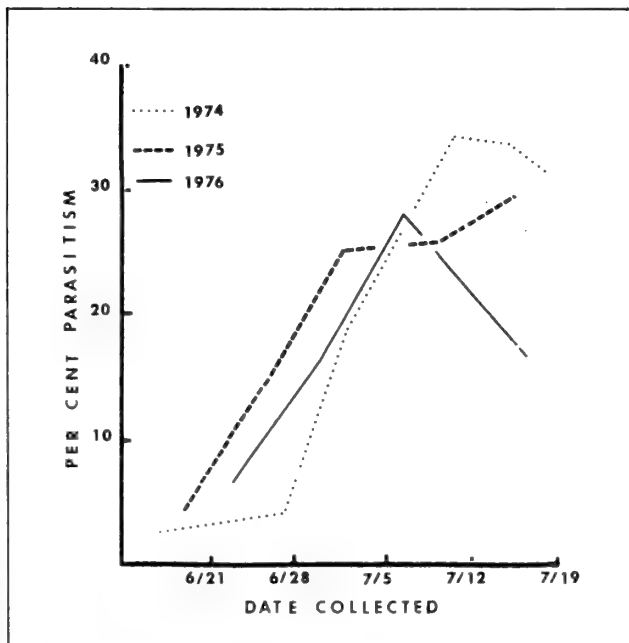


Figure 4.--Percent parasitism of gypsy moth larvae at Hawk Mountain by *Blepharipa pratensis* in 1974, 1975, and 1976.

when at its peak. The abundance of this parasite is in contrast to reports of some previous studies in the U.S. Barbosa *et al.* (1975) reported only 12 out of nearly 4000 larvae were parasitized by *P. silvestris*, and Tigner (1974) found that numbers of *P. silvestris* were always relatively small in sites studied in New York. In a much earlier study in Hungary, Crossman (1924) found that *P. silvestris* was by far the most abundant parasite of the late instars, killing about 40 percent of them.

Figure 5 shows the total parasitism of larvae and pupae at Hawk Mountain during each of the 3 years. With the exception of 1974, when *A. melanoscelus* was abundant, the gypsy moth larvae were relatively free of parasites during the first month after hatch. Parasitism of large larvae was much greater, peaking each year at about 70 percent of the larvae collected. Crossman (1924) also reported tachinid parasitism of the last two larval stages of an *L. dispar* population in Hungary to exceed 70 percent. This peak parasitism is occurring in large larvae nearing pupation. At that time, the larval population is at its

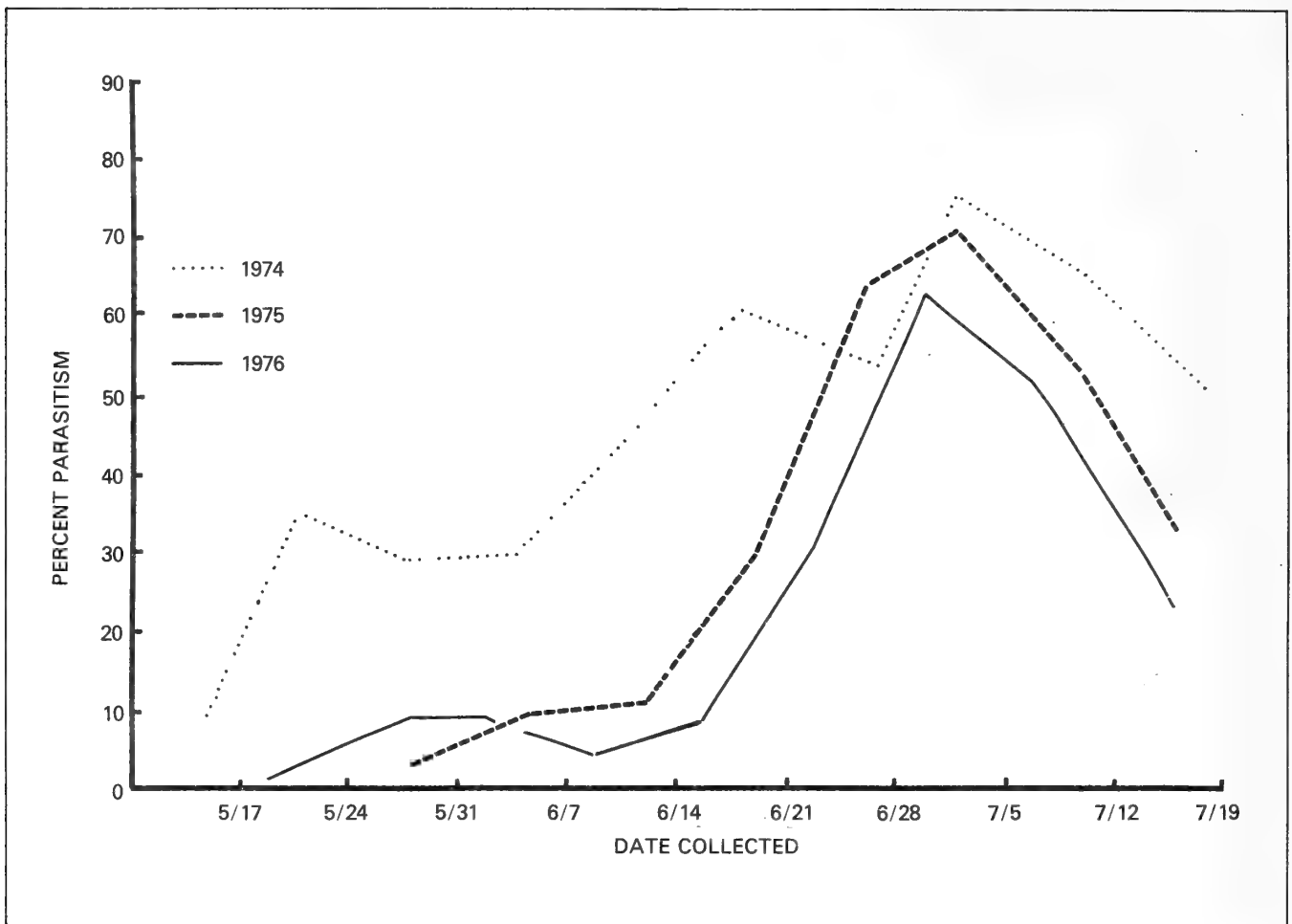


Figure 5.--Total percent parasitism of gypsy moth larvae at Hawk Mountain in 1974, 1975, and 1976.

lowest level because many of the various mortality factors affecting insects have taken their toll. Parasitism of 70 percent of the remaining larvae is then a primary factor in reducing the subsequent gypsy moth population. In addition, it should be noted that this amount of parasitism is conservative in that it represents parasitism only at its peak.

We recognize that even though egg and larval parasitism of the gypsy moth is high, it is not high enough to single-handedly cause a great reduction in the population of an insect with the biotic potential of the gypsy moth. Other regulating factors such as weather, predation, and disease, which vary from year to year, make their contributions to mortality. The gypsy moth population at Hawk Mountain has not increased over the 3 years of this study, and the data presented here clearly show that parasites are an important factor in maintaining this balance.

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V. NOVEL APPROACHES TO FOREST INSECT CONTROL

Exploiting Olfactory Interactions between Species of Scolytidae

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Insect chemical communication is not limited to pheromones, i.e., within-species messages. Insect receptors are exposed to a vast array of chemicals, many of which are produced by co-existing and competing species.

Interaction between the attractant pheromones of two sympatric species of Scolytidae in California, *Ips paraconfusus* Lanier and *I. pini* Say, was demonstrated by Birch and Wood (1975). The two species apparently do not respond to each other's pheromone, as evidenced by trap catches in the field (Lanier *et al.*, 1972), although both attack and infest ponderosa pine. This apparent lack of cross-attraction is a result of inhibition of each species by one or more components of the pheromone of the other. Thus, a bolt containing males (the pheromone-producing sex) of both species side-by-side attracted significantly fewer beetles of each species than did bolts containing males of either species alone.

The chemical basis for the inhibition of *I. pini* by *I. paraconfusus* is ipsenol (2-methyl-6-methylene-7-octen-4-ol) (table 1). Since ipsenol is only one of the three synergistic compounds required to elicit attraction by *I. paraconfusus* (Silverstein *et al.*, 1966), it could be used to inhibit *I. pini* from attacking susceptible host material without at the same time attracting *I. paraconfusus*.

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Table 1.--Response (trap catch) of *I. pini* to bolts containing male *I. pini* separately and together with male *I. paraconfusus* or ipsenol¹

Treatment	Response ²
50 ♂♂ <i>I. pini</i>	45.0 (15-90) a
50 ♂♂ <i>I. pini</i> +	2.8 (0-8) b
50 ♂♂ <i>I. paraconfusus</i>	
50 ♂♂ <i>I. pini</i> + ipsenol (1 mg/24 hr)	4.0 (0-15) b

¹ McCloud, California, 7-12 July 1973.

² Data from Birch and Wood, 1975.

Numbers are means (ranges in parentheses). Those figures followed by the same letter are not significantly different ($p < 0.05$). Sex ratios of responding beetles are not different between treatments ($\sigma:\varphi:1:1.8-1.9$).

This approach has been evaluated in N. California, where attack of *I. pini* on felled ponderosa pines baited with male *I. pini* was successfully prevented by eluting ipsenol around the trunk (Birch and Light 1977).

In 1975, we started to explore the interactions between five sympatric bark beetles in the southern United States to determine if a similar possibility for using inhibitors existed there. Our aims were: (1) To determine the sequence of attack and degree of competitive interaction between five species, (2) to investigate the role of olfaction as a mechanism of behavioral interaction between competing species, and (3) to determine how behavioral interactions might modify the pattern of host utilization between species. The species are: *Dendroctonus frontalis* (Zimmerman), *D. terebrans* (Oliver), *Ips avulsus* (Eichhoff), *I. calligraphus* (German), and *I. grandicollis* (Eichhoff).

They are being studied as they infest loblolly pine (*P. taeda*) in E. Texas.

D. terebrans is an ubiquitous species found in the base of most attacked trees. However, it is also usual to find three of the other species, and sometimes all four, attacking the same tree (Birch and Svihra, unpublished). From the outset, it thus seemed likely that the type of inhibitory pheromone interaction which maintains breeding distinction between *paraconfusus* and *I. pini*, was not prevalent in this group.

To study the sequence of attack and distribution of species, 28 recently attacked *P. taeda* were felled and sampled over a 12-month period (fig. 1). From concurrent field experiments on the rate of development of four species (excluding *D. terebrans*), we attempted to estimate the time of attack of each species (fig. 2). In spite of the range in development times, it is apparent that all species attack within a short time period. *D. frontalis* consistently appears to be the pioneering species followed closely by *I. avulsus* and *I. calligraphus*. *I. grandicollis* rarely attacks the trunks of standing trees (0.8 percent), but is more frequently found in the branches. Only two trees in the study were attacked solely by *D. frontalis*. A detailed analysis of arrival and distribution is currently underway (Birch, Svihra and Paine, in preparation).

To examine the role of olfaction in behavioral interactions between these species, we conducted two-way interaction tests following the methods of Birch and Wood (1975), and one test where all four species were forced to bore in the same bolt.

In contrast to the almost complete lack of cross-attraction between *I. paraconfusus* and *I. pini* in California, there is considerable cross-attraction between all four species tested in E. Texas. None of the *Ips* species appeared to influence the response of *D. frontalis*. Although *I. grandicollis* and *D. frontalis* are generally cross-attractive, the trap catch of *I. grandicollis* is reduced by 70 percent when males of *I. grandicollis* are forced to bore in the same log as females of *D. frontalis* (table 2). This corroborates Werner (1972), who determined that frontalin, one of the volatile components associated with *D. frontalis*, inhibited the response of *I. grandicollis* to its own pheromone in laboratory assays. In our field tests, frontalin also reduced the response of *I. grandicollis* to ipsenol.

I. grandicollis is also inhibited by the simultaneous presence of boring male

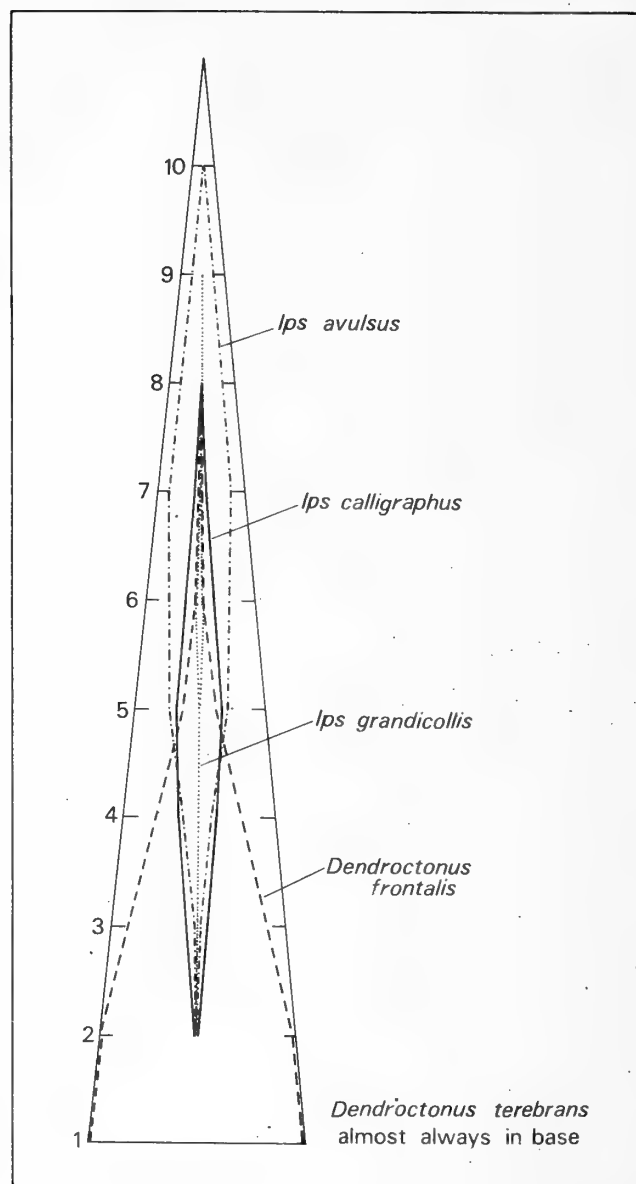


Figure 1.--Area of main trunk of *P. taeda* occupied by each of five bark beetle species in 28 sample trees. E. Texas, 1975-76. Numbers represent 30 cm sample sections taken at 1/10 intervals of the entire trunk.

I. calligraphus. This may explain the absence of *I. grandicollis* from trees containing *D. frontalis* and *I. calligraphus*, or its confinement to the branches, even when *I. grandicollis* is abundant and capable of attacking the same region of the host tree.

The high degree of cross-attraction and absence of mutual inhibition between the southern species reflects their different habitat utilization from the California *Ips* species. In California, suitable host mater-

ial for *Ips* (before the advent of lumbering) is rare, and, in the case of wind throw material and logging slash, it can be colonized by the beetles immediately after it is located. Consequently, there is a discernible advantage for the first colonizers to repel other species and to reserve the habitat.

In contrast, the southern *Ips* species often attack standing trees and successful colonization depends on overwhelming the tree's resistance mechanisms as rapidly as possible. Rapid attack, facilitated by pheromone cross-attraction, favors the survival of all attacking species. Inhibitive pheromone interactions must be looked for in delimiting areas of the trees that are attacked by each species.

There are no obvious pheromonal interactions that can be exploited as novel control strategies in the southern species studied. However, in studying interactions between species, we have been forced to sample entire attacked trees, to evaluate the involvement of several species of Scolytidae in the phenomenon of tree killing and colonization, and hence to recognize that "the southern pine beetle problem" is not synonymous with *D. frontalis*. It should also be possible to predict which species are most likely to use competitive inhibition from when and what host material they attack.

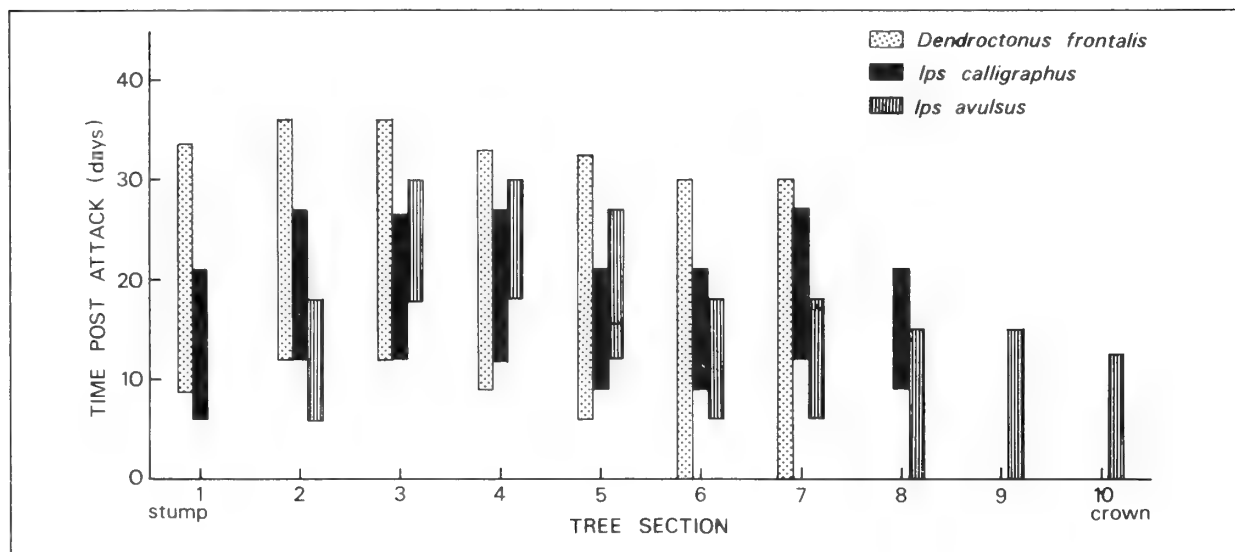


Figure 2.--Estimated time from first attack for each of three bark beetle species, calculated from the mean of the most advanced stage of development in each section at time of sampling, and from rate of development studies. E. Texas, 1975-76 (28 sample trees).

Table 2.--Response (trap catch) to bolts containing male *I. grandicollis* and female *D. frontalis* separately and together. E. Texas, May 11-16, 1976. Numbers are total catch from eight replications of each treatment. Sex ratios of responding beetles ($\sigma^{\circ}:\text{♀}$) in parentheses¹

Treatment	Response	
	<i>D. frontalis</i>	<i>I. grandicollis</i>
30 ♀♀ <i>D. frontalis</i>	68 ^a (1:0.5)	33 ^a (1:0.7)
30 ♂♂ <i>I. grandicollis</i>	3 ^b --	543 ^b (1:4.1)
30 ♀♀ <i>D. frontalis</i> +	29 ^a (1:0.6)	86 ^a (1:1.3)
30 ♂♂ <i>I. grandicollis</i>	6 ^b --	0 --
Control bolt, no beetles		

¹ Trap catches of one species are significantly different ($p < 0.05$) if followed by different letters; NSD if followed by the same letter (modified t -test).

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Development and Evaluation of Synthetic Inhibitors for Use
in Southern Pine Beetle Pest Management [27]
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Research on alternative methods of southern pine beetle control utilizing pheromones was begun in 1962 and resulted in the formulation of the attractant frontalure which consists of the insect-produced pheromone, frontalin, (Kinzer *et al.* 1969) and a compound from the pine host, α -pinene (Vite 1971).

In addition to attractants, other types of behavioral chemicals have been implicated as having a role in southern pine beetle attack behavior. The compounds, *endo*- and *exo*-brevicomin (Silverstein *et al.* 1968), the former found in small amounts in the beetles, were reported to reduce the attractiveness of frontalure when combined with the attractant mixture (Vite and Renwick 1971). Similarly, in 1974 and 1975 field tests using sticky traps, *endo*- and *exo*-brevicomin each reduced the attractiveness of frontalin plus loblolly turpentine (containing α -pinene) by approximately 50 percent (Payne *et al.* unpublished). When both compounds were combined with frontalin plus turpentine, the attractiveness was reduced approximately 80 percent.

These results prompted us to field-test the effect of the continual presence of both *endo*- and *exo*-brevicomin on the flight and landing activity of southern pine beetles in a natural infestation. We also evaluated a controlled-release formulation of the compounds that may have application in the operational deployment of these behavioral chemicals.

Methods and Materials

Study Area

The study site was located in a 500-tree, southern pine beetle infestation in a loblolly

pine-mixed hardwood forest in east Texas. Tests were conducted for 24 days, from October 9 to November 2, 1975.

Monitoring Flight and Landing Activity

Southern pine beetle activity was monitored with two types of unbaited traps, coated with Stickem Special[®]. Nine large wing traps (four vanes; 0.9 x 2.1 m/vane; 1/3 cm mesh; 3 1/2 m above ground) (Brown, personal communication) monitored distribution of the flying beetles (flight traps). The second trap, a single piece of hardware cloth (15 x 60 cm; 1/3 cm mesh), monitored landing activity (landing traps). Individual landing traps were nailed at 2 to 2.4 m to selected host trees in the infestation. All flight and landing traps were cleaned of southern pine beetles by 10:00 a.m. each day. The beetles were sexed and counted in the lab.

Compound Formulation and Handling

Endo- and *exo*-brevicomin were dispensed from Conrel[®] hollow-fiber controlled release strips prepared by FRL Corporation (fig. 1). Each dispenser consisted of 30 polyester fibers, each 3 cm x ca. 0.5 mm (length x ID). Alternate fibers contained *endo*- and *exo*-brevicomin, and each dispenser contained ca. 90 mg. of the compounds. The release rate per dispenser was determined cathetometrically as ca. 3.0 mg/day (1.5 mg/day per compound) at constant temperature (21° C) and humidity (65 percent). Each dispenser was estimated to provide ca. 30 days of continuous release.

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Each dispenser was halved (fig. 1) to provide ca. 15 days continuous release capacity. Thirty-six half dispensers were taped to index cards which were attached to host trees at selected release points in the plot. Purity was determined for one dispenser each, exposed under field conditions for 4, 8, or 12 days. These performance trial dispensers were exposed simultaneously with other dispensers in the same manner only 0.8 km from the plot. Compound purity was determined by GLC. Ten dispensers were measured at the end of the test as an estimate of the release rate under field conditions. All dispensers were stored at -60°C when not in use.

Experimental Design

Check and treatment tests were conducted sequentially in the same infestation. Check data were taken for 4 consecutive days without synthetic behavioral chemicals in the plot. Synthetic behavioral chemicals were then introduced and treatment data gathered for four consecutive dates, i.e., days 5 to 8 inclusive. At the beginning of the ninth day, the chemicals were removed and the second 4-day check period began. The procedure was repeated three times, providing three replicates of both the treatment and check tests.

The plot consisted of a 3 x 3 grid of adjacent 15 m square blocks (fig. 2) and had a total area of 0.202 ha. The grid did not encompass the entire infestation, but was limited to that area containing primarily freshly attacked and unattacked trees. The grid was repositioned after each complete treatment-check replicate to include the leading edge of the infestation. A flight trap was located at the center of each block within the grid. Sixteen landing traps were located at 15 m centers corresponding to the corners of each 15 m block. In addition, 18 landing traps were positioned at 7.5-m centers within the grid, with two traps per block, one each in the northeast and southwest corners.

A total of 36 dispensers was used in the plot during each treatment replicate. Four dispensers were positioned in each block on host trees at ca. 7.5 m centers. The dispensers were nailed to the north sides of the trees at 1.8-2.4 m above ground level. A landing trap was attached at two dispenser positions per block. The infestation was cruised daily and newly attached trees were flagged and mapped.

Landing trap catches for the treatment replicates were examined with T-test to check for possible positional effects due to trap and dispenser placement. Significant differences were not found at the 5 percent level. Therefore, landing trap catches were summed in subsequent analyses of variance tests.

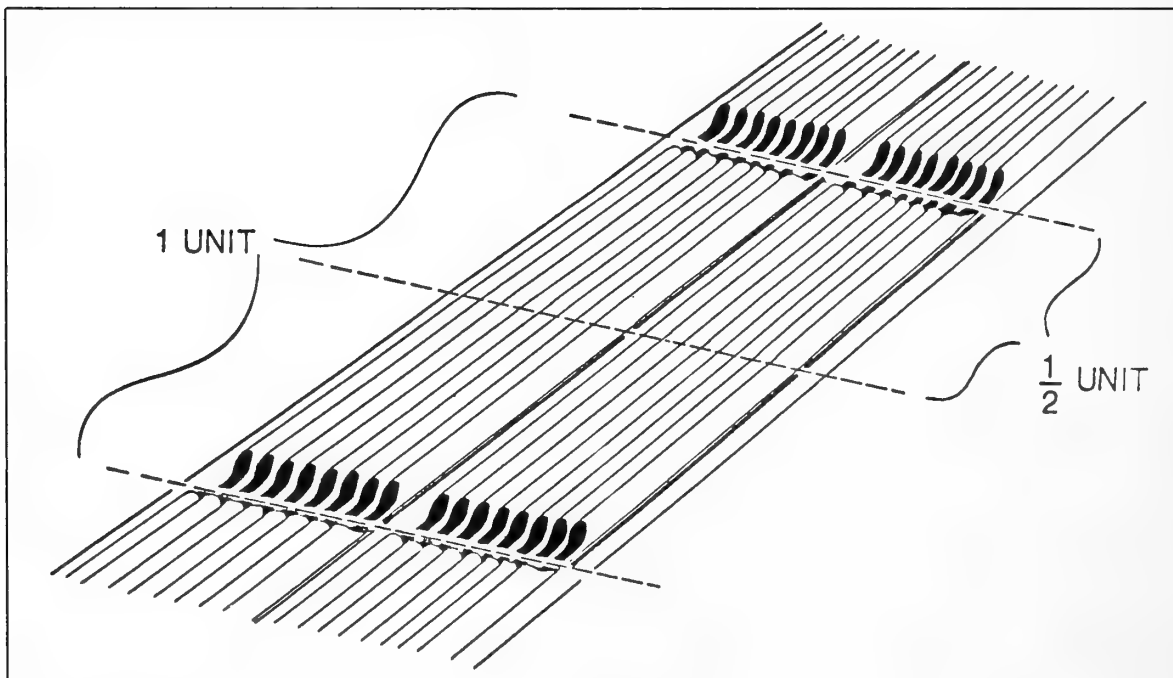


Figure 1.--Conrel[®] hollow-fiber dispenser unit.

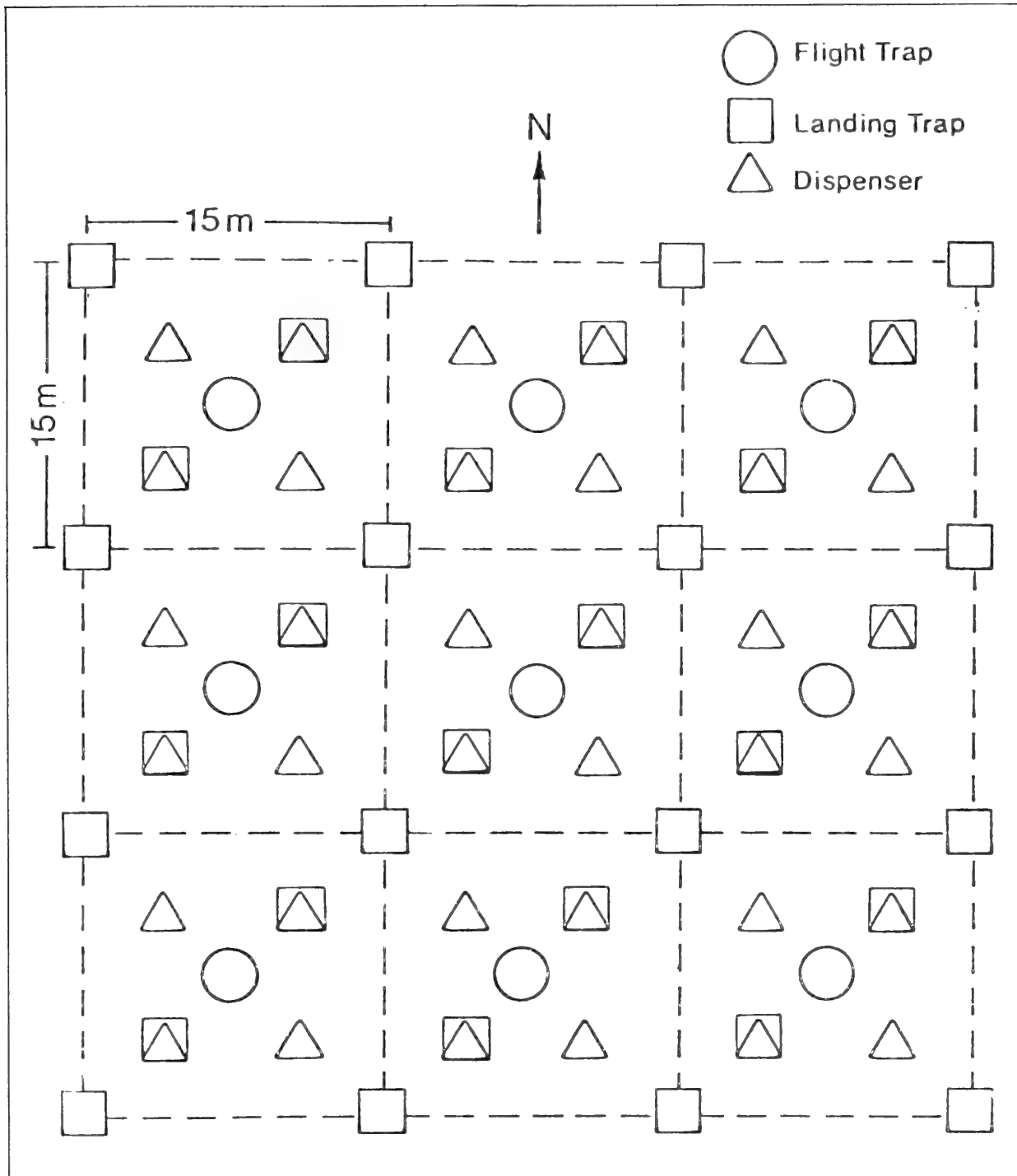


Figure 2.--Plot design for evaluation of effects of *endo*- and *exo*-brevicomin on flight and landing activity of southern pine beetle.

Results and Discussion

Mean total landing trap catch was significantly less during the period when *endo*- and *exo*-brevicomin were dispensed (treatment) as

compared to periods when the compounds were not present (check) (table 1). Landing activity was significantly less for treatment vs. check comparisons within each of the three replicates of the test (table 1). This reduction was significant for both sexes (table 2).

There was no significant difference in trap catch for treatment replicates between landing trap positions with dispensers and those without, or trap positions surrounded and not surrounded by dispensers.

Table 1.--Total and mean daily landing trap catches of southern pine beetles in synthetic *endo*- and *exo*-brevicomin-treated vs check tests for each 4-day replication

	Total	Numbers Mean ¹	Significance ²
Replicate 1			
Treatment	114	29 + 5.20	$\alpha \leq 0.005$
Check	458	115 + 30.24	
Replicate 2			
Treatment	438	110 + 30.14	$\alpha \leq 0.005$
Check	980	245 + 78.33	
Replicate 3			
Treatment	199	50 + 22.55	$\alpha \leq 0.005$
Check	1088	272 + 110.22	
Totals			
Treatment	751	63 + 15.43	$\alpha \leq 0.005$
Check	2526	211 + 46.46	

¹ Means \pm SE \bar{x} .
² Analysis of variance.

Table 2.--Total and mean daily landing trap catches of male and female southern pine beetles in synthetic *endo*- and *exo*-brevicomin-treated vs check tests

	Total	Numbers Mean ¹	Significance ²
Males			
Treatment	486	41 + 10.33	$\alpha \leq 0.001$
Check	1466	122 + 29.88	
Females			
Treatment	265	22.08 + 5.28	$\alpha \leq 0.001$
Check	1060	88.33 + 18.69	

¹ Means \pm SE \bar{x} for 3 replicates of 4 days each.
² T-test.

Flight trap catch showed no significant difference between treatment and check periods (table 3). There was, however, a significant difference in beetle catch due to plot location which indicated differences in flying beetle density among the three replicates.

The landing trap catches showed that the compound did inhibit or interrupt the landing

Table 3.--Total and mean daily flight trap catches of the southern pine beetle in synthetic *endo*- and *exo*-brevicomin-treated and check tests

	Total	Numbers Mean ¹	Significance ²
Treatment	24,528	2044 + 410	N.S.
Check	24,904	2075 + 755	

¹ Means \pm SE \bar{x} for 3 replicates of 4 days each.
² Analysis of variance.

of the southern pine beetle on host trees on an area basis, even though 16 of the 34 landing traps were not in direct association with the dispensers, and only 12 traps were surrounded by dispensers. Flight trap catches showed that intra-plot flight activity was not significantly affected by the presence of the compounds.

Compound purity remained >99 percent throughout the life of the units as determined by the analysis of the three field conditioned dispensers. The 10 dispensers measured at the end of the test showed a release rate of ca. 3.3 mg/day/dispenser or ca. 600 mg/ha/day (300 mg/ha/day/compound).

The results suggest the potential for development of these behavioral chemicals for southern pine beetle population control on an area basis. However, additional controlled field tests using different release rates and spacing, over extended periods of time, will be needed before these or any other behavioral chemicals can be adequately evaluated for use in southern pine beetle pest management. To our knowledge, the test reported here is the first demonstration of an area-wide influence of synthetic inhibitors on the landing behavior of the southern pine beetle in a natural infestation.

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214 Manipulating the Entomophagous-Mycetophagous Nematode, *Deladenus siricidicola*,
for Biological Control of the Woodwasp *Sirex noctilio* in Australia 1711

R. A. Bedding¹

Introduction

During the nineteenth century, a scarcity of endemic softwoods in Australia led to the introduction of various exotic pines. One of these, *Pinus radiata* D. Don (introduced in 1857), has flourished under Australian conditions and forms the bulk of commercial plantations which now exceed half a million hectares with an annual return approaching \$250 million; and the industry continues to expand rapidly. However, in 1952, *Sirex noctilio* F. was discovered in Tasmania, having been introduced probably via shipment of timber from New Zealand, and, within a decade, it has killed some 40 percent of radiata pine trees in a forest near Hobart. Thus, what is probably the most susceptible tree species (from California) was exposed to the most virulent siricid (originally from Europe) in the absence of any of its natural biological control agents.

When it was found in 1961 that *S. noctilio* had reached the mainland of Australia, the National Sirex Fund was established and one of the most extensive worldwide searches for natural enemies instituted. When initial attempts at eradication proved unsuccessful, a massive programme of "Search and Destroy" was carried out by the Forests Commission, Victoria, while a comprehensive research programme was instituted on various other aspects of control, including attractants, selective breeding of resistant trees, and the introduction of insect and nematode parasites. Despite all efforts to contain them, infestations of *S. noctilio* have spread steadily from the initial outbreak area near Melbourne over many thousands of hectares and are now only about 60 km from the vast coniferous forests surrounding Mt. Gambier (80,000 ha).

Following the discovery of nematodes infecting *S. noctilio* in New Zealand (Zondag 1962), CSIRO commenced investigations in 1965 into nematode parasites of various siricids and their parasitoids. The life history of these nematodes was shown by Bedding (1967, 1972a, and 1976b) to be an extraordinary one, involving profound female dimorphism associated with free-living mycetophagous and parasitic life cycles; seven species of *Deladenus* (Neotylenchidae) parasitic on siricids were described by Bedding (1968, 1974), and a detailed account of the use of *Deladenus siricidicola* Bedding in the biological control of *S. noctilio* was given by Bedding and Akhurst (1974).

Biology of S. noctilio

When female *S. noctilio* (usually several on one tree) drill into the wood of living pine trees to oviposit, they also insert toxic mucus and spores of the symbiotic fungus *Amylostereum areolatum* (Fr.) Boidin. The mucus and fungus kill susceptible trees (Coutts 1969) and *S. noctilio* larvae bore through and feed up on the fungus infected wood. Adult *S. noctilio*, which emerge 1 to 3 years after oviposition, are subject to predation by birds while immature stages are attacked by various ichneumonid, cynipid, and nematode parasites.

Biology of D. siricidicola

Shortly after investigations by CSIRO into the biology of *D. siricidicola* commenced, it was found that when sections of logs, from which all siricids had emerged 2 years previously, were placed in Baermann funnels, these yielded large numbers of nematode juveniles apparently identical to those from siricid hosts. This suggested that the nematodes were possibly feeding within the

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wood on siricid symbiotic fungus. Accordingly, juvenile nematodes removed aseptically from siricid hosts were placed onto cultures of the fungus *Amylostereum areolatum* growing on potato dextrose agar plates. The nematodes fed, matured, and laid eggs on the growing front of the fungus, and it was found that monoxenic cultures could be subcultured indefinitely without intervention of the siricid host; this, despite the fact that the original nematodes were fully parasitic in the host's haemocoel.

Parasitized *S. noctilio* larvae contain 1 to 100 cylindrical adult female nematodes, often bright green, 5 to 25 mm in length. The nematode's reproductive system remains undeveloped (about 0.5 mm in length) until the onset of host pupation and then expands rapidly, producing several thousand eggs which hatch within the parent; juvenile nematodes escape into the haemocoel of the host pupa and migrate into its reproductive organs entering the ovaries and eggs of female *S. noctilio* and testes of the male. Female *S. noctilio* are sterilized but since spermatozoa have already passed into the vesiculae seminales before invasion of the testes by juvenile nematodes, fertility in the male is unimpaired.

Parasitized female *S. noctilio* oviposit readily, implanting symbiotic fungus and eggs each containing up to 200 juvenile nematodes. These migrate from the hosts' eggs, feed on the developing fungus and grow into adult free-living nematodes (1.3 to 2.5 mm in length) which lay many eggs within the tracheids around *S. noctilio* oviposition holes. After the tree dies and as the wood dries out, the symbiotic fungus spreads throughout it and nematodes breed within tracheids, resin canals, and even beneath the bark. In these relatively monoxenic areas where fungus is sparse, juveniles develop only into mycetophagous forms, but in the vicinity of *S. noctilio* larvae (progeny of uninfected females attacking the same tree), where bacteria abound, juvenile nematodes may develop into adult infective females which are quite unlike the mycetophagous females. After insemination (by males morphologically identical to those fertilizing mycetophagous females, but having microspermatozoa), infectives penetrate *S. noctilio* larvae and grow up to a thousandfold in volume within a few weeks.

Because the relatively few nematodes introduced by parasitized *S. noctilio* can breed up through several generations so that they eventually occur in large numbers throughout the tree, they are able to achieve levels of parasitism often approaching 100 percent.

Utilizing *D. siricidicola* to Control *S. noctilio*

A thorough knowledge of the biology of this nematode has proven essential for its successful manipulation to control *S. noctilio* on a large scale. Aspects of greatest importance are its ability to sterilize female *S. noctilio*, the free-living cycle which can be utilized for establishing and maintaining cultures and mass rearing; its specificity to the symbiotic fungus (which restricts it to the environment of siricid larvae); and an inability to affect important insect parasitoids.

The importance of being able to culture readily and therefore store nematodes after removal from their hosts cannot be over-rated. Some 22,000 insects of 34 different species from 31 tree species and hundreds of localities in 28 countries have been dissected and nematodes cultured (Bedding and Akhurst, 1978). This has meant that an armory of many different species and strains of *Deladenus* could be stored for evaluation over several years. It has made possible the rapid screening of hundreds of cultures for new species by crossbreeding experiments on fungal culture (Akhurst 1975), and has enabled extensive testing to determine the effect of various nematode species and strains on insect parasitoids.

Evaluation

Important aims of evaluation have been to determine which species and strains will parasitize and sterilize *S. noctilio* without harming the insect parasitoids and which will be the most efficient parasites.

Of the seven species of nematodes isolated from siricids, it was soon found that only two could successfully utilize the fungus *A. areolatum* (as opposed to *A. chailletii* from most siricid species) and of these only *D. siricidicola* gave good parasitism of *S. noctilio* without harming the parasitoids. However, many strains of *D. siricidicola* were cultured from Europe, Japan, and New Zealand. After eliminating those few that parasitized but did not sterilize female *S. noctilio*, several strains were tested in comprehensive experiments to determine the relative levels of parasitism achieved. In these experiments, some strains were obviously inferior to others and were eliminated.

Since the nematode relies for its distribution on *S. noctilio* females, the extent to which parasitism affects flying and oviposition capabilities is important. Comprehensive experiments using flight mills, although they showed that flight capabilities were highly variable, indicated that there was no significant difference between parasitized and unparasitized *S. noctilio* of the same size (Bedding and Akhurst, in preparation). However, the largest females of *S. noctilio* flew up to 10 times as far as the smallest, and there is a relationship between decrease in size of *S. noctilio* and the presence of nematodes. Various strains of *D. siricidicola* differed in this respect and two strains which had little significant effect on the size of emerging *S. noctilio* as well as giving the highest levels of parasitism were therefore selected for liberation. Size is, of course, also important in relation to the number of eggs laid and the number of juvenile nematodes produced within the host.

Mass Rearing Nematodes

The use of host insects, which have a life cycle of from 1 to 3 years, to rear large numbers of nematodes for release would be both tedious and expensive; taking advantage of the nematodes free-living cycle is far more efficient. Although potato dextrose agar culture plates will each produce only a few thousand nematodes, these may be used to inoculate flasks containing autoclaved wheat (100g wheat and 150 ml water per 500 ml flask), which yield from 3 to 10 million juvenile nematodes within 4 to 6 weeks after incubation at 24°C (Bedding and Akhurst 1974). Since the contents of a single flask are sufficient to inoculate about 100 metres of *S. noctilio*-infested tree trunk, no attempts were made to scale up the process.

Inoculation of Trees

In order to introduce *D. siricidicola* to *S. noctilio* infestations, a number of easily accessible infested trees scattered throughout the infested area are usually felled and inoculated as they lie. Most female *S. noctilio* emerging from correctly inoculated trees are parasitized, and these oviposit on trees which usually are also attacked by wild unparasitized *S. noctilio*. The techniques used for inoculation are important; early methods resulted in low, variable, or no parasitism, but the methods currently used regularly produce over 99 percent parasitism.

Both preparation of inoculation holes and the medium used to inoculate are of critical importance: normal drilling of wood results in twisted tracheids which impede nematode entry; water suspensions are rapidly adsorbed leaving the nematodes to desiccate. Although chisel cuts proved fairly suitable for nematode entry a wad punch mounted to form a hammer has proven the most efficient tool for making inoculation holes and aerated 12 percent gelatin with 4000 nematodes per ml the most satisfactory medium (Bedding and Akhurst 1974). (Other gel media, such as agar, were much less satisfactory because nematodes failed to emigrate). A spacing of one inoculation per metre was found adequate to produce almost 100 percent parasitism. Heavier inoculation resulted in early competition between nematodes and *S. noctilio* larvae for fungal food and thus smaller *S. noctilio* females in the next generation.

Field Liberations

Experimental liberations in Tasmania (Bedding and Akhurst, in preparation) have indicated that *D. siricidicola* establishes, spreads, and achieves high levels of parasitism rapidly. In a 400 ha forest in Northern Tasmania with a low infestation of *S. noctilio*, some 50 parasitized females were allowed to emerge from a single point in one corner of the forest during 1970. By 1972, nematodes had spread to 37 percent of siricid infested trees in the whole forest and 92 percent in the compartment of liberation (over 70 percent of *S. noctilio* emerging from any nematode infested tree were parasitized). Two years later, over 70 percent of all trees contained nematodes (with over 90 percent of *S. noctilio* emerging from these parasitized), and the number of trees killed by *S. noctilio* in the next year dropped dramatically. As of this writing, no trees have been found that were killed in 1976. In a nearby forest of similar size, several thousand trees were killed annually by *S. noctilio*, but after a heavy inoculation program designed to achieve 10 percent parasitism during the first year (1972), over 90 percent parasitism resulted in the following year. The year after this, only 200 trees were killed by *S. noctilio*; the next year only five, and now no fresh *S. noctilio*-killed trees can be found either by ground or aerial survey. The nematode has also spread naturally to other nearby forests 2, 7, 8, and 13 kilometres away, and the level of parasitism is already high.

During 1970, some 1000 inoculated billets were sent from Tasmania to the Forest Commission, Victoria for distribution in *S. noctilio*-infested areas. Since then, hundreds of millions of nematodes in oxygenated water have been sent to Victoria and, in a major program of liberation by the Forests Commission (which at one stage had 10 mobile crews searching for and inoculating trees in infested forests, nematodes have been liberated throughout most of the *S. noctilio*-infested areas in Victoria. *D. siricidicola* is now established over most of Victoria, and high levels of parasitism are already in evidence.

The program of nematode control is complemented by and coordinated with a similar one for insect parasitoids (Taylor 1976), and it is expected that the manipulation of both nematodes and parasitoids will become standard forestry practice. In this respect, nematodes are most easily and cheaply reared in the laboratory, but both kinds of agents can usually also be introduced to new *S. noctilio* infestations by transfer of infected billets from one forest to another. Comprehensive evaluation experiments are being continued in both Tasmania and Victoria, but it will be many years before the full impact of biological agents can be assessed.

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Reproductive Incompatibility in *Pityogenes chalcographus* (L.) c 7/1

by Erwin Führer¹

Introduction

It is well known that speciation within an animal species can proceed without conspicuous changes in morphology and biology. Its striking indication is reproductive incompatibility between allopatric populations of the same species. *Culex pipiens* is a well studied example (Laven 1967) and *Rhagoletis cerasi*, the European cherry fruit fly, is becoming a second one (Russ, personal communication). In both insects, incompatibility represents the basis for a novel approach to genetic control concepts.

A kind of intraspecific incompatibility in bark beetles already has been recorded for *Ips grandicollis* Eichhoff and *Dendroctonus pseudotsugae* Hopkins. Crossing beetles of different origin result in reduced progeny (Lanier 1970; Johnson and Furniss 1967).

At Göttingen, a crossing program between different populations of the polygamous scolytid *Pityogenes chalcographus* (L.)² has been started. Its main host tree is the Norway spruce. Material was taken from sites in Central and Northern Europe, considering the natural distribution pattern of the host tree. This natural distribution is characterized by some disjunctions, providing a certain degree of geographical isolation of the inhabiting *Pityogenes* populations for many thousand years. The *Pityogenes* beetles of different origin were bred separately in the laboratory, in this way supplying the material needed for the crossing experiments.

The first step was to compare egg production and egg mortality for pairings between sympatric and allopatric partners, respectively. The numbers of emerged larvae per fe-

male serve as a measure of fertility. Larval mortality was initially disregarded.

Results and Discussion

Ten different strains of *Pityogenes chalcographus*, coming from Finland, Norway, Denmark, Germany, and Austria, were integrated into the first crossing program. Reliable data from 57 of 100 possible combinations are available now, each representing the results from 20 to more than 100 pairings (Führer 1976).

Essential to all further interpretations is the fact that, in the sympatric experiments, fertility of the different strains was on a comparable and high level. From this is concluded that the breeding conditions and the substrate in the laboratory were suitable to the beetles regardless of origin. The range of 30 to 45 larvae per female is considered average for the fertility of normally compatible parents. Significant downward deviations from this category may be considered as indications of incompatibility.

Pairings of allopatric parents frequently result in reduced fertility. In the combinations tested, the average number of larvae per female ranges from 1.8 to 47.0. Table 1 demonstrates the effects of pairing females of the South German strain No. 8 with males of the complete series of strains arranged from south to north. Similar to this, but not as pronounced, are the results of pairing females of the Alpine strain No. 10 with males of the others. These results give evidence of reproductive incompatibility between allopatric populations of *Pityogenes chalcographus*.

Incompatibility is most pronounced between females from South Germany and Austria, respectively, and males from Scandinavia. There is great variation as to its degree, and, for the present, the incompatibility pattern in Europe cannot yet be completely understood.

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² Coleoptera: Scolytidae.

Table 1.--Fertility of *Pityogenes* females, strain No. 8, after pairing with males of different strains¹

♀	♂	r	Eggs/♀ av.	Egg mort. percent	Larvae/♀ av.
8	8	63	43.1	2.3	42.1
8	10	40	20.2 ***	5.8 ***	19.0 ***
8	9	32	39.9	6.0 ***	37.5
8	7	58	20.9 ***	7.5 ***	19.3 ***
8	6	62	29.2 **	9.2 ***	26.5 ***
8	5	56	32.4 *	8.4 ***	29.6 *
8	4	29	16.3 ***	15.2 ***	13.8 ***
8	3	17	4.1 ***	40.0 ***	2.5 ***
8	2	29	2.1 ***	16.1 ***	1.8 ***
8	1	36	5.0 ***	40.8 ***	2.9 ***

¹ Strain No: 1 = Finland, 2 = Finland, 3 = Norway, 4 = Denmark, 5 = North Germany, 6 = Central Germany, 7 = West Germany, 8 = South Germany, 9 = South Germany, 10 = Austria.

Significance levels: * = .05, ** = .01, *** = .001.

Incompatibility, expressed by the average number of larvae per female, probably derives from physiological and genetic reasons. Egg mortality is rather low; in females, which have mated with sympatric males, it ranges from 1 to 3 percent. In crossings between allopatric parents, egg mortality usually is increased significantly up to 10 or 20 percent, only exceptionally up to 40 percent (table 1). Embryonic stages presumably die for cytogenetic reasons.

Much more pronounced than egg mortality is the decrease of egg numbers. Egg production usually is at its maximum, when pairings have occurred between sympatric parents. Crossing of allopatric parents, however, results in more or less reduced egg production. This effect can be very strong. Average egg numbers 50 or even 95 percent below the normal levels frequently were recorded (table 1).

An important point is the problem of mating between incompatible partners. Since extensive tests did not indicate parthenogenesis in *Pityogenes*, mating doubtlessly occurred, because females laid fertile eggs. Nearly unproductive females were dissected and sperm could be observed in the spermatheca. Moreover, females mated only once produced up to 50 fertile eggs, if the males were of the same strain. From these results, it is concluded that the reason for the decrease in egg numbers must be other than a mating barrier.

The decrease of egg production, therefore, is attributed to a physiological dis-

cordance. A phenomenon like this can be understood, if a stimulation of egg maturation by sperm transfer or by paragonial substances of the male is implied. On this assumption, biochemical differences specific to the various strains could be responsible for insufficient stimulating effects of mating.

Evidence of reproductive incompatibility within a bark beetle species raises many new biological and genetic questions. Furthermore, it stimulates reflections, such as whether this fact opens new aspects to bark beetle control. Certainly, research has only begun. Nevertheless, some ideas should be mentioned in respect to the use of incompatibility in bark beetle control.

Practical use of reproductive incompatibility would be restricted to preventive measures against bark beetle outbreaks. The extent of successful primary attack on living trees depends on the beetle's population level, which usually increases after excessive damage by storm, snow, or fire. The opportunity for extensive multiplication lasts for a short period only. The population level attainable during this time is determined by the amount of brood material as well as by the rate of multiplication per generation.

The increase of a mixed population, consisting of two incompatible strains, theoretically must be delayed, because progeny would be produced by pairings of compatible partners only. Provided that incompatibility is total and bidirectional, and that the chance of mating with an incompatible partner is 50 percent, the multiplication rate would fall by half. It is presumed that an effect like this would be sufficient either to prevent extensive epizootics in many cases or to improve the chances of control success. A remarkable advantage of this kind of prevention would be its continuous effect, because the coexisting strains would propagate independently on a reduced rate, and loss of progeny by incompatibility would happen generation by generation.

One must remember that this model is very much simplified and theoretical. The principle of incompatibility as a basis of preventive measures has a chance of success, only if a number of conditions is given, such as: incompatibility must be sufficiently high and bidirectional; its reasons must be well understood; the incompatible strains must correspond bionomically, ethologically, and ecologically; the properties of hybrids between partially incompatible partners have to be investigated critically in regard to epidemiology. Hence, many important questions need investigation. These studies will establish only the basis for an estimation of how far

reproductive incompatibility is appropriate for prevention of bark beetle outbreaks.

There are good reasons to expect incompatibility also in other forest pests with wide areas of distribution. Moreover, the results obtained in *Pityogenes chalcographus* confirm the actuality of the problem of strain evolution in forest pests.

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Arthur Retnakaran¹

The introduction of chlorinated hydrocarbons as insecticides resulted in unprecedented control of insect vectors of human disease and agricultural insect pests. The undesirable side effects of one of these insecticides, DDT, became apparent in the early sixties, nearly 20 years after it was first introduced. The main reasons for the environmental hazard of these compounds were their broad spectrum of activity, persistence in the environment, and characteristics for biological concentration in the environment (Pimentel 1971). In forest situations, the ecological concern becomes even more acute than in agricultural spraying where the areas to be treated are well contained. Forest spraying usually covers large areas. In Canada, for instance, it has been a practice to spray over 2 1/2 million acres every year to control the spruce budworm, *Choristoneura fumiferana* (Angus 1973). Repeated spraying of DDT in the province of New Brunswick during 1954-56 resulted in significant reduction in woodcock populations, and young salmon were almost eliminated in the Miramichi River. Similar spray operations in British Columbia resulted in almost total mortality of the Coho salmon (O'Brien 1967).

The solution to these problems is to find candidate compounds that are selective in their action, affecting the target insect pest with very little impact on non-target species. The ideal, of course, is to have species-specific control agents. Unfortunately, economic constraints make a compound attractive only when it is active on several key insect pests. Development of a compound that will act only on a specific insect pest will not be economically attractive to industry. Thus, the returns often dictate the type of compound being developed. Fortunately, in recent years, the widespread environmental concern has forced

scientists to look for more selective insecticides even if at higher cost. In the words of O'Brien (1967): "It is not unreasonable that to enjoy the advantages of cheap agricultural commodities and undamaged flowers and trees, along with full streams and a noisy spring, one should pay a little more."

One of the approaches toward such a goal is the development of the so-called Insect Growth Regulators (IGR). Basically, they are slow-acting chemicals that adversely affect the growth and development of insects. There are two groups of such compounds, Juvenile Hormone Analogs (JHA) and Inhibitors of Chitin Biosynthesis (ICB).

The chemistry and physiology of insect juvenile hormones and the potential of JHA in insect control have been extensively reviewed (Burdette 1974, Gilbert 1976, Menn and Beroza 1972, Slama *et al.* 1974, Staal 1975). There are three possible ways in which JHA can be used for insect control. First is the ovicidal action of many such compounds. When applied to the eggs, the embryo ceases to develop beyond a certain stage (Retnakaran 1970, Riddiford and Williams 1967). In our laboratory, we tested several JHA for ovicidal activity against the spruce budworm (table 1). Compounds such as ZR-777 and ZR-619 showed good activity when the egg masses were treated topically (table 2). When JHA were sprayed on potted balsam fir and white spruce trees containing eggs, very little ovicidal activity was observed. Since the egg masses are laid on the undersurface of the needles, the compounds failed to reach the eggs. Whether JHA can be used as ovicides against other forest insect pests remains to be tested.

The second type of control with JHA is possible in insects that go into diapause as adults. It has been shown that diapause in adults occurs as a result of a lack of juvenile hormone (de Wilde and de Boer 1961). When JHA is applied to such insects, it induces diapause development. The white pine weevil, *Pissodes strobi*, has an obligatory diapause (Harmon and Kulman 1967). When the weevils

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Table 1.--Juvenile Hormone Analogs (JHA) tested for ovicidal activity against the spruce budworm


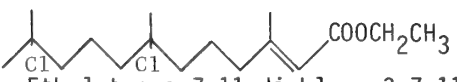

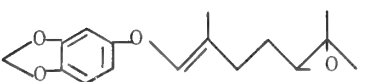
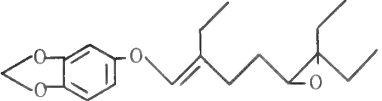
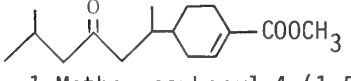
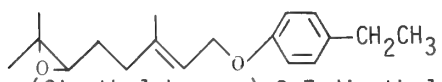
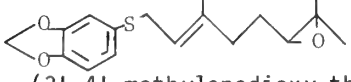
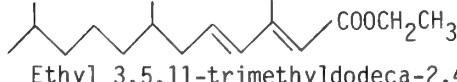



Formula	Chemical name
 <p>Methyl rac-10, 11-epoxy-7-ethyl-3,11-cis-trideca-2-trans,6-trans-einoate.</p>	Juvenile hormone (Hoffmann-La Roche, Nutley, N.J.)
 <p>Ethyl trans-7-11-dichloro-3,7,11-trimethyl-2-dodecenoate.</p>	Dichloro analog (Hoffman-La Roche)
 <p>1-Methoxy-3,7,11-trimethyl-2-cis/trans,6-trans,10-dodecatriene.</p>	Farnesyl methyl ether Hoffman-La Roche)
 <p>3,7-Dimethyl-6,7-epoxy,octa2-enol-3'4', methylene dioxy phenyl ether.</p>	Methyl-aromatic terpenoid ether (Dr. W.S. Bowers, Cornell Univ., Geneva)
 <p>3,7-Dimethyl-6,7-epoxy,octa2-enol-3'4', methylene dioxy phenyl ether.</p>	Ethyl-aromatic terpenoid ether (Dr. W.S. Bowers)
 <p>1-Methoxycarbonyl-4-(1,5-dimethyl-3-oxohexyl) cyclohex-1-ene.</p>	Juvabione (Hoffman-La Roche)
 <p>(3'-ethylphenoxy)-3,7-dimethyl-6,7-epoxyoct-2-ene Exoxidized aromatic ether of geraniol</p>	Stauffer Compound (Stauffer Richmond, Calif.)
 <p>(3',4'-methylenedioxy-thiophenoxy)-3,7, dimethyl 6,7-epoxyoct-2-ene.</p>	Thioether (Eco-Control, Cambridge, Mass.)
 <p>Ethyl 3,5,11-trimethyldodeca-2,4-dienoate.</p>	ZR-512 (Zoecon, Palo Alto, Calif.)

Table 1. (Continued)

Formula	Chemical name
 <p data-bbox="66 367 679 419">Isopropyl 11-methoxy-3,7,11-trimethyldodeca-2,4-dienoate.</p>	ZR-515 (Zoecon)
 <p data-bbox="66 530 668 582">Ethyl 11-methoxy-3,7,11-trimethyldodeca-2,4-dienethiolate.</p>	ZR-619 (Zoecon)
 <p data-bbox="66 691 733 721">Prop-2-ynyl,3,7,11-trimethyldodeca-2,4-dienoate.</p>	ZR-777 (Zoecon)

are treated with JHA before they go into diapause, the insect becomes sexually mature and the fat reserves are mobilized (table 3). They no longer have the ability to overwinter (Retnakaran 1974). Although these effects have been shown in the laboratory, field evaluation remains to be tested.

The third type of control with JHA is possible during the last larval instar. During this stage, the titer of juvenile hormone drops precipitously. If JHA is applied to the last larval instar, it moults abnormally into a larval-pupal intermediate or a supernumerary larva and dies. It becomes intuitively obvious that when the adult is the damaging stage, morphogenetic control by applying JHA to the last larval instar will be very effective. In cases like that of the spruce budworm, where the damage is caused by larval feeding, controlling the last larval instar will not provide foliage protection in the year of application, but during the subsequent year the trees will be protected from defoliation provided immigration of moths is not significant. Although many JHA showed good activity against the spruce budworm in the laboratory, field evaluation indicated that high concentrations are required for control (Retnakaran 1973, Retnakaran *et al.* 1977). Two compounds, RO-10 3108 (Hoffman La Roche) and ZR-515 (Zoecon), were ineffective at 5 oz/acre. The former compound at 8.5 oz/acre gave 92 percent control (table 4, Granett 1977). The eastern hemlock looper, *Lambdina fiscellaria fiscellaria*, unlike the spruce budworm, is sensitive to JHA at lower concen-

trations. At 3 oz/acre, ZR-515 gave 97 percent control (table 5, Retnakaran *et al.* 1973).

The IGR that act as inhibitors of chitin biosynthesis (ICB) are less selective than JHA. One such compound is Dimilin (Thompson-Hayward, Kansas City), and it has been extensively studied. It appears to inhibit chitin biosynthesis at the terminal step and manifests its effect during the moult (Post and Vincent 1973, Wellinga *et al.* 1973). Dimilin has been tested against three forest species: spruce budworm, forest tent caterpillar, (*Malacosoma disstria*), and the gypsy moth, (*Lymantria dispar*). As with JHA, the spruce budworm was the most refractory species among the three. When the last larval instar was sprayed at 2 oz/acre, over 70 percent reduction in population was achieved (Retnakaran *et al.* 1977). Dimilin was less effective when earlier instars were treated (Granett and Retnakaran 1977, Retnakaran and Smith 1975). Dimilin was effective at less than 1 oz/acre on the gypsy moth (Granett and Dunbar 1974). When forest tent caterpillar infestations were treated with a 1 percent solution of Dimilin using a mist blower, the effect was dramatic (table 6, Retnakaran *et al.* 1976). Total foliage protection was achieved.

Recently, another ICB (EL-494, Elanco Ltd., Indianapolis) has been introduced. Laboratory and greenhouse testing has indicated that this compound is more effective on the spruce budworm than Dimilin. Field testing is currently in progress.

Table 2.--Ovicidal activity of some JHA on spruce budworm (egg masses were treated with the candidate compound in acetone)

Treatment No.	Amount, $\mu\text{g}/\mu\text{l}/$ egg mass	Number treated	Number hatched	Percent hatch
1) Control (no treatment)	0	371	353	95
2) Control (acetone)	0	350	322	92
3) Hydrochlorination reaction mixture (Law's)	2	240	228	95
	20	252	38	15
	150	231	0	0
4) "Cecropia" juvenile hormone	10	147	97	66
	25	137	18	13
	50	153	0	0
5) Dichloro analogue	25	147	8	5
	50	141	0	0
6) Farnesyl methyl ether	25	141	31	22
	50	157	17	11
	100	139	0	0
7) Methyl aromatic terpenoid ether	25	213	59	28
	50	210	27	13
	100	199	12	6
8) Ethyl aromatic terpenoid ether	25	207	32	15
	50	191	17	9
	100	186	0	0
9) Juvabione	57	139	7	5
	114	185	0	0
10) Stauffer compound	5	421	97	23
	10	401	36	9
	20	449	26	6
11) ZR-512	5	335	24	7
	10	315	5	2
	50	300	1	0
12) ZR-515	5	190	37	20
	10	345	12	4
	50	360	2	1
13) Thioether	10	380	105	28
	50	313	8	3
	100	392	4	1
14) ZR-619	10	250	1	1
	20	300	0	0
15) ZR-777	5	233	27	1
	10	200	0	0

The toxicology of IGR indicates that they are environmentally less hazardous than the broad spectrum insecticides. JHA appear to be environmentally safer than ICB. To illustrate the point, the toxicology of ZR-515 (JHA) and EL-494 (ICB) as provided by the respective manufacturers is summarized in tables 7 and 8. A more detailed account is given by Wright (1976).

The prognosis for use of IGR in forest insect control appears good. The ICB, because of their activity, will probably come into use before the JHA although a more active JHA would be environmentally preferable. A new class of compounds that show anti-JHA activity is being actively developed (Bowers 1976). The IGR on hand and the ones that are being developed will certainly reduce our dependence on broad spectrum insecticides in the years to come.

Table 3.--Effects of some juvenile hormone analogs on adult white pine weevils in the pre-diapause state

Analog	Dosage (μg in 1 μl acetone)	No. treated		No. alive on day 20		Development of:		
		σ	♀	σ	♀	Testes	Ovaries	Fat bodies (σ and ♀)
-	(acetone con- trol)	4	6	3	6	+	-	+++
ZR-515	10	3	7	1	3	+	++	-
ZR-515	100	5	5	3	3	+	+++	-
ZR-777	10	5	5	2	2	+	++	-
ZR-777	100	6	4	0	1	(-)	+++	-

Note: + to +++ indicates degrees of development; - indicates no development.

Table 4.--Spruce budworm pre-adult population control in plots treated with RO 10-3108/018 on 18 June 1976, in Maine

Plot no.	Rate (aI/acre)	Assay date	Total pre-spray counts (in branches)		Total post-spray counts	Survival percent	Control ¹ percent
7	4.4 oz	29 June	251	(20)	56	22	0
		9 July	413	(40)	95	23	0
8	8.5 oz	29 June	324	(20)	21	6.5	63
		9 July	162	(10)	2	1.2	92
	check	29 June	418	(20)	74	18	
		9 July	418	(20)	60	15	

¹ Percent control = $\frac{\text{Percent survival in check minus percent survival treated}}{\text{percent survival in check}} \times 100.$

Table 5.--Effect of ZR-515 treatment of eastern hemlock looper larvae in Anticosti Island on July 19, 1973

Plot	Pupae/burlap trap	Entomo- phthora	Parasitized	Total healthy pupae	Healthy pupae/ tree	Control Percent
Control (airport)	1984/10	226	139	1619	161.9	0
^A (3 oz/2 gal/acre)	86/15	10	4	72	4.8	97
^B (1 oz/2 gal/acre)	156/15	18	3	135	9.0	94
^C (0.25 oz/2 gal/acre)	593/15	72	30	491	32.7	80

Table 6.--Effect of Dimilin on first instar forest tent caterpillar

Plot	Sample values	No. trees sampled	Tree height (M)	No. larvae/tree	Hatched egg bands/tree	Defoliation	Larvae in underbrush around each tree
Control	\bar{x}	10	5.5	56.0	>30	Total	Numerous
	Range	-	3.6 - 7.5	10 - 118	all >30	All total	All numerous
Treatment	\bar{x}	10	6.1	0	>30	Nil	Nil
	Range	-	3.6 - 9.0	0	all >30	All nil	All nil

Table 7.--Toxicological properties of ZR-515 (Zoecon Ltd.)

Test	Effect
Acute oral toxicity	LD ₅₀ >34,500 mg/kg
Rat	No deaths at highest single dose which could be administered.
Dog	LD ₅₀ = 5000-10,000 mg/kg
Subacute oral toxicity (dog and rat)	No toxic effect
5000 ppm for 90 days	No mortality, no irreversible deleterious effects
5000 ppm for 90 days	
Primary skin and eye irritation (rabbit)	Nonirritating
Acute dermal toxicity (rabbit)	LD ₅₀ = 3000-10,000 mg/kg
Subacute dermal toxicity (rabbit)	
For 21 days at 400 mg/kg	No abnormal or toxic effects
Acute aerosol inhalation	
Rat and guinea pig	LD ₅₀ >210 mg/l.
Subacute inhalation (rat)	
At 20 mg/l. for 21 days	No toxic effects
Three generation reproduction	
Rats fed 2500 ppm	No toxic or reproductive effects, including mortality, pregnancy and fertility rates, food consumption values, length of gestation periods, offspring viability at parturition, offspring survival, litter survival, or sex ratios.
Teratology studies (rat, rabbit)	
Rat, 1000 mg/kg to pregnant animals	No teratogenic effects
Rabbit, 500 mg/kg to pregnant animals	No teratogenic effects
Dominant lethal mutagenicity (rat)	
Single dose, 2000 mg/kg	No lethal mutagenic effects
Static fish toxicity studies	
Blue gill	TL ₅₀ = 4.62 ppm
trout	TL ₅₀ = 4.39 ppm; TL ₅₀ (aerated water) = 106 ppm
Channel catfish	TL ₅₀ = 100 ppm
Coho salmon	TL ₅₀ = 32 ppm
Crustacean toxicity studies	
Crayfish, freshwater shrimp	LC ₅₀ = 100 ppm
White and pink shrimp	LC ₅₀ = 100 ppm
Subacute oral feeding studies	
Mallard duck	LC ₅₀ >10,000 ppm
Bobwhite quail	LC ₅₀ = 10,000 ppm
Chicken	LC ₅₀ = 4640 ppm
Reproduction studies	
Bobwhite quail (30 ppm continuous feeding)	No effect
Mallard duck (30 ppm continuous feeding)	No effect
Mammalian hormone bioassay	
Mouse and rat	No estrogenic, androgenic, anabolic, or glucocorticoid activity

Table 8.--Toxicological properties of
EL-494 (Elanco Ltd.)

Species			
Mouse	Technical	oral	LD ₀ > 500 mg/kg
Rat	50W	oral	LD ₀ > 2 g/kg
	50W	inhalation	LD ₀ > 2 g/kg
Rabbit	50W	dermal	LD ₀ > 2 g/kg
	50W	ocular	Slight conjunctive redness, cleared by 72 hours
Rainbow trout	Technical suspension		LC ₀ > 10 ppm

Note: Ames Test: negative.

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Using Behavior Modifying Chemicals to Reduce Western Pine
Beetle-Caused Tree Mortality and Protect Trees [20]

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Introduction

Each year from 1900 to 1950, the western pine beetle (*Dendroctonus brevicornis* LeConte)⁵ killed between 0.5 and 3.5 billion board feet of timber (Miller and Keen 1960). Since then, losses have not been comparably assessed, but they are continuing at an unacceptably high level. Tree mortality occurs under a wide variety of conditions and land uses. The value of killed trees ranges from high for those around homes to low for those in remote areas.

To date, direct control methods to suppress western pine beetle populations and thereby reduce tree killing have not been fully satisfactory. Such methods have usually taken two forms: logging killed trees and use of toxic chemicals. By logging beetle-killed trees, timber values can be recovered that otherwise might be lost. But as a suppression technique, logging is usually inadequate because too many beetles emerge before the trees can be removed (Miller and Keen 1960). Toxic chemicals have a number of drawbacks. They are expensive to apply -- largely because infested trees must be found, felled, and treated (Keen 1966). And they are controversial on the grounds of both unproven efficacy and environmental hazards (Koerber 1976).

A new approach using attractants and interruptants offers much promise for suppressing beetle populations and protecting trees (Bedard and Wood 1974). These behavior modifying chemicals are used by the beetles to coordinate their attacks on trees in order to overcome the natural resistance mechanisms of their hosts. The chemical messages they convey are essential to beetle survival (Wood 1972; Wood and Bedard 1977). Thus, they could be effective for direct control if they could be used to misguide the beetles or otherwise interrupt this vital communication system. Attractants and interruptants are nontoxic, and generally do not affect the behavior of other organisms (Wood 1977). In the long run, they could prove to be less expensive than toxic chemicals because it would not be necessary to find, fell, and treat infested trees.

This paper describes three experimental methods of using behavior modifying chemicals to suppress western pine beetle populations and to protect ponderosa pine (*Pinus ponderosa* Laws.) trees from infestation: (a) Trapping beetles with synthetic attractants; (b) interrupting the response to natural attractants by synthetic attractants; and (c) interrupting beetles from aggregating on trees by non-attractants.

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Suppression Based on Trapping

Suppression based on trapping is intended to suppress western pine beetle populations over a large area (>5,000 ha). Traps are baited with pheromones -- the host terpene myrcene and the synthetic (racemic) attractants *exo*-brevicomin and frontalin (Bedard *et al.* 1970; Wood 1972). If enough beetles are trapped, subsequent beetle-caused tree mortality can be reduced to acceptable levels. Experimentation with this approach is difficult and expensive because the possible major treatment effects must be monitored over a large area for several beetle generations (Bedard and Wood 1974). These effects include a change in the distribution and abundance of the beetle and its natural enemies and of the trees that are killed.

We studied the effects of two simultaneous trapping treatments in one 65-sq-km area, at Bass Lake, Madera Co., California. Including pre- and post-treatment evaluations, five generations of the western pine beetle were studied (Bedard and Wood 1974). In one treatment, 99 traps were deployed on 0.8-km centers for three generations. In the other treatment, four suppression plots, each 1.3 sq km, contained 66 traps deployed on about 161-m centers for one generation (spring generation). The total number of emerging and attacking beetles was estimated.

In all, nearly 1 million western pine beetles were caught. Tree mortality declined throughout the treatment period. The beetle generation prior to treatment killed a total of 283 ± 94 trees (± 2 standard errors⁶); the third generation, which was exposed to attractants, killed a total of 91 ± 28 trees (C.J. DeMars *et al.*, unpublished data). Trees near traps were attacked, and some were killed. It appears that, for the three generations exposed to the treatment where traps were deployed on an 0.8-km grid, a constant proportion of the population (estimated from emergence densities) was caught. And, after traps were removed, the number of trees killed by beetles declined further, to a total of 49 ± 8 for two generations, and remained low for the next 4 years. These results suggest that trapping may suppress the western pine

beetle population below some critical level and have lasting effects. But we cannot rule out entirely other explanations for the decline in tree mortality.

The effects of trapping beetles with synthetic attractants have potential advantages and disadvantages that should be considered when planning further research. In addition to advantages already mentioned, the technique: 1) Can suppress beetle populations over large areas; 2) may be effective against low pest populations; and 3) may reduce tree mortality beyond treatment plots. Its principal disadvantage is that trees are killed near traps. We surmise that this problem would be more severe if the treatment were used against higher beetle populations and in high-density stands.

Although the tests point to the efficacy of the synthetic attractants, other information must be acquired before these compounds could be considered for registration by the U.S. Environmental Protection Agency. The agency subjects behavior modifying chemicals to the same scrutiny as toxic chemicals (Phillips 1976). The research to meet the requirements for registration could be costly (Djerassi *et al.* 1974; Ospenson 1977).

The attractants used in the trapping study were nontoxic in our panel of tests on acute oral and dermal toxicity, inhalation toxicity, and eye and skin irritation to laboratory mammals (W.D. Bedard, unpublished data). In the light of these results, we believe that much of the data required for environmental safety tests could be waived because the compounds: 1) Occur naturally (Wood 1972, Browne *et al.*); 2) will be applied only in their normal environment; 3) will be applied at rates that do not exceed those found in nature (Browne *et al.*); and 4) are not introduced directly into plant, animal, soil, or aquatic systems. They are simply allowed to evaporate into the air, similar to the naturally occurring compounds.

On the other hand, meeting the requirements needed to demonstrate efficacy could be expensive. Efficacy could be demonstrated by beetle suppression or tree protection or both.

⁶ Standard error = square root of the estimated variance of the estimate of the number of infested trees.

⁷ Browne, L.E., D.L. Wood, W.D. Bedard, R.M. Silverstein, and J.R. West. Quantitative estimates of the attractive pheromone components, *exo*-brevicomin, frontalin, and myrcene, of the western pine beetle in nature. *J. Chem. Ecol.* (accepted for publication).

Given present technology, the demonstration of beetle suppression is difficult and expensive, especially over the large areas involved. Tree protection is easier to demonstrate, but it is only an indirect treatment effect and as such would have to be repeated several times under different conditions. Thus, it too would be expensive to demonstrate.

Interruption Using Attractive Pheromones

Interruption using attractants is designed to prevent western pine beetles from killing ponderosa pine trees over a large area. Pheromones -- myrcene and synthetic (racemic) *exo*-brevicomin and frontalin -- are broadcast to interrupt the beetles' normal aggregative response. Thus, in theory, trees are protected, and beetle populations are suppressed when beetles either fail to concentrate adequately to overcome tree resistance and thereby are killed or they leave the treatment area. Release of pheromone components from many sites in a 0.81-hectare square during test periods of 1 day caused significant reduction in the catch of beetles in the center of the square on a trap baited with either the same compounds or attractant portions of the bole removed from a tree under attack (Bedard *et al.*, unpublished data; Wood and Bedard 1977). The effect was observed when attractants were released in a wide range of release rates and densities. Test runs for longer than 1 day resulted in less interruption, i.e., beetles were caught in greater proportions at the centrally located source. As attractant release rate increased, the number of beetles attracted into the area increased, and trees near the edge of the plot were attacked (Bedard *et al.*, unpublished data).

We must be cautious about predicting the possible outcome in the operational use of this method because these were short-term, small-scale tests. Therefore, the following advantages and disadvantages are rather speculative. The potential advantages of interruption using attractants are these: 1) The method could be inexpensive; and 2) it could be prescribed with little modification for a diverse array of beetle population levels and land management objectives, including very high population levels over large areas. Potential disadvantages are the long time and high cost needed to solve technological problems and determine the feasibility of their solution. The problems in their application are: 1) Controlled release formulation and application technology; 2) tree killing where attractant gradients develop, such as at treatment plot boundaries or where there are

irregularities in application or performance of the controlled release formulation; and 3) the introduction of formulated compounds into plant, animal, soil, and aquatic systems thereby requiring extensive safety data for registration (Phillips 1976).

Interruption Using Non-Attractants

Interruption using non-attractants seeks to protect individual, pre-selected trees from western pine beetle attacks by the release of verbenone from the tree bole. In theory, the trees are protected when the beetles' aggregative response is interrupted by the presence of verbenone so that the attack rate is insufficient to overcome the host's resistance. Although verbenone might be suitable for broadcast treatments aimed at protecting trees in an extensive area, we are now studying it primarily as an individual tree protectant. The following discussion is limited to that use.

We found that verbenone reduced the catch of beetles responding to either the attractive portions of the bole removed from a tree under attack or to the synthetic attractants (Bedard *et al.*, unpublished data; Wood and Bedard 1977). We tested the potential of verbenone to protect trees by suspending myrcene and the synthetic (racemic) attractants *exo*-brevicomin and frontalin between pairs of trees. Verbenone was released from the bole of one and not the other. Trees without verbenone were visited (i.e., landed upon) by many beetles and attacked (i.e., bored into) and killed, while trees with verbenone were visited by only a few beetles and were not attacked (Bedard *et al.*, unpublished data). These results clearly establish the possibility of verbenone as a tree protectant.

The advantages of verbenone as an individual tree protectant are these: 1) It could be formulated so that it is easy to apply; 2) in forested areas it could be used by small landowners or forest managers who are interested in protecting a few trees without the cooperation of others who would be required to successfully execute an area-wide treatment, such as the trapping method; 3) in urban and developed areas, it could be used by small landowners or groups of landowners to protect high value trees; 4) the costs of developing the environmental safety data that might be required for registration could be low because the compounds could be released into the air from controlled release devices attached to trees and thus the compounds would not be introduced into plant, animal, soil, or aquatic

systems; and 5) the cost of developing the efficacy data that might be needed for registration could be low because tests to demonstrate efficacy are small and straightforward and therefore inexpensive.

The disadvantages of verbenone for individual tree protection are these: 1) It may be too expensive to be used in an extensive forest area; and 2) a long time span and great expense are needed to determine optimum release rates that will protect trees under a variety of conditions. However, the research needed to develop the individual tree protection method to the operational stage is judged to be much less than that required to develop either the methods of trapping or of interruption using attractive pheromones.

Conclusions

Behavior modifying chemicals offer a promising approach in a western pine beetle pest management system (Wood 1977). The cost of further research and development is high, and resources available for such work are now limited. Therefore, future developmental work, including work on registration of these materials and methods, must be selective.

Interruption with attractants could some day have the widest use and be the least expensive. But it appears to be more expensive to develop than the trapping method because of the problems already described. If the trapping method proves to be ineffective against high beetle populations, it may have more limited use than the interruption method using attractants. The efficacy of the interruption-with-attractant method against high populations, however, remains to be established. Among the three experiment methods, interruption using non-attractants for individual tree protection would have the most specialized use. And, it appears to be least expensive to obtain the data required for registration of this method. If estimated cost to develop and register the behavior modifying chemicals is the sole criterion for selecting future studies, individual tree protection using anti-attractants would probably receive priority attention. However, because its potential use is so limited and because toxic chemicals are already available for this use, we have sought a method that could be used over large areas. We plan to continue our efforts to develop the trapping method, since we already have made a significant investment in the research and, as a consequence, have developed a considerable understanding of how this method can be made effective.

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VI. FOREST INSECT ECOLOGY AND CONTROL

Several Types of the Mycetangia Found in (Scolytid and) Platypodid Ambrosia Beetles L 711

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Ambrosia beetles bore deep tunnels in the wood of felled trees, logs, or stumps. The beetles cultivate their symbiotic fungi in the tunnels, and the fungi cause great damage to the quality of wood. Such ambrosia beetles have specialized structures in their bodies called mycetangia that play a role in fungus transmission.

Recently, the mycetangia have been examined especially from the viewpoint of the relationship between the ambrosia beetles and their symbiotic fungi.

Francke-Grosmann (1967) classified the mycetangia of several scolytid ambrosia beetles into 13 groups based on the location of their mycetangia. In the family Platypodidae, however, the mycetangia were found only in a few species.

The mycetangia of several species of the family Platypodidae were examined. For histological studies, serial sections of 15 μ thickness were cut from whole beetles, and for surface examination, the beetles were scanned with a scanning electron microscope. Hitherto, the mycetangia found in the platypodid ambrosia beetles were classified into five groups.

In group A, the mycetangium is developed only in the female. The mycetangium is a single spherical tissue, about 0.2 mm in diameter, situated at the back of the preoral cavity. *Crossotarsus niponicus* Blandford belongs to this group.

In group B, the male has a different mycetangia from those of the female. The female has tens or hundreds of integumentary

pit-type mycetangia crowded on the caudal half of the pronotum. Each pit is oval or round in shape and is 10 μ or so in diameter. On the posterior wall of each pit, a small process, about 1 to 3 μ in length, projects forward. The function of this inner process is not clear, but it may play a role in transferring fungus material from the gallery-wall into the mycetangial openings in the newly emerged adult. A few minute holes, 0.5 to 1.5 μ in diameter, are situated on the posterior wall of the pit. They may lead to ducts which transport secretions from the glands associated with the mycetangia.

The male has two types of mycetangia. One is the pit-type mycetangia which are similar to those of the female, and the other is the enlarged forecoxal and mesocoxal cavity-type mycetangia, which represent the main mycetangia. Many fungus specimens occur in the enlarged coxal cavities. *Platypus severini* Blandford, *P. caliculus* Chapuis, *P. solidus* Walker, *P. jansonii* Chapuis, and *P. calamus* Blandford belong to this group. *P. forficula* Chapuis and *P. pseudocupulatus* Chapuis tentatively belong to this group.

In group C, the mycetangia of both sexes are almost the same in type, and are similar to those of the type of female in group B. The mycetangia of the male are, however, somewhat less developed. The forecoxal and mesocoxal cavities of the male are not enlarged. *Platypus curtus* Chapuis and *P. shoreanus bifurcus* Schedl certainly belong to this group, while *P. shoreanus mutilatus* Schedl may belong to this group.

In group D, the mycetangia of both sexes show two types of openings. There are a long transverse crevice and about 20 to 30 integumentary pits, the one situated near the posterior margin of the pronotum, and the other situated slightly forward of the crevice. The inner processes of the pits and

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of the crevice are wide, polydactyl, about 20 to 30 μ in length, and extend out of the mycetangia. *Diapus quinquespinatus* Chapuis belongs to this group.

In group E, the mycetangia consist of a few large pores, about 40 to 45 μ in diameter, situated near the base of the pronotum. The inner process of the pore is flat, slender, polydactyl, and about 40 μ in length. *Diacavus philippinensis* Schedl belongs to this group. *D. abdominalis* Schedl may tentatively be placed in this group

It seems likely that beetles of the family Platypodidae may generally have mycetangia of some types similar to those found in scolytid ambrosia beetles.

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M. W. Stock^{1 2}

Introduction

Larvae of the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, are some of the most destructive defoliators of true fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) forests of western North America. Documented outbreaks have occurred approximately every 7 to 10 years since about 1900. The severe outbreak in the Pacific Northwest from 1971 to 1974 covered over 800,000 acres and caused extensive damage with concentrated tree mortality on about 89,000 acres (Graham *et al.* 1975). Controversy over the use of DDT against the tussock moth led to widespread support for seeking other, more environmentally sound ways of suppressing this pest. In 1975, the USDA began an expanded 3-year research and development program to find new answers to the tussock moth problem.

Although Wellington (1977) and others have emphasized that recognizing and evaluating intrinsic diversity within economically important insect groups is essential for realistic and effective pest management, studies of this type have been nonexistent or secondary compared to research on external environmental variables affecting insect numbers. But only when genetic variation and relations among subgroups of pests are understood can the results of studies of environmental variables (such as insecticides or climatic events) on one population be extrapolated accurately to other populations. Consequently,

one new approach incorporated into the tussock moth research program is the application of biochemical genetic methods to define and quantify population diversity within the species.

This report describes key information obtained to date in these genetic studies of the tussock moth, our future plans, and the significance and potential value of this work toward eventual prediction and control of tussock moth outbreaks. Primary objectives include:

1. Identification of genetic characteristics of Douglas-fir tussock moths associated with different stages in the outbreak episode (release, epidemic, and decline phases).
2. Development of methods to predict the genetic makeup of field populations prior to their emergence.
3. Evaluation of the genetic relations and diversity among tussock moth populations over western North America.

Methods

In cooperation with U.S. Forest Service and various university personnel associated with the Douglas-fir Tussock Moth Research

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California at Berkeley and with the Canadian Forestry Service, Victoria, B.C., for providing larvae used in this study, and for their interest and help in providing associated information which will aid in present and future work. She is especially indebted to Mr. J. D. Guenther for his invaluable assistance in acquiring data used and to Drs. M.W. McFadden, M.L. McManus, G.B. Pitman, F.M. Utter, and F.W. Allendorf, and to Mr. G. Milner and Ms. M. Brookes for critical reading of the manuscript.

and Development Program, we obtained samples of over 2,100 late-instar larvae from diverse field locations and laboratory colonies in spring and summer 1976 (fig. 1). We also had laboratory-reared larvae from egg masses collected during fall 1975. Variables represented by these samples included sibling groups (progeny of single-pair matings); dif-

ferent geographic locations (from New Mexico to British Columbia); high-density (Trigo Canyon, New Mexico; Denver, Colorado; Kamloops, B.C.) and low-density (California; Winema National Forst, Oregon) populations; continuing (Trigo Canyon; Denver) and collapsing (Kamloops) outbreaks; different collecting times in a single season; and colony-reared larvae.



Figure 1.--Sources of samples of Douglas-fir tussock moth larvae used in genetic studies during 1976.

We use biochemical genetic methods (starch gel electrophoresis) to examine and quantify genetic features of, and relations among, these populations. In recent years, this method has proved uniquely valuable for providing precise data on the genetic makeup of populations and species because of its direct reflection of genetic differences coupled with its ease of application (Utter *et al.* 1974, Avise 1974). The method is based on the fact that proteins (such as enzymes) produced by different alleles at a single gene locus often differ in charge and can be separated in a gel medium by an electric current. Specific enzymes (and variants of these enzymes or "isozymes") are revealed by supplying the appropriate substrate and cofactors which involve a product of the enzymatic reaction in a colorproducing reaction. The colored product is then deposited on the gel at the precise location of the specific enzyme, forming visible banding patterns for individual insects which can be directly related to specific gene expression (fig. 2). Because codominant expression of most variant alleles occurs on starch gels (that is, each allele is expressed as a single distinct protein), banding patterns from individuals can be read directly from the gel as genotypic and allelic frequencies for statistical analysis of population samples. Data from single, few, or many loci can provide information useful in different ways. Burns (1975) discusses how electrophoretic information from several loci (representing a sample of the genome as a whole) can have systematic value, but he also points out how data on a few or even single loci have been used to show selective divergence or as genetic markers of specific population types.

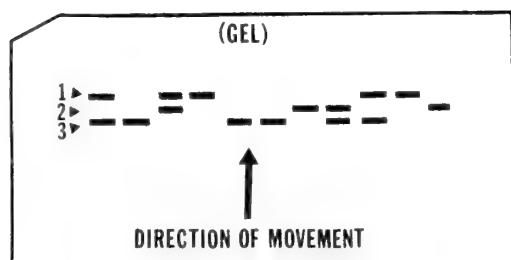


Figure 2.—Diagram of a gel showing the EST-1 locus with a single run of 11 insects. Each vertical row of bands represents a single insect for a single enzyme system. Here, a single gene locus coding for the enzyme has three alleles producing isozymes varying in electrophoretic mobility. Heterozygotes show up as double bands and homozygotes are single bands. Genotypes can be read across as 1-3, 3-3, 1-2, 1-1, etc.

During 1976, we tested over 25 tussock moth enzyme systems with a variety of buffer and stain combinations. We now have standardized methods for routine analysis of 12 enzymes, eight of which are polymorphic (variable) in one or more of the populations samples (see tabulation below).

Enzymes for which assays were developed during 1976 for Douglas-fir tussock moth genetic analysis:

- *Aspartate aminotransferase (AAT)
- *Acid phosphatase (AcP)
- *Esterase (EST)
- *Glutamic pyruvic transaminase (GPT)
- α -Glycerophosphate dehydrogenase (AGPDH)
- *Isocitrate dehydrogenase (IDH)
- *Hexokinase (HK)
- *Leucine aminopeptidase (LAP)
- Malate dehydrogenase (MDH)
- Malic enzyme (ME)
- Transferrin (TFN)
- *Phosphoglucomutase (PGM)

*Polymorphism observed in some or all samples.

Despite the preliminary nature of our analyses to date, certain interesting and relevant aspects of this work are beginning to emerge. I will use specific examples from our data, particularly from the highly polymorphic esterases, to illustrate key points.

Seasonal Shifts in Gene Frequency

Our first objective is to detect unique features of populations at different phases in the outbreak episode and at different densities. We found the majority of genetic variation characteristic of different populations to be stable over the season. However, when the genetic makeup of samples taken on two different dates during the summer from epidemic populations at Kamloops, B.C., and Denver, Colorado, were compared (table 1), several interesting differences were observed. There was a difference in the frequency of occurrence of variants at the first esterase locus (EST-1) between the two dates at each site. In both populations, allele 1 occurred less frequently and allele 2 occurred more frequently later in the summer. The difference at Kamloops is highly significant ($p < .01$), but the difference between the Colorado

Table 1.--Occurrence of three enzyme types, esterase (EST-1), isocitrate dehydrogenase (IDH), and aspartate aminotransferase (AAT), in two epidemic tussock moth populations during 1976

		Lowry Air Force Base, Denver, Colorado		Kamloops, British Columbia	
		7 July	20 July	7 July	19 August
<u>EST-1</u>	Genotypes				
	1-1	90	16	178	71
	1-2	23	7	17	39
	2-2	5	2	2	3
	N	118	25	197	113
	Frequency				
	p(1)	.86	.78	.95	.80
	p(2)	.14	.22	.05	.20
χ^2		2.9		32.1**	
<u>IDH</u>	Genotypes				
	1-1	100	49	238	79
	1-2	0	0	0	9
	2-2	0	0	0	7
	N	100	49	238	95
	Frequency				
	p(1)	1.0	1.0	1.0	.88
	p(2)	0	0	.0	.12
χ^2				59.7**	
<u>AAT</u>	Genotypes				
	1-1	17	2	210	215
	1-2	40	7	0	0
	2-2	66	24	0	0
	N	123	33	210	215
	Frequency				
	p(1)	.30	.17	1.0	1.0
	p(2)	.70	.83	.0	.0
χ^2		4.7*			

samples is not. There are several plausible explanations for these differences, the most obvious of which is simply population heterogeneity and the sampling of two different subgroups or population mixtures on the different dates. While care was taken to reduce this possibility (the same person collected at the same site each time), it cannot be discounted. If, however, the shift in gene frequency is real, the greater change at Kamloops could possibly be related to the relatively longer time between collection of samples there (43 days compared to 13 days in Denver). The shift could also be associated with the fact that the Kamloops epidemic collapsed during summer 1976 while the Denver populations did not and will be epidemic again in 1977. When the first Kamloops sample was taken, there were over 117 larvae per 50 sq. ft. of foliage.

Larvae were extremely difficult to find at the time of the second sampling, following a sharp drop in numbers associated with nucleopolyhedrosis virus disease. The second Kamloops sample was also unique in that we found genetic polymorphism at the isocitrate dehydrogenase (IDH) locus in this sample, but in all others, including the first from Kamloops, IDH was consistently monomorphic (table 1). We do not know the significance of this variation, but can hypothesize that the variant form is present at very low frequencies in normal high-density or stable low-density populations. Possibly, when population numbers dropped drastically in mid-August, the rare gene was concentrated in the last survivors.

The Denver population was unique in being the only group sampled that was poly-

morphic at the aspartate aminotransferase (AAT) locus (table 1). This population, in contrast to the other two epidemic populations sampled (Trigo Canyon, Kamloops), has been subjected to heavy insecticide stress for the past 2 years.

During 1977, we will obtain a sequence of larval samples from epidemic locations to determine the validity of the genetic differences observed in 1976. We will also carry out genetic analyses in association with insecticide bioassays to determine if the selective effect of insecticide stress could be related to some of the genetic differences observed between populations.

Low-Density Populations

Larval samples of adequate size for statistical analysis of genetic data were difficult to obtain from low-density populations. We often had to work with samples of less than 20 larvae. While we have found that the genetic composition of samples this small sometimes closely matches the genetic makeup of larger samples (100 or more) from the same population in high-density areas, the large confidence interval associated with small samples makes inferences derived from them subject to serious question. We did obtain a sample of 75 larvae from low-density areas in California, however, and found these insects unique in that they all lacked allele 2 at the EST-1 locus, a common allele in all other populations sampled.

Laboratory-reared sibling groups were used to test the genetic basis of biochemical variation by comparing genotype ratios to simple models of Mendelian inheritance (table 2). For example, if sibling genotypes were identical for a particular enzyme type,

we could infer that the parents were homozygous for that gene. Similarly, if a genotype ratio of 1:1 was observed, we could infer that one parent was homozygous and the other heterozygous. By inferring parental genotypes in this manner, we obtained small "samples" (the parents) from several areas, including low-density populations, where moths could not otherwise be collected.

During 1977, in conjunction with Forest Service personnel, we will obtain live adult males in areas of low tussock moth density from pheromone traps during flight periods in the fall. These insects will provide more data on genetic features of low-density populations that cannot be sampled by other means.

Predicting the Genetic Composition of Populations

Our second objective is to develop methods to predict the genetic makeup of populations prior to their emergence in the field. In some cases, we found a close correlation between the small samples obtained by inferring parental genotypes from laboratory-reared larvae in the spring (table 2) and the actual field population that later emerged. For example, EST-1 gene frequencies observed in a sample from the summer 1976 Kamloops epidemic (.88, .10, .02, N = 318) (table 3) were similar to frequencies derived from sibling groups from five egg masses reared during spring 1976 (.80, .05, .15, N = 10). However, as previously noted, variances calculated from such small samples for determination of confidence intervals ($s^2 = \frac{p(1-p)}{2N}$) must

be considered in estimating the accuracy of data from samples of such small size.

During 1977, we will rear larvae from a limited number of egg masses from specific

Table 2.--Data obtained from sibling groups, single tussock moth egg masses, showing: (1) confirmation of genetic basis of variation observed by comparison with models of simple Mendelian inheritance; and (2) inference of parental types which constitute another small sample from the original wild population

Egg mass	Larval Genotypes (EST-1 Locus)						Approx. ratio	Inferred parental genotypes
	1-1	1-2	2-2	1-3	2-3	3-3		
1	11	-	-	12	-	-	1:1	(1-1) (1-3)
2	20	-	-	-	-	-	1:0	(1-1) (1-1)
3	10	8	-	-	-	-	1:0	(1-1) (1-2)
4	12	8	-	11	6	-	1:1:1:1	(1-3) (1-2)

Table 3.--Esterase (EST-1) gene frequencies for all field samples (multiple samples pooled) of tussock moth larvae assayed during 1976¹

	Sante Fe, N. Mexico	Trigo Canyon, N. Mexico	Denver, Colorado	Kamloops, B.C.	California
<u>Genotype</u>					
I-1	30	35	106	249	55
1-2	26	91	30	56	0
2-2	5	93	7	5	0
1-3	11	2	2	6	15
2-3	7	0	1	0	0
3-3	2	0	0	2	2
N	81	221	146	318	72
<u>Allelic frequencies</u>					
p(1)	.60	.37	.84	.88	.87
p(2)	.27	.62	.15	.10	0
p(3)	.13	.01	.01	.02	.13

¹ All populations, except those from Colorado and British Columbia, exhibited differences in genetic makeup significant at the 95 percent and 99 percent levels.

sites to determine how many egg masses are necessary to predict the genetic constitution of the later-emerging field larvae with desired accuracy. Once genetic indicators of specific tussock moth population features are identified, prediction during spring of the genetic constitution of the future field population will have particular significance as an aid in making decisions for regional control operations.

Genetic Relationships

Our third objective is to evaluate genetic relationships and diversity among all populations. We found much variation between and among samples at certain loci. For example, among all populations tested, the frequency of allele 1 at the EST-1 locus ranged from .37 at Trigo Canyon, New Mexico, to .88 at Kamloops, B.C., while the frequency of allele 2 ranged from zero in California samples to .62 in the Trigo epidemic (table 3). All populations were significantly different (at the 99 percent confidence level) at this locus except the two epidemic populations from Denver and Kamloops which were strikingly similar (chi-square at 2 d.f. = 5.13). Similarity coefficients (e.g., Rogers 1972) can be calculated from data from several loci from each sample based on the number of shared alleles between populations. Addition of genetic information on more loci during 1977 will enable us to further quantify genetic relations among tussock moth subgroups.

Further Ramifications

Pooled data from larvae collected at several sites in a low-density infestation in Winema National Forest, Oregon, contained an excess of homozygotes at the EST-1 locus when observed genotypes were compared to expected values derived from the Hardy-Weinberg equilibrium equation (table 4). One possible cause of this observed genetic imbalance is the Wahlund effect, created by pooling data from sites between which gene flow is restricted. Because the collecting area in Winema National Forest was large compared to that of other sampling areas, such pooling of separate populations could easily have occurred. When data were broken down by site, gene frequencies for allele 1 varied from .10-.95 and for allele 2, .05-.90, and genetic equilibrium, based on Hardy-Weinberg expectations and indicating random gene flow, was found in four of five cases. Furthermore, despite the small size of these samples, differences in gene frequency significant at the 95 percent confidence level were observed (fig. 3). Thus, it appears that the deficiency of heterozygotes in pooled data from this location results from local differentiation among populations. Information of this type can be helpful in analysis of similar data. We would know when and when not to pool data and which collecting areas might be observed more closely for unique selective features affecting insect numbers.

The Berkeley tussock moth colony was virtually identical in genetic makeup (as

Table 4.--Pooled data for the EST-1 locus from tussock moth larva collected at five sites in a low-density infestation in Winema National Forest, Oregon¹

Genotype	Observed number	Expected number	Observed -Expected
1-1	14	7.8	6.2
1-2	11	23.5	-12.5
2-2	24	17.6	6.4
N	49		
Frequency		$\chi^2 = 13.9^{**}$	
p(1)	.40		
p(2)	.60		

¹ Genetic disequilibrium, as indicated by the high chi-square value, results from a deficiency of heterozygotes.

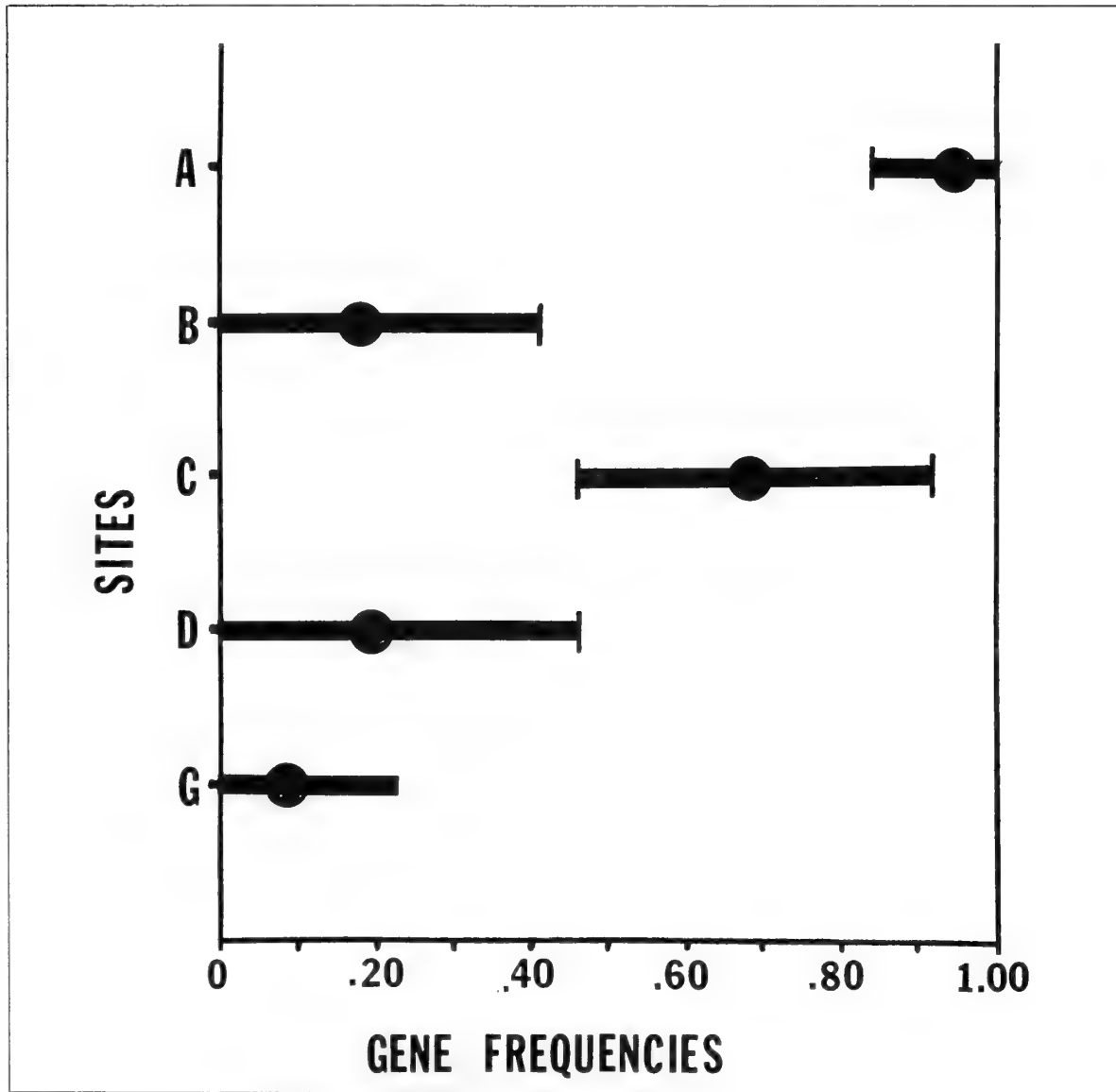


Figure 3.--Gene frequencies (+ 1 s.d.) at the EST-1 locus for five collections sites at Winema National Forest, Oregon. Populations are usually considered to be differentiated at a locus at the 95 percent confidence level if these lines do not overlap. Thus, populations at sites B and G are genetically distinct from these at sites A and C.

might be expected) to the Trigo Canyon, New Mexico, population from which it was established only one generation previously (table 5). Comparison of these populations did, however, permit us to gain information on the minimum number of egg masses necessary to establish a colony that is genetically similar to the wild source. In addition, such comparisons suggest how, if colonies are kept over many generations in the laboratory and subjected to inbreeding and the differential selection pressures of a laboratory environment, monitoring by biochemical genetic

methods could be of value for detecting genetic divergence between the colony and any wild populations upon which results of laboratory experiments are to be applied. In 1977, we plan to explore in more detail the subject of monitoring the genetic quality of laboratory colonies.

A final report of this work on tussock moths will be prepared in 1978 and will demonstrate further how genetic studies of this type can contribute to the development of insect pest-management programs.

Table 5.--Esterase (EST) and phosphoglucosmutase (PGM) gene frequencies in samples of tussock moth larvae¹

Allelic or gene frequencies	Triego Canyon, N. Mexico			Berkeley colony			Denver, Colorado		
	7 July	22 July	pooled	6 June	2 July	pooled	7 July	20 July	pooled
EST									
N	157	64	221	99	76	175	121	25	146
p(1)	.37	.36	.37	.28	.40	.33	.85	.78	.84
p(2)	.62	.63	.62	.70	.53	.63	.14	.22	.15
p(3)	.01	.01	.01	.02	.07	.04	.01	0	.01
PGM									
N			20			23			33
p(1)			.65			.63			.47
p(2)			.35			.37			.53

¹ The slight divergence of each sample of the Berkeley colony from the wild New Mexico population from which it was derived and the similarity of pooled data from the two populations are illustrated. Data from the Colorado samples are provided for contrast.

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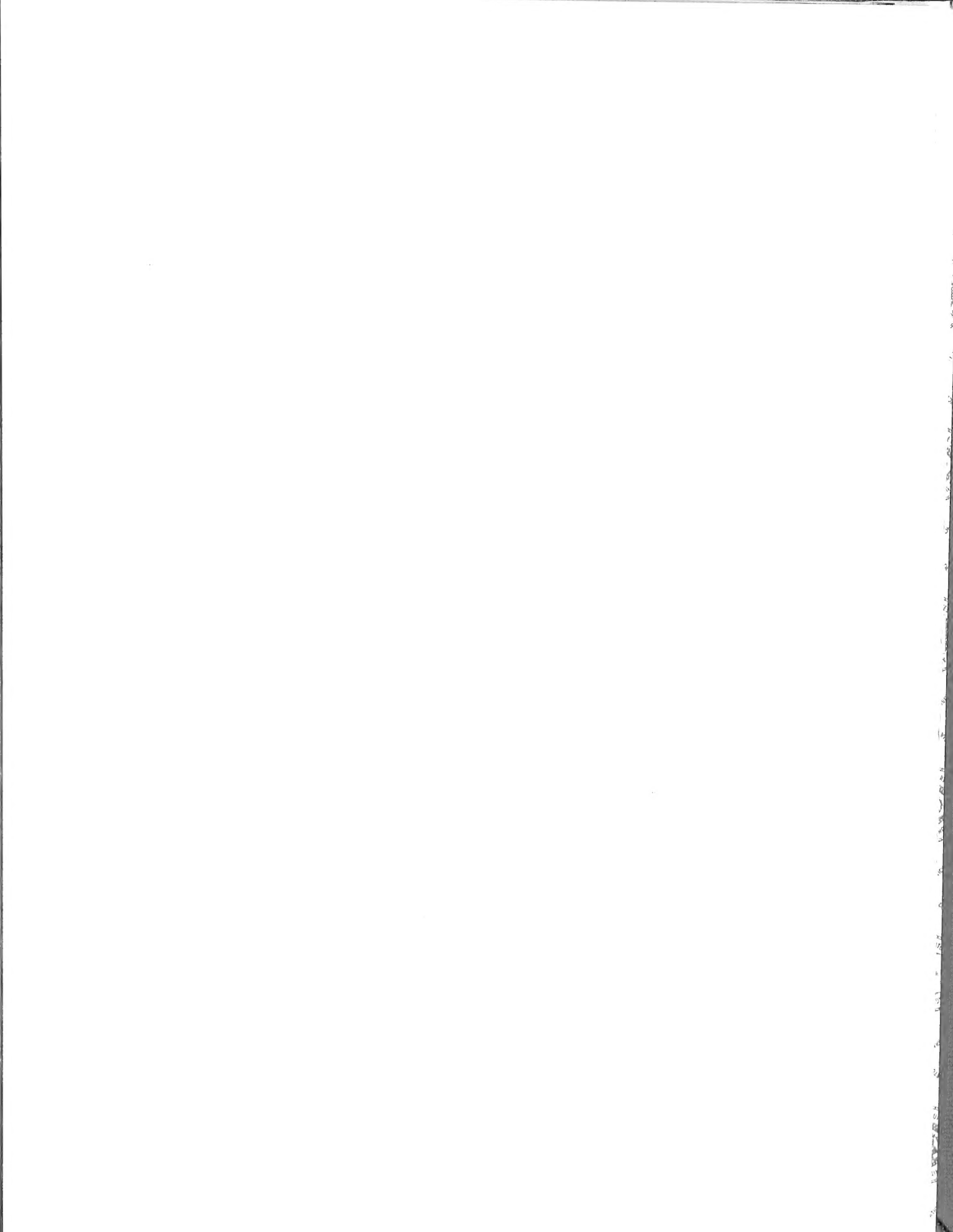
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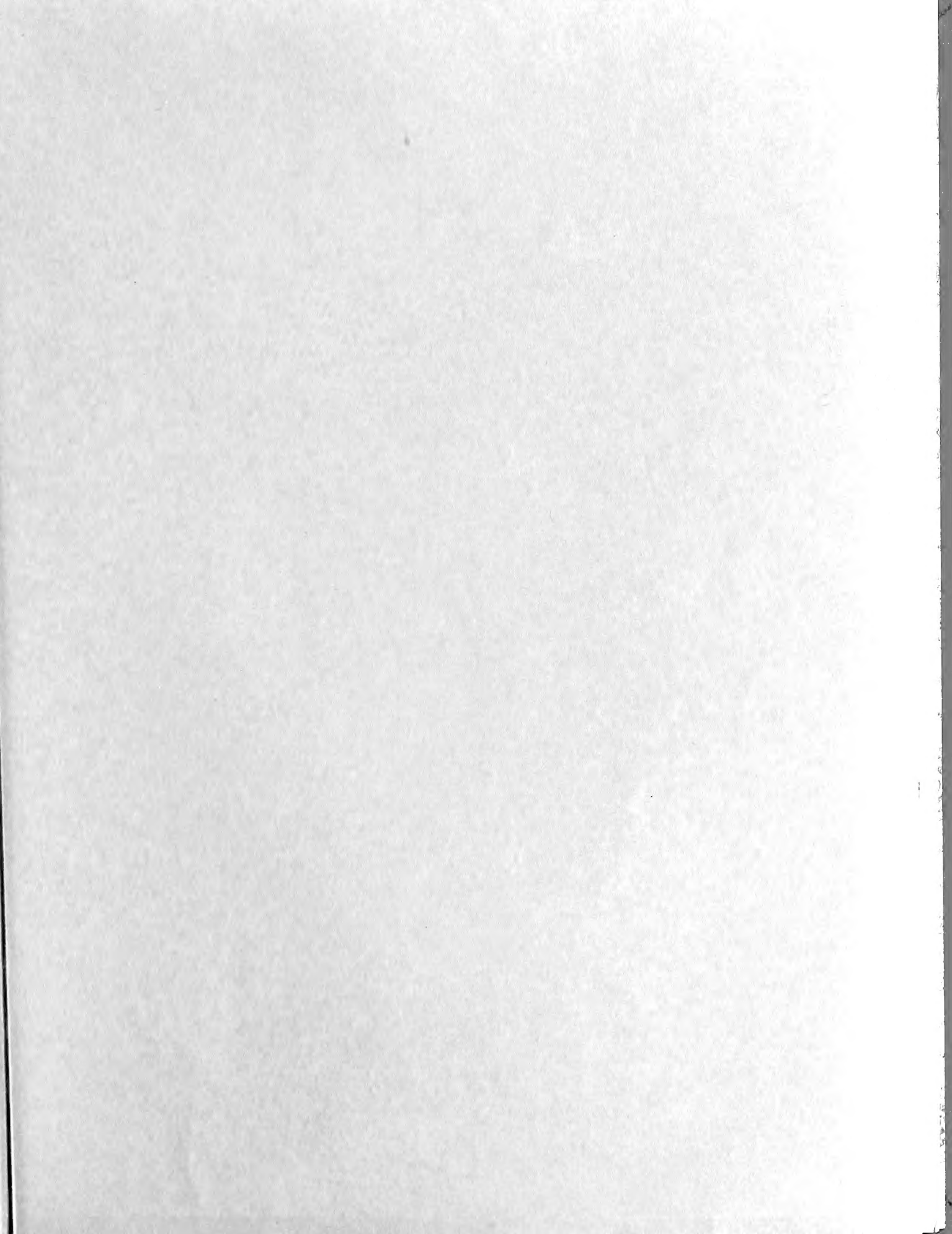
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