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OPTIMAL MANAGEMENT OF THE SPRUCE-FIR FOREST AGAINST THE SPRUCE BUDWORM

by

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Submitted in Partial Fulfillment of the Requirements for the Senior Scholars Program

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ABSTRACT

Proper management of the softwood forest-budworm ecosystem is vital to the future prosperity of Maine. In choosing a management strategy, economic as well as ecological effects must be considered. This paper constructs a computer simulation model of the budworm-forest ecosystem in order to better evaluate effects of different types of forest management.

The budworm-softwood forest ecosystem is a highly complicated system involving three dynamic population systems: the host tree population, the budworm population and the foliage population. Each system is modeled, by regression analysis, to observations collected by entomologists over the past half century. There are large gaps of knowledge that must be filled before more accurate models can be created. It is hoped that this paper will point future research in the right direction.
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CHAPTER 1

INTRODUCTION

The spruce budworm is an exception to forest insects in Maine. At periodic intervals their population densities will increase to an epidemic level and consume foliage (green buds and spindles) of the soft wood forest (balsam fir and spruce trees) over periods of five to ten years, Stedinger(34, pp. 1-1). Defoliation, by the budworm, in turn, will indirectly cause up to seventy percent volume loss in tree biomass, due to mortality, Batzer(9, pp. 36). This results because, as trees lose their foliage, they lose their ability to produce energy through photosynthesis. The trees become very weak and are highly susceptible to fungi, which will kill the trees.

1.1 History of the budworm in North America

There is documented evidence that budworm epidemics have existed in eastern North America since the early 1700's and has probably been here for several thousand years since the end of the ice age, Baskerville(7, pp. 139). Budworm epidemics occur under two necessary and sufficient conditions: a. the composition of the forest consist of large, continuous areas of mature and over mature host trees and b. two to three consecutive years of warm, dry spring weather, Baskerville(7, pp. 138). Surprisingly, in spite of the random nature of the weather, the budworm epidemics have occurred in near forty year cycles. Outbreaks have occurred in North America in 1770, 1806, 1878, 1910
and intermittently since 1950, Stedinger (34, pp. 1-1).

The pulp-paper and saw log industries have used the resources of the soft wood forest since the beginning of the twentieth century. Before this time there was no economic value of balsam fir and spruce trees. Hence, there was no economic loss when large amounts of tree biomass was destroyed by the budworm.

There was no reason to control budworm outbreaks.

Since the epidemic of 1910 - 1919 seriously depleted the biomass inventory of the forest based industries, causing economic loss, budworm control has become a very important consideration. There has been a lot of research put into both silviculture (planting and cutting strategies) and insecticide sprays over the last sixty years.

The state of Maine began spraying its forest to protect against budworm outbreaks in 1954. See Figure 1-1, Stedinger (34, pp. 1-3). The spraying program has been partially successful, in that it has prevented the loss of much of the forest's biomass. However, as will be explained in the next section of this paper, it has left the forest composition in a state which is still highly susceptible to budworm attack. Thus epidemics are still possible as soon as the right weather conditions occur. This is why over the past thirty years Maine has had epidemics almost every six to ten years.

The current policy, used in North America, is not acceptable as a long run consideration. A master plan is needed to satisfy the budworm problem in an economical as well as an
Figure 1-1
Aerial Spraying for Spruce Budworm Control in Maine

<table>
<thead>
<tr>
<th>Year</th>
<th>Insecticide</th>
<th>Acreage Treated</th>
</tr>
</thead>
<tbody>
<tr>
<td>1954</td>
<td>DDT</td>
<td>21,000</td>
</tr>
<tr>
<td>1958</td>
<td>DDT</td>
<td>302,000</td>
</tr>
<tr>
<td>1960</td>
<td>DDT</td>
<td>217,000</td>
</tr>
<tr>
<td>1961</td>
<td>DDT</td>
<td>53,000</td>
</tr>
<tr>
<td>1963</td>
<td>DDT and B.t.</td>
<td>480,000</td>
</tr>
<tr>
<td>1964</td>
<td>DDT and Malathion</td>
<td>59,000</td>
</tr>
<tr>
<td>1967</td>
<td>DDT, Fenitrothion and Mexacarbate</td>
<td>103,000</td>
</tr>
<tr>
<td>1970</td>
<td>Fenitrothion</td>
<td>210,000</td>
</tr>
<tr>
<td>1971</td>
<td>Mexacarbate</td>
<td>8,700</td>
</tr>
<tr>
<td>1972</td>
<td>Mexacarbate</td>
<td>500,000</td>
</tr>
<tr>
<td>1973</td>
<td>Mexacarbate and B.t.</td>
<td>474,000</td>
</tr>
<tr>
<td>1974</td>
<td>Mexacarbate</td>
<td>430,000</td>
</tr>
<tr>
<td>1975</td>
<td>Fenitrothion, Carbaryl and others</td>
<td>2,200,000</td>
</tr>
<tr>
<td>1976</td>
<td>Carbaryl and others</td>
<td>3,500,000</td>
</tr>
<tr>
<td>1977</td>
<td>Carbaryl and others</td>
<td>930,000</td>
</tr>
</tbody>
</table>
ecological manner.

To construct a responsible and effective management policy, all the ramifications of altering the intricate ecological balance of the forest must be considered. First, observe how the forest and the budworm coexist in their ecosystem. It is important to understand all the events that are occurring in the stable limit cycle of the budworm-forest. As Gordon Baskerville (7, pp. 139) noted:

Left alone the budworm and the forest are not changing much in the long run and contrary to commonly held opinion the fir component of the forest is not increasing as a result of budworm attack.

1.2 The role of the budworm in the ecosystem

The relationship between succeeding forest generations and the spruce budworm has varied with geographical location, the quality of the stand, and the specific host species. However, the functional pattern between the budworm and its host is the same, Baskerville (7, pp. 138). The behavior of the budworm-host ecosystem can be viewed as a stable limit cycle with a large amplitude, Holling (16, pp. 14). This will be demonstrated clearly by examining a typical site over a specified period of time.

In eastern North America, the balsam fir is the primary host of the budworm. Red spruce is also a host species but is less desirable. As a result red spruce suffers less mortality in a budworm epidemic, Stedinger (34, pp. 2-4).

As stated earlier, a necessary condition for a spruce budworm epidemic, is a large continuous area of predominant balsam
fir trees of mature and over mature age (forty to sixty years old). In Green River, New Brunswick, in the mid 1870's, the forest was as described above with interspersed areas of dense, uniform immature forest also predominantly fir. The dense fir is suppressing the growth of the less tolerant spruce and birch, Baskerville (7, pp. 138).

In 1877 the budworm population rose sharply, escaping the control of its natural predators and parasites. As a result, the mature and over mature component of the Green River Forest was almost completely destroyed except for a few mature spruce and all non-host trees. This component was replaced by a thick, dense mat of fir and spruce regeneration that stood less than two feet high. The dense immature fir component of the forest was significantly thinned by the outbreak. A good percentage of the immature fir survived along with the non-host and spruce trees, whose growth is no longer suppressed by the formerly dense fir component, Baskerville (7, pp. 138).

The outbreak now comes to an end after about seven years because there is no longer enough food (foliage) to support such a large population. This is a direct result of the fact that young trees have less foliage than mature and over mature trees. Hence because of starvations and the fact that younger trees do not support budworm life as well as older trees the population collapses to endemic levels, which pose no threat to fir growth.

After thirty years the forest composition has changed
again to where the thinned immature component has grown to an open mature and over mature stand, predominantly of fir. The thick, dense immature stand has grown to a thick, dense immature stand, which inhibits growth of the less tolerating spruce and birch, Baskerville (34, pp. 138). The amount of foliage in the forest has also increased substantially. In fact, enough so that it could again support a five to seven year outbreak. Again the budworm population exploded in 1912, as a result of two consecutive warm, dry springs. This new outbreak lasted from 1913 to 1919, Baskerville (34, pp. 138). In 1920 the forest looked much the same as it had in 1885.

This cycle will continue indefinitely if left undisturbed in its ecosystem. The budworm has a natural role in the maintenance of this cycle. First the budworm preserves less tolerant species such as birch and spruce by thinning out the fir component and allowing these trees to grow freely, Baskerville (7, pp. 140). This prevents the forest from evolving into an all fir forest. In turn, this ensures that the forest will not be completely extirpated by the budworm. And finally this ensures that the budworm will always have a food source that will not be extinguished.

What the above discussion has described is a system which is able to absorb change and still maintain the same relationships between their state variables (population levels). This persistent ability of a system is termed its resilience. This contrasts stability, which is the ability of a system to re-
turn to equilibrium after a disturbance, Holling (16, pp. 14).
Thus the budworm-forest is not a stable system:

C. S. Holling (16, pp. 15) argues via these above definitions that:

The budworm-forest is a highly unstable system and it is because of this instability that it has enormous resilience.

In light of this fact, we must be extremely careful not to weaken the resilience of the budworm-forest system by trying to stabilize the populations. C. S. Holling (16, pp. 21) warns:

The very approach that assures a stable maximum sustainable yield of a renewable resource might so change these deterministic conditions that the resilience is lost or reduced so that the occurrence of a rare event can trigger a sudden dramatic change and loss of structural integrity of the system.

Holling has thus raised the unthinkable catastrophe: could our management strategy cause the extinction of our forest? We must make sure to be extremely careful in what our management decisions should be.
CHAPTER 2

BUDWORM-FOLIAGE-FOREST MODEL

This section presents a new model of the budworm-fir forest. The goal, in constructing a new model, is to establish a continuous, dynamic, feedback system that is dependent upon as few state variables as possible. By creating this particular format, techniques of optimal control theory and phase plane analysis can be used.

There are four state variables which completely describe the state of the budworm-fir forest. The variables are:

1. budworm egg density (in eggs/tsf - number of budworm eggs per ten square foot plot of foliage)
2. the mode of the forest distribution
3. new foliage growth (amount in foliage units of year old foliage)
4. old foliage growth (two to ten year old foliage)

Note that new foliage is distinguished from old because budworms survive better on new foliage, Stedinger (34, pp. 2-7,10).

New and old foliage levels are described in terms of foliage units. A completely undefoliated tree will possess one new foliage unit per ten square feet (max(F1)=1.0 FU/tsf) and 2.8 foliage units of old foliage (max(F2)=2.8 FU/tsf). However do not confuse foliage unit measurement with the total foliage that a tree posses. A completely undefoliated ten year old and a completely defoliated forty year old tree will both
have 3.8 FU/tsf but the forty year old tree has much more total
foliage. See table 2-1, Bakuzis and Morris(25).

2.1 Budworm dynamics

The budworm dynamic submodel is broken down into different
stages of development to account for interactions with the
other variables. This follows exactly the same procedure that
Stedingger (34) used in the construction of his model. The
major submodels are:

1. small larvae survival (Instar I-II)
2. large larvae survival (Instar III-VI)
3. adult survival
4. fecundity factor

Budworm eggs hatch into instar larvae I, which undergo
wind-blown dispersal, in the late summer. These larvae
land on trees and spin hibernacula in which they overwinter.
Instar larvae II emerge in the spring when there is an instance
of consecutive warm, dry days. Over the next few months the
larvae develop from instar II-VI in which feeding is their
main activity. The larvae then pupate and become adult moths.
Next, there is a mating period followed by further dispersion
of females, which try to lay their eggs, where there will be
good food sources for its offspring, Stedingger (34, pp. 2-28).
See figure 2-1 for the general time periods in which the six
instar larvae develop, Greenbank (15, pp. 458).

There are many factors which effect the budworm survival
at its various stages of development. A general relationship
of budworm survival can be observed from table 2-2, Morris
<table>
<thead>
<tr>
<th>Stand Age (years)</th>
<th>Average Stand Diameter at Breast Height for Site Index 60 (60 ft ht at 65 years)</th>
<th>Morris's Branch Surface Area, in Thousands of 10 ft² Per Acre (1,000 tsf/acre)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>20</td>
<td>1.0</td>
<td>15.4</td>
</tr>
<tr>
<td>35</td>
<td>3.6</td>
<td>27</td>
</tr>
<tr>
<td>45</td>
<td>5.2</td>
<td>40</td>
</tr>
<tr>
<td>55</td>
<td>6.6</td>
<td>45</td>
</tr>
<tr>
<td>65</td>
<td>7.8</td>
<td>38</td>
</tr>
<tr>
<td>80</td>
<td>8.6</td>
<td>20</td>
</tr>
</tbody>
</table>
Percentage distribution of the larval population according to instars at Green River

Figure 2-1
Table 2-2

Life Table for Spruce Budworm Based on Mean Values

<table>
<thead>
<tr>
<th>x</th>
<th>(N_x)</th>
<th>(S_x)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Age</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>200</td>
<td>.81</td>
</tr>
<tr>
<td>Instar I</td>
<td>162</td>
<td>.18</td>
</tr>
<tr>
<td>Instar III</td>
<td>29.2</td>
<td>.14</td>
</tr>
<tr>
<td>Pupae</td>
<td>4.10</td>
<td>.66</td>
</tr>
<tr>
<td>Adults</td>
<td>2.71</td>
<td>.51</td>
</tr>
<tr>
<td>Porportion Female</td>
<td>1.38</td>
<td>.47</td>
</tr>
<tr>
<td>Fecundity</td>
<td>.65</td>
<td>160 eggs /female</td>
</tr>
</tbody>
</table>

Eggs after one Generation 104
This budworm table gives ballpark figures to judge the accuracy of the model by.

2.1.1 Small larvae survival

Instar larvae I and II survival is dependent upon which mode tree diameter the budworm is feeding and upon the mean number of foliage units the trees possess. Observed relationships between small larvae survival and tree diameter, as reported by Stedinger (34, pp. 2-38), are shown in figure 2-2.

The tree diameter-survival relationship is basically a quadratic function with a few modifications. The assumptions used in this regression fit are the following:

1. The maximum survival (31%) is at the 4.4 inch dbh class (4.4 inch diameter at breast height for a forty year old tree with a site index of 60). This corresponds to trees which possess the most total foliage (see table 2-1).

2. Survival is very poor in sapling stands due to instar larvae I's inability to overwinter on the sapling stand's smooth bark, Jones (19).

3. Survival is still quite good on fifty to eighty year old stands because, although the total foliage drops off, there is still enough total foliage available to support large populations of larvae.

The strategy is to compute small larvae survival with respect to the mode diameter class: and with the foliage level initially assumed constant at 3.8 FU/tsf. After this computed, the small survival at 3.8 FU/tsf, \( S_{3.8}(X) \), will be modified to account for all foliage levels.

By assumption 1

\[ X = 4.4 \text { dbh} \]

\[ \text{maximum } S_{3.8}(X) \]
Observed Relationship Between Small Larval Survival and Tree Diameter (Points are means computed from number of sets indicated)
This implies
\[ S''_{s3.8}(X) < 0 \]  
(1)
\[ S'_{s3.8}(X) = 0 = a(X-4.4) \]  
(2)

With a being negative. Integrating (2) gives:
\[ S_{s3.8}(X) = a(X+2/2 - 4.4X + c) \]  
(3)

From table 2-2
\[ S_{s3.8}(4.4) = a(4.4^2/2 - 4.4^2 + c) = .31 \]  
(4)
\[ S_{s3.8}(8.3) = a(8.3^2/2 - 4.4^2 + 3.8 + c) = .13 \]  
(5)

(5) - (4) gives
\[ -.18 = a(.25\cdot8.3 - 4.4^2)/2) \]  
(6)

Solving (6) for a solves to \( a = -.024 \). Now plug a back into (4)
and solve for c
\[ c = .31/a + 9.68 = -3.06 \]  
(7)

This gives the unique solution for (3).
\[ S_{s3.8}(X) = -.024(X+2/2 - 4.4X - 3.06) \]  
(8)

As stated earlier small larvae survival also depends on
the mean foliage level of the stand. See figure 2-3 for small
larvae survival on a forty year old tree with respect to dif­
ferent foliage levels, Stedinger (34, pp. 2-38). This curve
is interpreted in an ecological sense as foliage levels in­
crease, the budworm's survival will increase. The budworm will
survive best at 3.8 Fu/tsf and where \( S_s(X,F) = S_{s3.8}(X) \).

Define \( S_{s40}(F) \) to be the percentage of \( S_{s3.8}(X) \) that sur-
Figure 2-3

Modeled Small Larval Survival as a Function of Fall Foliage

Total Fall Foliage

( FU/tsf )
vives at a given foliage level, F. Hence

$$S_s(X,F) = S_{s3.8}(X) \cdot S_{s40}(F)$$  \hspace{1cm} (9)$$

There are some distinctive properties about $S_{s40}(F)$:

1. The shape of $S_{s40}(F)$ should look similar to the shape of figure 2-3.

2. $F = 0$ implies $S_s(X,0) = 0$

3. $F = 3.8$ implies $S_{s40}(3.8) = 1$ implies $S_s(X,3.8) = S_{s3.8}(X)$

4. Figure 2-3 calculates survival with respect to fall foliage levels. This effects $S_{s40}(F)$ because it is calculated with respect to spring foliage levels. As will be seen in the foliage dynamic section, the fall foliage will generate new shoots, which will make the spring levels higher. This implies that there is an increasing return to scale of fall foliage to spring foliage. Hence the $S_{s40}(F)$ curve should be slightly more pessimistic at each level of foliage. That is if $S_{s40}(F)$ and figure 2-3 were in scale then $S_{s40}(F)$ would be less than or equal to figure 2-3 at all levels of F.

By properties 1 and 2, let

$$S_{s40}(F) = a\sqrt{F}$$  \hspace{1cm} (10)$$

And by property 3

$$S_{s40}(3.8) = a\sqrt{3.8} = 1$$  \hspace{1cm} (11)$$

Solve for $a$

$$a = \frac{1}{\sqrt{3.8}} = .513$$  \hspace{1cm} (12)$$

This gives the solution of (10)

$$S_{s40}(F) = .513\sqrt{F}$$  \hspace{1cm} (13)$$

Solve for small larvae survival using (8) and (13)

$$S_s(X,F) = S_{s3.8}(X) \cdot S_{s40}(F)$$

$$= [-.024(X+2/2 - 4.4X - 3.06)] \cdot .513\sqrt{F}$$  \hspace{1cm} (14)$$
Solve for the third instar larvae population level, \( N_3 \):

\[
N_3 = S_3(X,F) \cdot N_1 \tag{15}
\]

### 21.2 Large larvae survival

The large larvae survival factor is represented as the product of the instar larvae III-IV and instar larvae V-VI survival factors.

\[
S_L = S_{34} \cdot S_{56} \tag{1}
\]

Two stage large larvae survival allows for a more accurate survival due to spraying factor, which occurs in the fourth instar larvae stage, Stedinger (34, pp. 2-37).

The factors of large larvae survival are parasitism, defoliation, weather and density-dependent factors. As in the Maine Model, the density-dependent and weather factors are accounted for in both stages of large larvae survival by taking the square root effect as a subfactor in each stage.

Parasitism is calculated solely in the fifth-sixth instar survival period and the defoliation effect on survival is computed separately for each stage. This gives the general form of the two stages in large larvae survival:

\[
S_{34} = P \sqrt{S_w} \cdot S_{dd}(F,N_3) \tag{2}
\]

\[
S_{56} = S_{Para} \sqrt{S_w} \cdot S_{dd}(F,N_{s5}) \tag{3}
\]

Where

- \( P \) = Proportion of an individual larvae's demand for new foliage fulfilled
- \( S_F \) = Foliage survival factor
- \( M_s \) = Mortality due to spraying
\[ N_{55} = \text{Fifth instar larvae population after spraying} \]
\[ = N_5(1-M_5) \]
Substitute (2) and (3) into (1)
\[ S_L = S_{\text{Para}} \cdot P \cdot S_{F} \cdot S_{w} \sqrt{S_{dd}(F, N_3) \cdot S_{dd}(F, N_{55})} \]

**Weather**

There is an overwhelming amount of evidence which correlates budworm outbreaks to the weather because of a significantly higher large larvae survival rate in warm, dry springs, Greenbank (15, pp. 45) Miller's warm-dry day index explained 64% of observed variation in budworm survival from 1946-1970, Miller (23).

\[ S_w = \exp[.09(w-18.9)] \]  
(4)

Where

\[ w = \text{the number of warm, dry days in budworm development} \]

Miller estimated mean\((w) = 18.9 \text{ and var}(w) = 40.1\). In this model the number of warm, dry days, \(w\), will be represented as a continuous cyclic function, in order to keep the model a closed feedback system. Dr. Mott believes that this type of estimate is just as valid as a random number estimate of the weather and there is no reason not to use it when considering management decisions. Let:

\[ w = w(t) = 18.9 + 18.9\sin(\pi t/4) \]  
(5)

Thus the number of warm, dry days in the spring will vary from zero to thirty-eight days and cycle with a period of eight years.
Density-dependent survival factor

Initial studies of the density-dependent factor on budworm survival comes from Stedinger's analysis in the Maine Model. However, the functional relation of survival of the budworm versus budworm density is too pessimistic, especially at the low population density levels. That is, in using the Maine Model's density-dependent factor, budworm populations levels go extinct after the end of an outbreak and also there is no possibility of an outbreak without a tremendous influx of eggs into the stand (about 150 eggs/tsf). Stedinger's density-dependent factor is modified to correct this.

The assumption used in the modified version of the density-dependent factor is an increase in survival as egg densities approach zero. It should be noted here that not much is known about endemic levels of egg density because of the difficulty which entomologists have in collecting such data, Mott (26) and Seymore (30). Test runs of the completed budworm-forest, to chose the modified factor which best describes the observed behavior, are described later. The modified version of the Maine Model looks as follows:

\[
S_{dd}(F, N_3) = (1 - \theta)[.1 + .7N_3/93 + N_3]
\]
\[+ \theta \cdot [b + a/N_3 + .7N_3+3/(68800 + N_3+3)](6b)
\]

where

\[ b + a/N_3 \equiv \text{modifies survival at low densities} \]
\[ N_3 \equiv \text{third instar larvae density} \]
\[ F \equiv \text{total foliage unit level (} F_1 + f_2) \]
\[ \theta = \text{weighting factor which depends on degree of defoliation} \]

Theta weights the large larvae survival for different levels of infestation. The first part of the equation, (6a), represents survival in moderately infested areas, see figure 2-4, Stedinger, (34, pp. 2-45). The second part of the equation, (6b), accounts for survival in heavily infested areas, see figure 2-5. Data for these curves comes from the Green River study, Morris (25, pp. 57-58 and 144-149).

The weight for survival versus infestation levels is given in the Maine Model as:

\[
\begin{align*}
\theta &= 2 - 2F/3.8 & \text{for } F \leq 1.9 \\
&= 1 & \text{otherwise}
\end{align*}
\]  

(7a) (7b)

This equation is modified because it is not differentiable at \( F=1.9 \). Theta is approximated with a polynomial regression fit given as:

\[ \theta = .97 + .199F - .122F^2 \]  

(8)

The fit is good to the 5% level, see figure 2-6 for a comparison of the Budworm-forest and the Maine Models of theta.

Third-fourth instar larvae survival

The third-fourth survival of the budworm depends on the square root of the density-dependent and weather factors multiplied with the proportion of foliage consumption demand for new foliage which is fulfilled. Proportion of foliage that is fulfilled is defined as:

\[ P = \frac{CN}{.0008/N_3} \]  

(9)

Where

CN = actual new foliage consumed (discussed in foliage dynamics section)
Figure 2-4

Large Larval Survival in Moderate Infestations

Third Instar Density (larvae/ft²)

(Solid line is modeled survival. Points represent mean of at least ten sets of data.)
Figure 2-5
Large Larval Survival in Severe Infestations

Third Instar Density (larvae/tsf)
(Solid line is modeled survival for $F = .95$ and 1.80 foliage units.)
Figure 2-6
Moderate-Heavy Infestation Weighting Functions

Value of Weighting Function

Rudworm-forest Model  Maine Model

Total Foliage After Fourth Instar Feeding
.0008N₃ = foliage demanded by third instar larvae
.0008 Fu/tsf = foliage demand of a third instar larval

This gives:

\[ S_{34} = P/S_w(t) \cdot S_{dd}(F,N_3) \]  \hspace{1cm} (10)

The fifth instar population after spraying is:

\[ N_{s5} = (1-M_s) \cdot S_{34} \cdot N_3 \]  \hspace{1cm} (11)

Where

\[ M_s = \text{mortality rate of fourth instar larvae due to spraying} \]

Note that actual foliage consumed in the third-fourth instar larvae feeding period is new foliage. This is because third and fourth instars survive poorly on old foliage, Blais (10).

Survival of Instar V-VI

Instar five and six is the last instar period in budworm development. This section will discuss parasitism and defoliation survival factors.

The majority of parasites attack the fourth-sixth instar larvae. The functional relationship for survival in moderate unsprayed infestation levels is given in Morris (25, pp. 242).

\[ S_{\text{Para}} = 1 - .35\exp[-.0026N_3] \]  \hspace{1cm} (12)

This is modified to account for spraying by replacing \( N_3 \) with \( N_{s3} \). Hence:

\[ S_{\text{Para}} = 1 - .35\exp[-.0026(1-M_s)N_3] \]  \hspace{1cm} (13)
Survival and Defoliation

Instar V and IV can survive on old foliage, but prefer new foliage. Generally most new foliage in an area will be consumed before the Instar V-VI begin feeding on old foliage, Blasis(i3). The following terms are defined for purposes of this discussion:

- \( \text{FD} \) = total foliage demand = \( .25N_5 \)
- \( \text{OFD} \) = old foliage demand
- \( \text{OFC} \) = old foliage consumption
- \( \text{NFC} \) = new foliage consumption
- \( \text{FSS} \) = foliage-search survival
- \( \text{F}_{14} \) = new foliage remaining after fourth instar consumption
- \( \text{F}_{24} \) = old foliage remaining after fourth instar consumption

Thus new foliage consumption of Instar V-VI is the minimum of new foliage left and total foliage demand.

\[
\text{NFC} = \min[\text{F}_{14}, \text{FD}] \quad (14)
\]

This is approximated into a continuous multivariable function in the foliage dynamics section. Stedinger (34, pp. 2-50) gives the foliage-search survival factor as:

\[
\text{FSS} = .25 + .75\frac{\text{NFC}}{\text{FD}} \quad (15)
\]

This is the prop. of larvae which survive to feed on old foliage. Now old foliage demand will be larvae surviving the foliage search times the remaining foliage demand.

\[
\text{OFD} = \text{FSS}(\text{FD}-\text{NFC}) \quad (16)
\]

The foliage survival factor is the percentage of foliage consumed out of new consumption added to a modified percentage of foliage demand consumed out of old foliage to account for
extra searching. Stedinge (34, 2-50) gives the relationship

\[ S_F = \frac{(NFC + 0.250 FC/KSS)}{FD} \]  \hspace{1cm} (17)

This completes the discussion of large larvae survival, the survival of the budworms through the instar periods III-VI.

The pupal population density is given by

\[ N_p = S_L N_3 \]  \hspace{1cm} (18)

2.1.3 Adult Survival

The adult survival factor includes survival of pupae and adult moths from predation, mating failure, failure of females to lay all their eggs, and females laying eggs in a non-host areas. However, variation in pupal survival has very little significance in the variation of the general survival of the budworm, Morris(25, p. 35). Thus the pupae survival factor is taken as a constant, the value of the mean pupae survival, \( S_{pupae} = 0.66 \). This model also takes the survival in the adult phase, the ratio of observed egg density deposited to the expected density based on pupae density and fecundity, to be a constant at \( S_{adult} = 51\% \), Morris(25, p. 99). This is because of the immensely complex relationships are not modeled very well to date.

2.1.4 Proportion Female and Fecundity

The average proportion of females observed in the unsprayed area of the Green River study is 47%, Morris(28, pp. 75), and will be used in this model. Fecundity is the number of budworm eggs laid by a female larvae. This effect is important because it determines the actual egg densities of next year's budworm density. This model uses the equation given in the Maine Model,
Blais (10) reports that the mean fecundity of larvae fed on new foliage is 185 while fecundity of old foliage fed larvae is 79, hence:

$$FEC = 185\frac{NFC}{FD} + 790\frac{FC}{(FSS \cdot FD)}$$  \hspace{1cm} (19)

where

$$\frac{NFC}{FD} = \text{prop of V-VI demand fulfilled with new foliage}$$

$$\frac{OFC}{(FSS \cdot FD)} = \text{prop of demand fulfilled with old foliage consumed}$$

### 2.1.5 Budworm Dynamics

In this section a differential equation will be approximated which represents the continuous growth function of the budworm. The assumption here is that BW levels correspond to budworm egg density in the spring and that one time unit is one year. Hence:

$$BW(t + 1) = BW(t)S_sS_pS_pupaeS_{adult}FEC$$  \hspace{1cm} (20)

let:

$$BW(t + 1) = BW(t) + \Delta BW(t)$$  \hspace{1cm} (21)

And substitute in (20):

$$\Delta BW(t) = -BW(t) + BW(t)S_sS_pS_pupaeS_{adult}FEC$$  \hspace{1cm} (22)

This is the equation which gives the continuous growth function of the budworm over time with respect to the foliage levels, BW level, and the mode diameter class.

### 2.2 Foliage Dynamics

Foliage is the critical resource without which the budworm-forest could not survive. The evolution of a mature stand and a budworm epidemic depends directly on the level of foliage in the stand. The section on budworm dynamics demon-
strates the correlation between budworm survival and foliage levels. The next section will show how the vitality of the forest also depends critically on the foliage level.

This section will talk about how much foliage is actually consumed by the BW, i.e. NFC and OFC etc. The regeneration phase of foliage is also modeled. This is combined to form a difference equation which is approximated by a differential equation as in the budworm section.

Defoliation by the budworm occurs in the second through sixth instar larvae stages, large larvae. This model has a defoliation factor for the third-fourth and fifth-sixth instar levels.

2.2.1 Defoliation in Instar III-IV

This model assumes that there will be no survival by consuming old foliage at this stage of budworm development. Therefore, no old foliage consumption takes place in this period. In the budworm dynamics section, foliage consumption, CN, was defined. Stedinger (34, pp. 2-47) models foliage consumption as:

\[ \text{CN} = F_l[1 - \exp(-0.0008N_3/F_l)] \]

Where

\[ \frac{(0.0008/N_3)}{F_l} = \text{Percentage new foliage demand to total new foliage} \]

Foliage levels after Instar IV is given by:

\[ F_{l4} = F_l - F_l + \exp(-0.0008N_3/F_l) \]
\[ = \exp(-0.0008N_3/F_l) \]  
\[ F_{24} = F_l \]
2.2.2 Defoliation in Instar V-VI

In this stage the budworm eats both new and old foliage. However, almost all the new foliage is eaten before the budworm begins feeding on old foliage. Old foliage consumption is modeled in the same form as foliage consumption, CN, in the defoliation effect of Instar V-VI. Define old foliage consumption as:

\[
OFD = F_{24}[1 - \exp(-OFD/F_{24})] 
\]

where

\[
OFD/F_{24} = \text{Percentage old foliage demanded to foliage available}
\]

The old foliage left in the fall is:

\[
F_{24}^{\text{fall}} = F_{24} - F_{24} + \exp(-OFD/F_{24}) 
\]
\[
= \exp(-OFD/F_{24})
\]

New foliage consumption was defined in the BW section as:

\[
NFC = \text{min.}[F_{14}, FD]
\]

In this model new foliage consumption is approximated by a continuous multiple regression curve. The independent variables of new foliage consumption are the independent variables of both the new foliage after the fourth instar equation and the foliage demand equation. Thus:

\[
FD = FD(N_1, X, F_1, F_2)
\]
\[
F_{14} = F_{14}(N_1, X, F_1, F_2)
\]

Hence

\[
NFC = NFC(N_1, X, F_1, F_2)
\]

To get a good approximation of new foliage consumption a BASIC program is written, to vary all independent variables over a wide range and compute a table comparing combinations of inputs
with new foliage consumption. This data bank is inputed to COSAP, a software statistical package which performs the multiple regression analysis. New foliage consumption is computed with 176 different combinations of inputs and yields an F-ratio = 419, good to beyond the 1% level. New foliage consumption is defined:

\[ NFC = 0.046 - 0.014\text{LN}(N_1) + 0.81F_d - 0.0004X \quad (10) \]

Note that NFC does not vary greatly enough at different large larval survival factors to vary NFC with different approximation of large larval survival. This gives new-fall foliage as:

\[ F_{\text{fall}} = \exp(-0.0008N_3/FD) \quad (11) \]

2.2.3 Foliage Regeneration

Foliage regeneration depends on how much new foliage is produced and how much of the old fall foliage is retained. Foliage gradually loses its photosynthetic ability after about eight years, Stedinger (34, 2-26). This stage can be thought of as maximizing the trees photosynthetic abilities.

New spring foliage levels are determined by the amount of total foliage in the fall. A tree that is just slightly defoliated in the fall can produce a full new spring foliage unit due to increased productivity of the remaining foliage that is exposed to more light, Stedinger (34, pp. 2-25). Thus the regenerative abilities of foliage are better than a linear relationship between total fall foliage and new spring foliage. See figure 2-7 for a comparison with the actual and linear relationships. The assumptions of the foliage production function are:
Figure 2-7

New Foliage Produced

Total Fall Foliage

(FU/"w")
1. a better than linear reproductive ability

2. at zero total fall foliage units no new foliage is produced and the tree dies

3. the maximum new foliage produced is when the trees are completely undefoliated in the fall.

By assumption 1, a quadratic function is used. By assumption 3 the change in foliage production is:

\[ FP'(F_{\text{fall}}) = a(3.8 - F_{\text{fall}}) \quad (12) \]

Where

\[ FP(F_{\text{fall}}) = \text{foliage production function i.e. new foliage produced at given levels of total fall foliage} \]

Integrating both sides gives:

\[ FP(F_{\text{fall}}) = a[c + 3.8F_{\text{fall}} - F_{\text{fall}}^2/2] \quad (13) \]

By assumption 2:

\[ FP(0) = 0 = ca \quad (14) \]

This implies that \( c = 0 \).

Again by assumption 3:

\[ FP(3.8) = 1 = a[3.8 \cdot 3.8 - 3.8^2/2] \quad (15) \]

This gives a unique value for \( a \) by solving (15):

\[ a = \frac{2}{3.8^2} \quad (16) \]

Substitute (16) and (14) into (13) gives:

\[ F_{\text{spring}} = FP(F_{\text{fall}}) = 2F_{\text{fall}}/3.8 - F_{\text{fall}}^2/3.8^2 + 2/3.8^2 \quad (17) \]

The foliage retained by trees in the fall is the old foliage level in the spring. That is:

\[ F_{\text{spring}} = F_{\text{fall}} + SF_{2}\cdot F_{\text{fall}} \quad (18) \]

Where

\[ SF_{2} = \text{the old foliage survival function} \]
The old fall foliage survival function has the following properties:

1. When the maximum new foliage is produced (1 FU/tsf) only 65% of fall foliage will survive into the following spring. This leaves the maximum level of spring old foliage i.e. when:

   \[ F_{\text{fall}} = 3.8 \implies F_{\text{spring}} = 1 + 0.65 \times 2.8 = 2.8 \quad (19) \]

2. As the total fall foliage levels decrease, the old fall foliage survival will increase. The trees maintain their maximum photosynthetic capacities by holding more old fall foliage.

3. Old fall foliage survival rate is at most 82.5% because after eight years all the photosynthetic powers are lost. This rate corresponds to the survival level when no new spring foliage is produced \((F_{\text{fall}} = 1.9)\).

The survival of old fall foliage is approximated with a third degree polynomial regression fit good to beyond the 1% level. See figure 2-8 for a graph of the fall foliage survival function.

\[ S_F = 0.82 - 0.083F_{\text{fall}} + 0.068F_{\text{fall}}^2 - 0.049F_{\text{fall}}^3 \quad (19) \]
Figure 2-8
Old Foliage Survival ($S_2$)

Total Fall Foliage

( FU/tsf )
2.3 Host Forest Dynamics

The dynamics of the budworm-forest system is cyclical by nature. This section will develop a growth function for the forest, a tree mortality function, a tree density function, and a function which represents the budworm-forest. There is far less known about the growth patterns of the forest under varying levels of infestation. The function derived, especially the tree mortality function, represent "ball park" figures which will generally describe the forest i.e. mimic the observed forest behavior over the last two hundred years.

2.3.1 Uninhibited forest growth

Uninhibited forest growth is the rate at which trees grow in diameter (dbh) without any budworm interference. The objective of this section is to derive, by regression analysis, a growth versus diameter class size curve. Age versus mean diameter tables are available in Morris(25). Note that in this paper all state variables are measured on site indexes of sixty i.e. the average tree will grow sixty feet high in sixty-five years.

The first step is to compute a regression curve of the diameter with respect to time. Using the software package COSAP, a second degree polynomial is calculated good to the 1% level.

\[ \text{MODE}(t) = -3.96 + 0.266t - 0.0014t^2 \]  

(1)

The instantaneous velocity of the mode with respect to time is derived by differentiating the approximation of the mode
versus time, equation (1).

\[ \text{MODE}'(t) = 0.266 - 0.0028t \] (2)

The ordered pairs (MODE(t), MODE'(t)) at values of time ranging from ten to eighty years, are the data points for the regression fit of the mode versus the change in the mode. See table 2-3 for a comparison of the observed and the expected values of the no budworm world growth in the mode of the forest distribution.

\[ \text{MODE}'(t) = 0.21 - 0.0009\text{MODE} - 0.002\text{MODE}^2 \] (3)

The fit of (3) to the observed data is good to beyond the 1% level.

2.3.2 Budworm's effect on immature forest growth

The budworm's effect on the growth on the forest is not entirely clear from the research that has been done to date. Mott (26) and Seymore (30) claim that many trees which survive a moderate to heavy infestation will lose a significant amount of their normal growth. However, because the stand is now more open, from thinning from budworm induced mortality, each tree will get more sunlight and will compensate growth. In fact, in twenty years, budworm damage is no longer detectable. There are other complications.

Heavy infestations of the immature host forest result in an increase in the mode of the tree distribution, Seymore (30). See table 2-4 and figure 2-9 for results of the Kedgwick Control Area study in New Brunswick, Baskerville (4). As can be seen, in the table and graph, the average diameter class tree, that dies, due to budworm induced mortality, is less than mode dia-
### Table 2-3
Values for the Natural Growth Function

<table>
<thead>
<tr>
<th>Observed Growth</th>
<th>Expected Growth</th>
<th>Average Diameter</th>
<th>Tree Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>.210</td>
<td>.203</td>
<td>1.0</td>
<td>20</td>
</tr>
<tr>
<td>.182</td>
<td>.190</td>
<td>2.6</td>
<td>30</td>
</tr>
<tr>
<td>.154</td>
<td>.161</td>
<td>4.4</td>
<td>40</td>
</tr>
<tr>
<td>.126</td>
<td>.125</td>
<td>6.0</td>
<td>50</td>
</tr>
<tr>
<td>.098</td>
<td>.087</td>
<td>7.3</td>
<td>60</td>
</tr>
<tr>
<td>.070</td>
<td>.060</td>
<td>8.1</td>
<td>70</td>
</tr>
<tr>
<td>.042</td>
<td>.042</td>
<td>8.6</td>
<td>80</td>
</tr>
<tr>
<td>.014</td>
<td>.027</td>
<td>9.0</td>
<td>90</td>
</tr>
</tbody>
</table>
### Table 2-4

#### Defoliation History

<table>
<thead>
<tr>
<th>Year</th>
<th>Percentage Defoliation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1948</td>
<td>0</td>
</tr>
<tr>
<td>1949</td>
<td>0</td>
</tr>
<tr>
<td>1950</td>
<td>20</td>
</tr>
<tr>
<td>1951</td>
<td>45</td>
</tr>
<tr>
<td>1952</td>
<td>91</td>
</tr>
<tr>
<td>1953</td>
<td>98</td>
</tr>
<tr>
<td>1954</td>
<td>98</td>
</tr>
<tr>
<td>1955</td>
<td>34</td>
</tr>
<tr>
<td>1956</td>
<td>92</td>
</tr>
<tr>
<td>1957</td>
<td>48</td>
</tr>
<tr>
<td>1958</td>
<td>2</td>
</tr>
<tr>
<td>1959</td>
<td>2</td>
</tr>
</tbody>
</table>

#### Mortality History

<table>
<thead>
<tr>
<th></th>
<th>Number of fir per acre</th>
<th>Diameter of average tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Living 1956</td>
<td>2,261</td>
<td>3.4</td>
</tr>
<tr>
<td>Dead 1957</td>
<td>471</td>
<td>2.7</td>
</tr>
<tr>
<td>Dead 1958</td>
<td>463</td>
<td>3.1</td>
</tr>
<tr>
<td>Dead 1959</td>
<td>254</td>
<td>3.5</td>
</tr>
<tr>
<td>Total dead</td>
<td>1,188</td>
<td>3.0</td>
</tr>
<tr>
<td>Residual</td>
<td>1,073</td>
<td>3.8</td>
</tr>
</tbody>
</table>
Figure 2-9

Tree and Basal Area Distributions for Living and Dead Balsam Fir in a Budworm Outbreak

[Diagram showing tree and basal area distributions for living and dead Balsam Fir with data for 1956 and 1957.]
meter class of the tree distribution. The result is an overall increase in the mode. This makes sense ecologically because a diameter class distribution, as described in the Kedgwick Control Study, is assumed to be of one age. This implies that the trees with below the mode diameter are suppressed and dominated by the more vigorous trees. Thus the budworm kills the weaker trees first and, as the outbreak lasts, larger diameter trees begin to die.

The object of this section is to model the effects of heavy to moderate budworm infestation on the mode of the immature host forest distribution. However, due to large gaps of knowledge about the actual effects of budworm infestation on forest growth, simplified assumptions for the Budworm-forest Model are made. It is assumed that the loss of growth in diameter size is offset roughly by the increase in the mode diameter size due to the loss of small diameter trees. Therefore, the net effect on the forest mode will be the change in the mode due to the uninhibited growth of the forest discussed in section 2.3.1.

Note that this assumption does not imply that there is nothing changing in the forest dynamics in heavy BW infestations. The Budworm-forest Model, as it stands, shows that there will be no change to the basic shape of the tree distribution. However, bw induced mortality does cause changes in the amplitude of the tree distribution, i.e, the tree densities.
2.3.3 Tree Density

Tree density decreases as trees get older and larger in diameter (dbh). See table 2-5 for relationships between age, diameter and tree density, for a site index of sixty, Morris (25). Mott (26) claims that a decrease in tree densities at larger diameters is due in part to mortality by suppression of less tolerant trees; but that much of the effect is from bw induced mortality in the immature stands. Tree density with bw thinning at immature diameter classes is approximated by regresional analysis giving:

\[ D(MODE) = 3687 - 1178\text{MODE} + 161\text{MODE}^2 + 7\text{MODE}^3 \quad (4) \]

This function will be used in the general forest distribution and is not modified for bw infestation at large diameter classes.

There is no need to model the effects of heavy infestation on large diameter class trees because the host population is completely destroyed. This effect is modeled, rather, as the regeneration of a thick, dense sapling stand.

2.3.4 Regeneration

Regeneration is represented in this model by setting the old age mode equal to the mode equivalent to a zero to ten year old stand. There must be an established threshold level at which the old age diameter class is ignored and the regeneration phase is introduced. This threshold will be termed the trees' CRASH Level. A mode will crash when the average foliage level is so low that the great majority of trees are lost.

The mortality function given by Stedinger (34) is used
### Table 2-5

Number of Trees per Acre in Fir-Spruce Stands

<table>
<thead>
<tr>
<th>Tree Density</th>
<th>Average Diameter</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>2675</td>
<td>1.0</td>
<td>20</td>
</tr>
<tr>
<td>1550</td>
<td>2.6</td>
<td>30</td>
</tr>
<tr>
<td>1025</td>
<td>4.4</td>
<td>40</td>
</tr>
<tr>
<td>825</td>
<td>6.0</td>
<td>50</td>
</tr>
<tr>
<td>775</td>
<td>7.3</td>
<td>60</td>
</tr>
<tr>
<td>750</td>
<td>8.1</td>
<td>70</td>
</tr>
<tr>
<td>740</td>
<td>8.6</td>
<td>80</td>
</tr>
<tr>
<td>735</td>
<td>9.0</td>
<td>90</td>
</tr>
</tbody>
</table>
to judge the percentage of trees lost at various foliage levels.

The basic equation for a forty year old tree is:

\[
M = \begin{cases} 
0 & F > 1.2 \\
1 - F/1.2 & F \leq 1.2 
\end{cases} 
\] (5)

Here 1.2 is the minimal level at which no mortality occurs, M_0. The crash level is figured by solving for the foliage level which causes a large percent mortality in the distribution, see Table 2-6 for details. A crash level function with respect to the mode of the distribution is approximated by regression analysis.

\[
\text{CRASH(MODE)} = -0.097 + 0.084\text{MODE} 
\] (6)

Thus the mode function modified for regeneration is:

\[
\text{MODE}_R = \text{MODE}'(t) - (\text{MODE} - 0.2)H[\text{CRASH(MODE)} - F] 
\] (7)

where

\[
H(x) = \begin{cases} 
0 & x < 0 \\
1 & x \geq 0 
\end{cases} 
\] (8)

Thus when the threshold is reached, the new mode will have a diameter of 0.2. Thus the approximate differential equation of (7) is:

\[
\text{MODE}'_R(t) = \text{MODE}'(t) - (\text{MODE} - 0.2)H[\text{CRASH(MODE)} - F] 
\] (9)

2.3.5 The Dynamic Tree Distribution

The forest dynamics of this model is represented by a moving probability distribution curve. Seymore (30) suggests that the Weibull Distribution is very appropriate because it drops quickly and asymptotically to zero as the independent variable approaches zero and ten. The Weibull Distribution is
Table 2-6

Foliage Levels Where Tree Population Crash

<table>
<thead>
<tr>
<th>Crash Level</th>
<th>Min. Zero Mortality</th>
<th>Tree Diameter</th>
<th>Number of Trees</th>
<th>Percent Trees Killed</th>
</tr>
</thead>
<tbody>
<tr>
<td>.30</td>
<td>1.2</td>
<td>4.4</td>
<td>1025</td>
<td>75</td>
</tr>
<tr>
<td>35</td>
<td>1.4</td>
<td>6.0</td>
<td>825</td>
<td>70</td>
</tr>
<tr>
<td>53</td>
<td>1.6</td>
<td>7.3</td>
<td>775</td>
<td>66</td>
</tr>
<tr>
<td>60</td>
<td>1.8</td>
<td>8.1</td>
<td>750</td>
<td>66</td>
</tr>
<tr>
<td>63</td>
<td>1.9</td>
<td>8.6</td>
<td>740</td>
<td>66</td>
</tr>
<tr>
<td>63</td>
<td>1.9</td>
<td>9.0</td>
<td>735</td>
<td>66</td>
</tr>
</tbody>
</table>
given by:

\[ W(x) = aBx + (B-1) \exp(-ax) \]  

(10)

The mode of the Weibull Distribution is found by differentiating with respect to \( x \) and setting the derivative equal to zero.

\[ W'(x) = aB[(B-1)x + (B-2) \exp(-ax) + x(B-1)(-aBx + (B-1)) \exp(-ax)] \]  

(11)

Collect common terms and set equal to zero:

\[ W'(x) = x + (B-2)aB \exp(-ax) \cdot [(B-1) - aBx + R] = 0 \]  

(12)

This gives mode:

\[ \text{MODE} = \left[ \frac{(B-1)}{aB} \right] + \left( \frac{1}{B} \right) \]  

(13)

In this model the shaping parameter is assumed equal to two.

Substitute into (13):

\[ \text{MODE} = \sqrt{\frac{57}{a}} \]  

(14)

The forest is represented as the sum of two Weibull Distributions. The forest is represented as having two modes which represent two diameter classes approximately different by forty years. This allows for a forest which closely resembles the forest described in the Green River Study, Baskerville (5, pp. 48). See Figure 2-10 for an illustration of the Green River Forest simulation.

\[ \text{FOREST}(\text{MODE}_1, \text{MODE}_2) = D(\text{MODE}_1)W(\text{MODE}_1) + D(\text{MODE}_2)W(\text{MODE}_2) \]  

(16)

Where subscripts are used to distinguish the individual modes. Note that over time the Weibull Distribution spreads out and flattens and the density function also decreases. This eventually reduces the old aged component of the forest to an insignificant level, i.e. has minimal effect on the over-
Figure 2-10

Schematic Representation of Host Forest Development with no Forest Management
all composition of the forest. Regeneration then replaces the old component.

2.4 Further Research and Modeling

The Budworm-forest Model is by no means the final word on budworm and forest dynamics. There is a great need to continue to improve upon the latest modeling efforts. The following are some of the more important omissions of the Budworm-forest Model:

1. The Budworm-forest Model avoids the problem of the interactions of individual components of the forest, i.e. interactions between balsam fir, red spruce, and hardwood trees. Each component of the forest should have its own growth equation dependent upon budworm infestation and a suppression factor of the rest of the forest.

2. The model should be properly "scaled" to represent a particular sized forest. This would make it possible to set up a multisite forest which could be set up in different stages of development.

3. A major sub-model of the multisite forest would represent budworm dispersal as a function of wind direction and the amount of foliage available in nearby sites.

4. Another very important addition to the existing Budworm-forest Model would be the development of an objective function representing total utility derived
from the forest as a renewable resource. This paper did not consider the economic significance of the forest in a quantitative manner. The economic benefits of the forest must be modeled in order to consider management options.

5. A great improvement in the Budworm-forest Model would be the separate sub-modeling of natural (uninhibited) growth of the host tree and effects of budworm controlled growth. This would allow for the calculation of the budworm's benefit to the forest under controlled conditions.
CHAPTER 3. MODEL SIMULATION AND MANAGEMENT STRATEGY

The final section of this paper will discuss how well the newly derived Budworm-forest Model works. A FORTRAN program call BUDMOD simulates the Budworm-forest Model over a period of one hundred years. Tests are made with various modifications of the large larvae survival factor. After a suitable modification is chosen, section 3.2 compares the Budworm-forest Model with the Maine Model, Section 3.3 will examine the spray policy strategies that Stedinger (34) considered in his thesis. Lastly, section 3.4 will summarize the author's views on proper management of the softwood forest against the spruce budworm.

3.1 Budworm-forest Model Modifications

The object of this section is to put the model on the computer and make changes that will "fine tune" the simulation to peculiarities of the system. The modifications to be discussed are the density dependent survival factor and new foliage consumption of the budworm and the natural growth rate of the forest.

The modifications needed in the density dependent survival stems from the fact that, in its unmodified state, the budworm will go extinct and also require great influxes of budworms from other sites in order to reach outbreak proportions. This state of the system is corrected by introducing the term

\[
a/N_3 + b
\]

(1)

to the heavy defoliation part of the density dependent equa-
tion. Minimum survival in heavily defoliated sites, \( b = 0.05 \). The factor by which this survival increases below one third instar per tsf is \( a = 0.1 \). This gives

\[
S_{dd} = (1 - \theta)(0.1 + 0.7N_3/(93 + N_3^3) + \theta(0.05 + 0.1/N_3 + 0.7N_3^3/(68800 + N_3^3)) \tag{2}
\]

These parameters are estimated by picking the lowest possible values which prevents extinction of the budworm at low densities and ensures that good weather and the right forest composition will induce an outbreak.

The new foliage consumption function presented problems for the computer simulation. When there were high budworm densities and low foliage levels (in the middle years of an outbreak) the NFC approximation actually was higher than the amount of new foliage available, Fl-CN. This caused the simulation to crash by sending budworm populations off to infinity. Due to the lack of time to approximate a better continuous NFC and not because it would be impossible to create such a function, the computer simulation of the Budworm-forest Model uses Stedinger's (34) equation for new foliage consumption:

\[
NFC = \min[FD, Fl_4] \tag{3}
\]

It is interesting to note that the original curve fit for NFC had an F-ratio = 430 which is an excellent fit. This is an excellent example of how precisely balanced this dynamic system is.

The last modification arises out of an awful blunder by the author in estimating the natural growth rate of the forest. Recall in Section 2.3.1 that the growth rate is:
\[ \text{MODE}'(t) = 121 - 0.0009 \text{MODE} - 0.002 \text{MODE}t^2 \quad (4) \]

This, however, is an instantaneous rate of change and gives very poor predictions for discrete periods of time used in the computer simulation. A somewhat better approximation of the natural growth rate of the forest is found by choosing data points as follows:

1. Use the mode versus time equation for the mode data points:
   \[ \text{MODE}(t_1) = -3.96 + 0.266t_1 - 0.0014t_1^2 \quad (5) \]
2. At time \( t_1 \) the average change in the mode is calculated from time \( t_1 \) to \( t_1 + 1 \):
   \[ \Delta \text{MODE}(t_1) = \text{MODE}(t_1 + 1) - \text{MODE}(t_1) \quad (6) \]
3. Now a polynomial regression fit is used to correlate data of (6) to (5):
   \[ \Delta \text{MODE}(t_1) = 0.06 + 0.04 \text{MODE} - 0.002 \text{MODE}t^2 - 0.29E^{-3} \text{MODE}t^3 \quad (7) \]

This discussion has effectively ironed out most of the roughness in the simulation.

3.2 Comparison of the Budworm-forest and Maine Models

The Budworm-forest Model was created to overcome the shortfalls of the Maine Model in the following areas:

1. Forest Structure
2. Budworm Survival

The forest structure of the Maine Model is an "all age class" structure, i.e. in each site there are 17 different age classes, each occupying one-seventeenth of the land, Stedinger, (34, pp. 2-4 to 2-10). Change in the basic structure never occurs. This means that Stedinger's model does not simulate
a change in forest compositions, thus does not take proper account of why the budworm explodes to epidemic proportions.

As mentioned earlier, Baskerville (7) and Mott (26) observed that a two tier age class structure is the natural unmanaged forest. This type of structure allows for the limit cycle of the forest as described in the first chapter and is exactly what is described in the double Wiebull Distribution used in the forest equation of the Budworm-forest Model. This type of model allows for a better representation of the role of age distribution in determining a budworm outbreak.

The Budworm-forest Model overcomes problems of budworm extinction and allows outbreaks to occur without outside influxes of budworms. The parameters which effect this change were discussed in section 3.2. In the Maine Model the budworm can go completely extinct after a severe outbreak. Note that there is very little known about what happens at low egg density population levels but it does make sense to assume survival increases at very low density populations. This thought brings up the very sticky question of low egg density spraying as a best spraying technique. How can anyone know what will happen at these low egg density levels.

3.3 Spraying Strategies

One of the major findings of the Maine Model simulations is that a low egg density spray strategy is more cost effective than a high egg density threshold. Stedinger (34)
claims that spraying when egg densities reach 300eggs/tsf, there would be less spraying over the lifetime of the tree than spraying at, say, 650eggs/tsf. The Budworm-forest Model predicts very similar results. The author believes that Steding's analysis is correct, but has reservations, as to its practical effectiveness, due to many uncertainties in the low egg density budworm dynamics.

In any case, spraying is not a suitable long term policy due to its harmful ecological side effects. Spraying, in the author's opinion, should be viewed as a policy that aides forest managers to delay certain economic disaster while to proper long term techniques are discovered and implemented.

§ Concluding Remarks

This paper concentrated on building an accurate understanding of the budworm-host interactions. This last section reviews the 'intuitive' arguments of Baskerville (6) for the successful management of the forest. Also the author will discuss other options being considered by scientists present at the Second Annual Eastern Spruce Budworm Research Conference held at Orono, Maine. Baskerville makes two suggestions for long term forest management, both having to do with modifications of the stand composition to reduce susceptibility. The first method is to plant a higher percentage of trees in the stand that are less susceptible to budworm attack. Studies have shown that thirty to sixty percent change in forest composition are required to effectively change the forest's susceptibility. This new forest would take about sixty to
one hundred years before this counter ecological process could be completed, Baskerville (6).

The other modification will develop the forest into an even and all age class structure so that susceptible trees are harvested before an outbreak can get started. This also has the benefit of creating an even flow of harvestable wood. Flow is the major problem of the forest related industries.

The budworm creates an economic threat to the forest industries because it does not allow for an even flow of wood supply. The question that has not been considered as yet is how can a constant flow of wood fiber be guaranteed without tampering with the environment? It would be far better to have the technology to store logs over long periods of time to protect against this problem. At the present time, logs will lose their value as raw material within months after the trees die. At the Eastern Spruce Budworm Research Conference this type of technology along with new processes that can use older logs are viewed upon with some hope of success.

I believe that tampering with the budworm-forest ecosystem is very risky business over the long run. Spraying should be phased out as soon as feasibly possible. The other management policies seem viable and should be explored fully.
BIBLIOGRAPHY


