

Richard A. Fleming

Environment Canada, Canadian Forestry Service,
Forest Pest Management Institute, Sault Ste.
Marie, Ontario, Canada P6A 5M7

Although it may soon be possible to alter stand foliage quality and thus reduce budworm reproductivity, the impact of such changes on the budworm-forest system remains unclear. There are currently a number of hypotheses concerning the key biological mechanisms which drive the budworm-forest system. The possible effects of changes in foliage quality are examined for four such alternative hypotheses. Each hypothesis suggests that in the short-term reducing foliage quality will lengthen the interval between outbreaks, increase the rate of stand wood volume production, and increase outbreak severity--and overall, improve the budworm problem in economic terms. The situation for the long-term is less certain: in some circumstances reducing foliage quality may even aggravate the budworm problem from an economic viewpoint.

Introduction

The eastern spruce budworm, *Choristoneura fumiferana* (Clem.), is a naturally outbreaking defoliator of spruce (*Picea* spp.) and balsam fir (*Abies balsamea* [L.] Mill.) in the boreal forests of eastern North America. Epidemic populations severely defoliate their host trees over wide areas causing reduced growth, top kill, and tree mortality which often results in considerable economic difficulties for the forest industry (Irland 1980).

Aerial application of insecticide has been the principal means of controlling budworm damage since the early 1950's. However, concerns about environmental impacts and cost-effectiveness (e.g., Swenson 1980) have motivated a search for possible alternative control methods. It has long been recognized that stands differ in their likelihood of budworm damage (Balch 1946; Morris 1963, pp. 189-292) and more recently it has been observed that several important nutritional parameters vary with needle age, tree species, stand maturity and other factors affecting budworm development and density (Kimmins 1971; Shaw et al. 1978; White 1974). As a consequence it has been suggested that certain stand characteristics could be manipulated through selective breeding (e.g., Zobel 1982) or fertilizer application (e.g., Shaw et al. 1978) to "favorably" alter budworm-forest dynamics. But before much investment in such research, it seems prudent to anticipate how changes in stand characteristics might affect the budworm-forest system.

This paper explores the impacts that changes in one such stand characteristic, foliage quality, might have on budworm-forest dynamics. Here foliage quality refers to the rate at which increases in foliage consumption per budworm are accompanied by increases in budworm reproductivity.

Anticipation of the effects of reducing foliage quality requires some understanding of the biological mechanisms underlying budworm-forest dynamics. Currently, there is considerable disagreement regarding the relative importance of these mechanisms. Blais (1974) concludes that budworm outbreaks require extensive areas of mature stands of balsam fir; Baskerville (1976) and Jones (1979) stress the effects of background predators; Stedinger (1977) suggests that all outbreaks are triggered by moth invasions; and Royama (1982) implies that a complex of numerically responding parasitoids and diseases may be a "universal cause" of budworm oscillations. Baskerville, Blais, Jones, and Stedinger assume that the depletion of food and ovipositing sites resulting from defoliation and tree mortality cause outbreak collapse.

Figure 1 illustrates the assumed interactions between the principal components of the

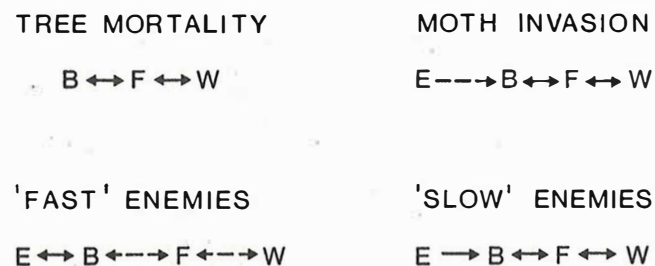
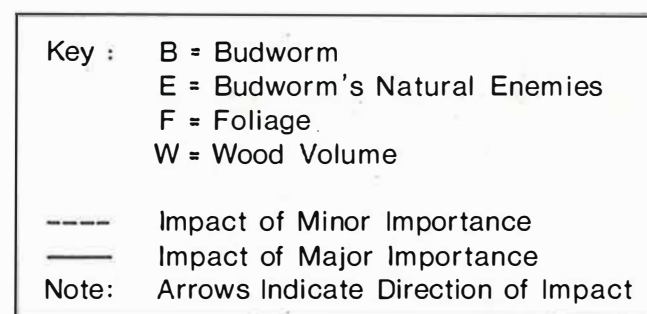


Figure 1. Hypotheses concerning the underlying mechanics of budworm-forest dynamics. The major components and their interactions are shown.

budworm-forest ecosystem for four hypothetical outbreak generating mechanisms. The 'tree mortality' hypothesis (Blais 1974) implies important and reciprocal impacts between budworm and foliage, and between foliage and wood volume. In the 'slow enemies' hypothesis,

Baskerville (1976) and Jones (1979) suggested that polyphagous non-synchronized predators and parasites limit the increase of low density budworm populations. Between outbreaks, these background enemies maintain their numbers by feeding on alternate prey as well as on budworm. During outbreaks, the numbers of budworm enemies increase much more slowly than budworm numbers so 'per capita' budworm losses to predation and parasitism decrease substantially. The lack of an arrow pointing from budworm to its slow enemies in Figure 1 reflects the assumed insignificance of the slow enemy numerical response to budworm densities.

Stedinger's (1977) moth invasion hypothesis (Fig. 1) encapsulates the behavior of his large scale simulation model of budworm-forest dynamics. In contrast to Baskerville and Jones, he concluded that the impact of natural enemies on budworm-forest dynamics was less important than that of moth invasion in terms of driving the outbreak cycle. According to his model, invasion is a prerequisite for outbreak: without it, low density mortality factors extinguish small budworm populations. Sufficient budworm invasion raises local populations to densities where these mortality factors are less important; population increase then continues until outbreak levels are reached, even in the absence of further moth immigration.

The 'fast' enemies hypothesis of Figure 1 represents a simplification of the conclusions Royama (1982) reached after reanalysing the Green River Project data (Morris 1963). According to Royama, mortality due to the combined action of parasitoids, pathogens, and a complex of unknown causes "apparently associated with the occurrence of disease(s) of an unknown nature is the most probable universal cause of population oscillation". The implication is that the mortality associated with certain synchronized parasitoid and pathogen populations increases quickly enough during budworm outbreaks to return budworm populations to low densities before resource limitation necessarily becomes important. Since budworm population collapse deprives these fast natural enemies of their principal food, fast enemy populations fall soon afterwards. A pattern of oscillations in natural enemy - budworm population sizes typical of predator-prey relationships (e.g., Krebs 1972, pp. 247-254) arises.

In what follows, I study the effects of reducing foliage quality on budworm-forest dynamics for each hypothesis illustrated in Figure 1. I hope to identify the range of impacts that can be expected on both a short and a long term basis.

A Simple Budworm-Forest Model

I begin by introducing a simple idealized model of the budworm-forest ecosystem. It will provide a standard of comparison by which to consider the complexity of budworm-forest dynamics in the field. Adopting a philosophy akin to that of laboratory work, the model is deliberately simplified so that the effects of reducing

foliage quality on budworm-forest dynamics can be examined in isolation. My approach is deductive: using data reported in the literature and assumption when data is lacking, I mathematically describe various aspects of the budworm-forest ecosystem; then, using computer simulation, I deduce the logical consequences of these mathematical descriptions.

The Forest Submodel

The model as a whole is intended to describe the dynamic relationships between budworm density, B , foliage quantity, F , and wood volume, W , in a representative balsam fir stand in Maine. To simplify model development, I initially ignore the budworm and concentrate solely on stand growth. Although the physiology of stand growth is poorly understood, the limited evidence available suggests that the annual increments of wood volume and foliage generally increase with the rates of photosynthesis and growth hormone production (Kramer and Kozlowski 1979). Since both these physiological processes occur in the foliage and use light energy captured by the foliage (Kramer and Kozlowski 1979), the model treats foliage as the 'engine' driving stand growth.

Stands use captured light for the maintenance of existing biomass as well as for the production of new biomass. Given the lack of knowledge about how captured light is partitioned between these processes, I assume a simple linear relationship (after Smith 1963). This linearity is evident in the following description of the relative rate (U) at which the stand 'consumes' captured light in year t to $t + 1$:

$$U = m.F(t) + g [F^*(t + 1) - F(t)] \quad (1)$$

$F^*(t + 1)$ is starred to indicate that it represents the potential stand foliage quantity in year $t + 1$ in the absence of budworm. The coefficients m and g represent the respective ratios of captured light allocated to maintenance and growth. It is implicitly assumed in this equation that foliage quantity is linearly related to stand biomass. The fact that the curvature of the relationship between wood volume and foliage quantity (Fig. 2) is small over realistic ranges suggests that this assumption may not be an unreasonable approximation. (For future reference, Table 1 alphabetically lists algebraic symbols used throughout the paper).

I also assume that in the absence of budworm, the annual 'per capita' rate of increase of stand foliage is proportional to A , the relative availability of limiting factors. It follows that the ratio of stand foliage quantities in successive years t and $t + 1$ can be written

$$F^*(t + 1)/F(t) = R.A + 1 \quad (2)$$

where R is the proportionality factor, the maximum annual 'per capita' rate of foliage production possible, and $F^*(t + 1)$ is the potential stand foliage quantity in year $t + 1$ in the absence of budworm.

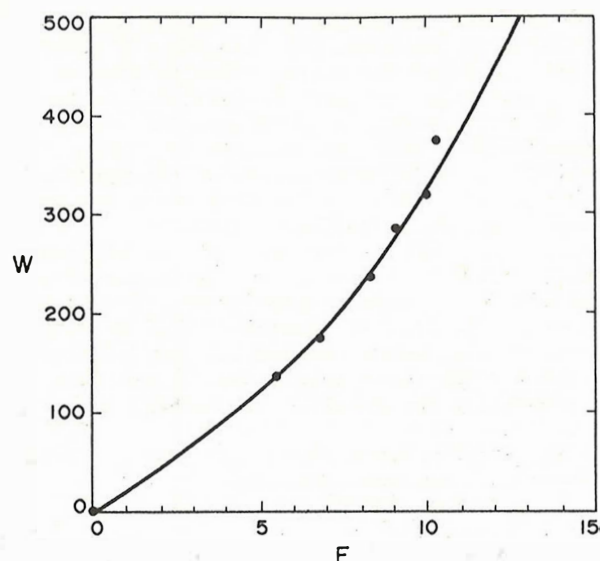


Figure 2. Wood volume, W (in m^3/ha) plotted against foliage surface, F (in $10^4 m^2/ha$). Solid circles indicate the means of field observations (Baskerville, 1965, Tables 5 and 9) averaged over every $50 m^3/ha$ interval of W starting from $W = 0$. The curve illustrates equation (6).

In light-limited conditions, A can be simply expressed as

$$A = 1 - U/U_{\max} \quad (3)$$

where $U_{\max}$ denotes the maximum rate at which the stand uses captured light. The existence of $U_{\max}$ follows from the existence of an upper bound on foliage quantity (Fig. 2). Hence, if $F_{\max}$ represents the maximum foliage quantity a stand can sustain, it follows from equation (1) that

$$U_{\max} = m \cdot F_{\max} \quad (4)$$

Substituting equations (1) and (4) into (3), substituting the result into (2), and then rearranging, the ratio of stand foliage quantities in successive years in the absence of budworm becomes

$$\frac{F(t+1)}{F(t)} = \frac{1 + R \cdot (1 - F(t)/F_{\max})}{1 + Z \cdot F(t)} \quad (5)$$

where $Z = R \cdot g / (m \cdot F_{\max})$. The parameter Z represents the maximum possible ration of captured light for foliage growth relative to the maximum for tree maintenance.

The economic value of a harvestable stand depends on its wood volume, and its wood volume, in turn, depends on its foliage quantity (Fig. 2). Expressing the relationship shown in Figure 2 mathematically:

$$W(t) = 544 F(t) / [268000 - F(t)] \quad (6)$$

where wood volume, W , is measured in m^3/ha . For consistency with the rest of the paper, the units of foliage quantity in Figure 2 have been converted from the originally reported kg/ha to m^2 of foliated branch surface per ha. This conversion was accomplished by comparing Baskerville's (1965) data of F in kg/ha against W (for immature stands) with Morris' (1955, p. 287) data of F in $ft^2/acre$ in stands 35 and 55 years old. By relating stand age to W through Figure 3 and assuming that stands of equal wood volume generally have equal foliage, it was estimated that .193 kg of foliage are the equivalent of a m^2 of foliated branch surface.

Table 1. Definitions of algebraic symbols*

A	relative availability of limiting factors (-)
B	budworm density (egg masses/ m^2 of foliated branch surface)
B_I	egg masses/ m^2 deposited by invading moths (B)
B_N	egg masses/ m^2 deposited in the stand by 'native' moths (B)
C	foliage to budworm conversion efficiency (B)
D	fraction of current foliage destroyed by budworm (-)
F	stand foliage quantity (m^2 of foliated branch surface/ha)
$F_{\max}$	maximum stand foliage quantity possible (F)
F_s	foliage quantity of typically susceptible stands (F)
g	fraction of 'captured' light used for stand growth ($1/F$)
L	amount of defoliation (F)
M	annual wood volume loss through tree mortality (-)
m	fraction of 'captured' light used for tree maintenance ($1/F$)
n	indicates the influence of foliage on budworm ovipositioning (-)
Q	foliage quality (-)
R	maximum annual 'per capita' foliage production (-)
t	time (years)
U	relative rate by which the stand consumes captured light (-)
$U_{\max}$	maximum value U can attain (-)
W	stand wood volume (m^3/ha)
W_M	stand wood volume when tree mortality begins (W)
$W_{\max}$	maximum stand wood volume possible (W)
Z	ratio of the maximum possible ration of light for foliage growth relative to the maximum for tree maintenance ($1/F$)

* Parentheses following definitions enclose the dimensionality; e.g. $1/F$ indicates that g is measured in ha/m^2 of foliated branch surface and - indicates A is dimensionless.

The assumption that the data reported in Figure 3 are appropriate for a representative balsam fir stand in Maine is implicit in this conversion of foliage units. The observation

that previous budworm outbreaks have left much of eastern North America's spruce/fir forest in a relatively even-aged condition (Baskerville 1976, p 8; Seymour 1980, pp 91-109) lends some support to this assumption. Whether data from a fully-stocked stand is representative is less certain.

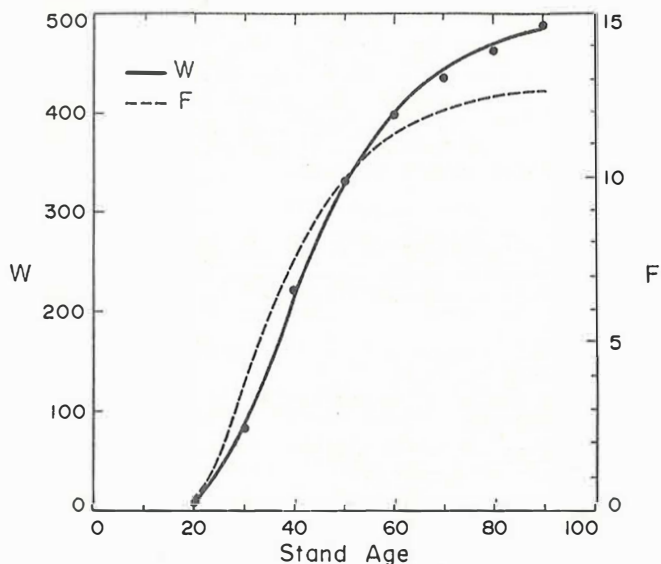


Figure 3. Wood volume, W (in m^3/ha), and foliage quantity, F (in $10^4 \text{ m}^2/\text{ha}$), plotted against age (years) for a fully-stocked even-aged balsam fir stand. The observations (solid circles) were taken from a good site (stand height = 18.3 m at age 65) in the northeast U.S. (Bakuzis and Hansen, 1965, Table 96). The solid and dashed lines show output of the forest dynamics submodel, equations (6) and (7), in the absence of budworm. These simulations began at $t = 20$ with $W = 9.1$.

Together, equations (5) and (6) constitute the foundation of the model's description of stand growth in the absence of budworm. A more specific description requires estimates of the parameters $F_{\max}$, R , and Z .

Extrapolation of the field data of wood volume against stand age in Figure 3 indicates a maximum stand wood volume of about $W_{\max} = 500 \text{ m}^3/\text{ha}$. Although the physiological mechanisms limiting volume growth to $W \leq W_{\max}$ are unknown, various observations are suggestive. First, the ratio of respiring tissue (e.g., stem cambium) to photosynthesizing tissue (foliage) increases with age (Möller et al. 1954). Second, translocation becomes more difficult as distances from the roots to the foliage increase with tree height (e.g., Kramer & Kozlowski 1979, pp 610-611). Third, mature stands generally exploit site 'carrying capacity', as reflected in light, water, and nutrient availability, more fully than very young stands (Baskerville 1965, p 2). But regardless of the physiological mechanism involved, given $W_{\max} = 500 \text{ m}^3/\text{ha}$, it follows from equation (6) that $F_{\max} = 128400 \text{ m}^2/\text{ha}$.

To estimate the parameters R and Z , numerical solutions to equation (5) with $F_{\max} = 128400 \text{ m}^2/\text{ha}$ were computed for various combinations of R and Z . These solutions were translated into time series of wood volumes through equation (6) and compared to the field observations of Figure 3. A search for an acceptable series of standardized residuals (Devore 1982, p. 459-464) and a low sum of squared residuals produced estimates of $R = .47$ and $Z = .00005$ to two and one significant figures, respectively; the extra significant figure reflecting the model's greater sensitivity to R . Hence, according to equation (5), the ratio of gross (i.e., before accounting for defoliation) foliage to the previous year's net (i.e., after accounting for defoliation) foliage is

$$\frac{F^*(t+1)}{F(t)} = \frac{1.47 - 3.6 \times 10^{-6} F(t)}{1 + .00005 F(t)} \quad (7)$$

Figure 3 shows that in the absence of budworm, the forest submodel, equations (6) and (7), can describe wood volume growth reasonably well. However, confidence gained in the forest submodel from the results displayed in Figure 3 is limited because three parameters (R , $W_{\max}$, and Z) were estimated from these data.

Defoliation

Completion of the forest submodel requires that the impacts of the budworm on the forest through defoliation and tree mortality be defined. Figure 4 illustrates the relationship

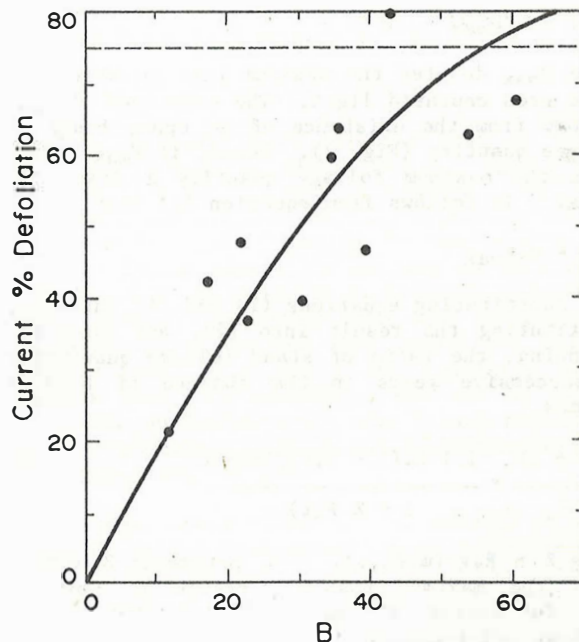


Figure 4. Plot of the % defoliation of new foliage against the number of new, healthy, budworm egg-masses per m^2 of foliated balsam fir branch surface. The solid circles show Miller's (1977, Fig. 3) data; the solid curve illustrates equation (8). Current defoliation is 75% along the dashed line.

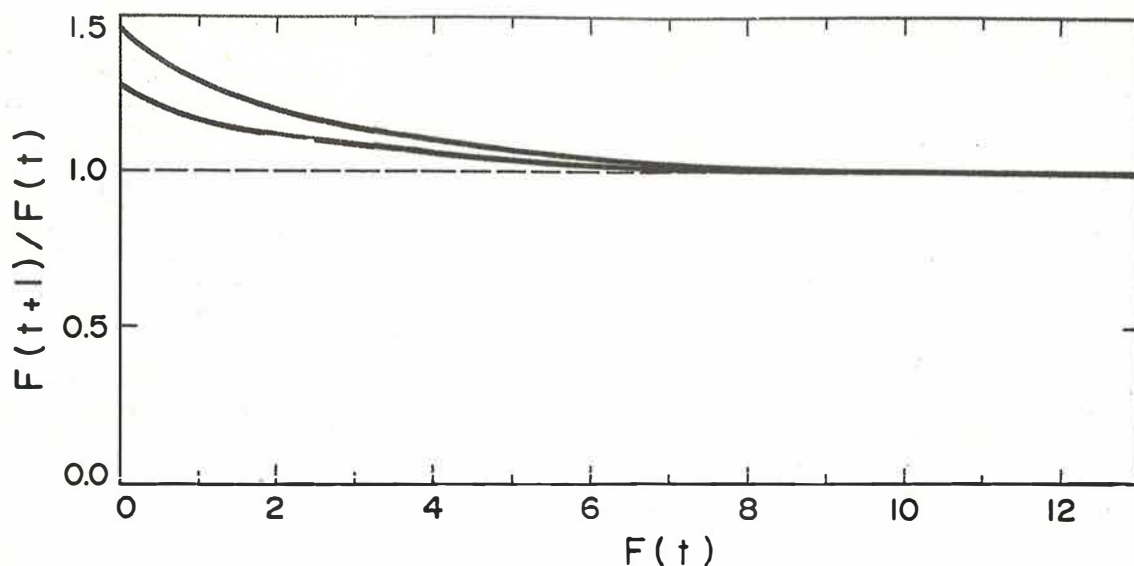


Figure 5. Foliage recruitment ratio, $F(t+1)/F(t)$, plotted against stand foliage quantity in year t , $F(t)$, in $10^4 \text{ m}^2/\text{ha}$. The upper and lower solid curves distinguish foliage recruitment ratios for budworm densities of 0.0 and 25.8 egg-masses/ m^2 , respectively. $F(t+1) = F(t)$ along the dashed line. The curves illustrate the system of equations: (7), (9), and (10).

between current defoliation and budworm egg mass density reported by Miller (1977, Fig. 3). The curve has been visually drawn to represent his data and to pass through the origin (since no defoliation is expected without budworm). The equation

$$D(t+1) = 1.82 B(t)/(B(t) + 84) \quad (8)$$

describes this curve where $D(t+1)$ is the fraction of current foliage destroyed in year $t+1$ by budworm larvae surviving from a population of B egg-masses/ m^2 in year t . Taking current foliage as $F^*(t+1) - F(t)$, it follows from equations (7) and (8) that the total amount of foliage destroyed by budworm in year $t+1$, $L(t+1)$, relative to the stand foliage in year t , $F(t)$, is

$$\frac{L(t+1)}{F(t)} = \frac{1.82 B(t)}{B(t) + 84} \times \frac{.47 - .000054 F(t)}{1 + .00005 F(t)} \quad (9)$$

Baskerville (1965, p 15) suggests $.25 F^*(t+1)$ as an alternative measure of the amount of current foliage. The implications of this possibility are presently under investigation.

Equation (9) completes the model's description of stand foliage dynamics when tree mortality is not a factor. The model computes net foliage as a function of budworm density and net foliage in the previous year from

$$F(t+1) = F^*(t+1) - L(t+1) \quad (10)$$

where gross foliage, $F^*(t+1)$, and losses to budworm, $L(t+1)$, are given by equations (7) and (9), respectively. The model then calculates $W(t$

$+1$) from equation (6), thus reflecting Peinés' (1980) conclusion that "balsam fir...growth reductions are expressed the same year as the first defoliation occurs".

Figure 5 illustrates the model's description of foliage dynamics for budworm densities of 0 and 25.8 egg-masses/ m^2 . This latter density represents the borderline between the 'moderate' and 'high' infestation classes of the Maine Forest Service (Fleming et al. 1983); it corresponds to 43% current defoliation (Fig. 4). The foliage recruitment ratio is a decreasing function of both foliage and budworm density.

Tree Mortality

Tree mortality usually begins after three to six years of "persistent, severe defoliation" (MacLean 1981) through some unknown physiological mechanism (Kramer and Kozlowski 1979, pp 676-677). Taking 'severe' defoliation as exceeding 75% current defoliation (after Baskerville and MacLean 1979), the model triggers the tree mortality process in the fifth consecutive year of budworm densities above 58.9 egg-masses/ m^2 (the density corresponding to 75% current defoliation in Fig. 4).

Once tree mortality begins, foliage is no longer the 'engine' driving wood production. Rather, the model reduces total stand foliage roughly in proportion to, and as a consequence of, losses in W , the wood volume contributed by live trees. (Since W excludes wood volume contributed by dead trees, using W to indicate stand value ignores any possible profit from salvage operations.)

If M is the fractional loss of wood due to tree mortality in any year while tree mortality is occurring, then the fractional survival rate is $1-M$. Therefore, since tree mortality continues for six consecutive years in a representative stand (MacLean 1981, Fig. 1), stand wood volume at the completion of tree mortality is

$$W(t_M + 6) = (1-M)^6 W(t_M)$$

where t_M is the year when mortality began. Algebraic manipulation of this equation shows that

$$M = 1 - \exp(.167 \ln[W(t_M + 6)/W(t_M)]).$$

MacLean (1981, Fig. 1) suggests that once triggered, cumulative tree mortality (in number of stems) reaches about 99% in mature stands and 55% in immature stands after six years. Since mortality in number of stems generally provides a reasonable approximation to mortality in wood volume (MacLean 1980), it follows from the equation above that $M = .54$ and $.12$ for mature and immature stands, respectively. Wood volumes corresponding to mature and immature stands were estimated from Baskerville and MacLean (1979, Table 7) as $450 \text{ m}^3/\text{ha}$ and $135 \text{ m}^3/\text{ha}$, respectively. Thus the model can use stand wood volume at the onset of tree mortality, W_M , as an indicator of stand age. A simple expression fitting these observations and the constraint that $M = 0$ when $W_M = 0$ is

$$M = 10^{-6} W_M^2 + .00075 W_M. \quad (11)$$

Summarizing, the model's tree mortality process begins in the fifth consecutive year of budworm densities exceeding $58.9 \text{ egg-masses}/\text{m}^2$ and continues for six years causing an annual volume loss of $M \times W$. The model treats the fractional loss of wood volume due to tree mortality, M , as a function of the stand's wood volume when tree mortality started, W_M . While tree mortality is occurring, foliage is calculated through the inverse of equation (6).

The Budworm Submodel

Although the spruce budworm - forest system has periodically been the object of intensive investigation, many questions remain to be answered regarding the reciprocal impacts between the budworm and its hosts. These uncertainties are necessarily reflected in the following submodel of budworm dynamics. This submodel is meant to provide a simple qualitative description of budworm population dynamics: it can claim to be neither definitive nor quantitatively accurate. Nonetheless, it will provide a useful basis for discussing the qualitative impacts of changes in foliage quality.

The development of the budworm submodel begins by distinguishing between the eggs laid by moths invading the stand and those 'native' to the stand. If B is the budworm density (in egg masses/ m^2 of foliated branch surface) then the annual change in budworm density is

$$B(t+1) - B(t) = B_N + B_I - B(t) \quad (12)$$

where B_N and B_I are the egg masses/ m^2 deposited in the stand by budworm which developed within and outside the stand, respectively. Thus B_N and B_I represent the egg deposition in the stand by 'native' and invading moths. The last term on the right side of equation (12) represents budworm mortality. Its form reflects the maximum budworm longevity of about 13 months: local extinction must exist, at least temporarily, following a complete lack of ovipositing within the stand (i.e., when $B_N = B_I = 0$).

Indirect evidence (Greenbank et al. 1980; Miller 1979; Morris 1963) suggests that dispersing moths favor stands with many large, mature, well-foliated balsam fir trees for oviposition. Miller et al. (1978) estimated that moths invading a heavily sprayed test block from the surrounding infested forest deposited about $10 \text{ masses}/\text{m}^2$. But budworm are reportedly rare between outbreaks (Baskerville 1976; Morris et al. 1958) so B_I is likely small in most stands lacking suitable foliage. Accommodating these assumptions and observations, the budworm immigration density can be expressed as an exponentially increasing function of foliage quantity:

$$B_I(t) = 10[F(t)/F_s]^n$$

where F_s represents the foliage quantity in a typical susceptible stand and n is a yet to be determined exponent indicating how abruptly immigration increases with increases in stand foliage.

Balch (1946) reports that moderately and highly susceptible stands generally exceed 40 and 60 years of age, respectively. Accepting the mean age of 50 years, the model assigns typically susceptible stands an average foliage quantity of $F_s = 10^5 \text{ m}^2/\text{ha}$ in accordance with Figure 3. Then, given respective practical maximums for F and B_I of $1.2 \times 10^5 \text{ m}^2/\text{ha}$ (Fig. 2) and $20-30 \text{ egg masses}/\text{m}^2$ (Miller et al. 1978), $n = 5$ to the nearest integer satisfies the expression for B_I above. Hence, the annual egg mass deposition by invading moths becomes

$$B_I(t) = 10 [F(t)/10^5]^5 \quad (13)$$

The density of egg masses deposited by native moths, $B_N(t)$, also depends on stand foliage, $F(t)$. Assuming the total number of eggs deposited by native moths in year t , $B_N(t) \times F(t)$, is proportional to the foliage consumed, $L(t)$,

$$B_N(t) = C.L(t)/F(t)$$

where C is the foliage to budworm conversion efficiency (i.e., the egg masses produced per m^2 of foliated branch surface destroyed). Since larval survival and moth fecundity reportedly increase as stand maturity increases (Morris et al. 1958; Morris 1963, p 189-202), and since moth fecundity declines exponentially as the duration of sustained severe defoliation increases (Morris

1963, pp 85-87), C is likely an increasing function of foliage. A simple possibility is

$$C = Q[F(t)/F_s]^n$$

where Q represents foliage quality in terms of budworm reproductivity and n is an unspecified exponent determining how sharply C accelerates as $F(t)$ increases. Combining the last two equations, and recalling that the amount of foliage of typical susceptible stands is $F_s = 10^5 \text{ m}^2/\text{ha}$, the annual egg mass deposit by native moths becomes

$$B_N(t) = Q \cdot L(t) \cdot F(t)^{n-1} / 10^{5n} \quad (14)$$

Equation (14) completes the model: equations (12), (13), and (14) constitute the budworm dynamics submodel; equation (11) describes the tree mortality process; equations (7), (8), and (9) link the budworm and forest submodels through defoliation, and equations (5) and (6) comprise the forest growth submodel.

Values for n and Q , however, remain undetermined in equation (14). Simulations of the complete model with initial conditions $W = 9.1 \text{ m}^3/\text{ha}$ (Fig. 3), $F = 4409 \text{ m}^2/\text{ha}$ [equation (6)], and $B = B_I = 1.7 \times 10^{-6} \text{ masses/m}^2$ [equation (13)] and with various values of n and Q displayed a variety of different outbreak cycles. Realistic cycles are generally 26-40 years in length (Royama 1982) with outbreaks lasting 6-15 years

in relatively unmanaged forests (Baskerville 1976; Stedinger 1977) and with budworm densities varying over four orders of magnitude (Baskerville 1976). Since $Q = .06$ and $n = 5$ produced the cycles which best met these criteria and which had a realistic range (c.f. Fleming et al. 1983) of budworm egg mass densities, these values were adopted as reference points for other simulations.

Model behavior, however, may also be acceptable for very different values of n and Q . Nonetheless, this is unlikely to affect the range of qualitative behavior exhibited by the model as Q varies: the model is behaviorally consistent for changes in n (excluding n values which do not admit acceptable outbreak behavior). Therefore, since this paper deals only with the qualitative behavior of the model, such behavior will be discussed only for $n = 5$ below.

A final comment on the form of equation (14) - the function $B_N(t)$ represents the product of the survival of the local population from eggs in year $t-1$ to moths in year t times the local reproductivity of those moths. Moreover, the (generation) survival component of $B_N(t)$ is itself the product of the survival rates for each of the six larval instars. Hence, since many of these instar survival rates probably increase with foliage (Thomson 1979), there is some theoretical basis for writing $B_N(t)$ as a function of $F(t)$ raised as high as the fourth power.

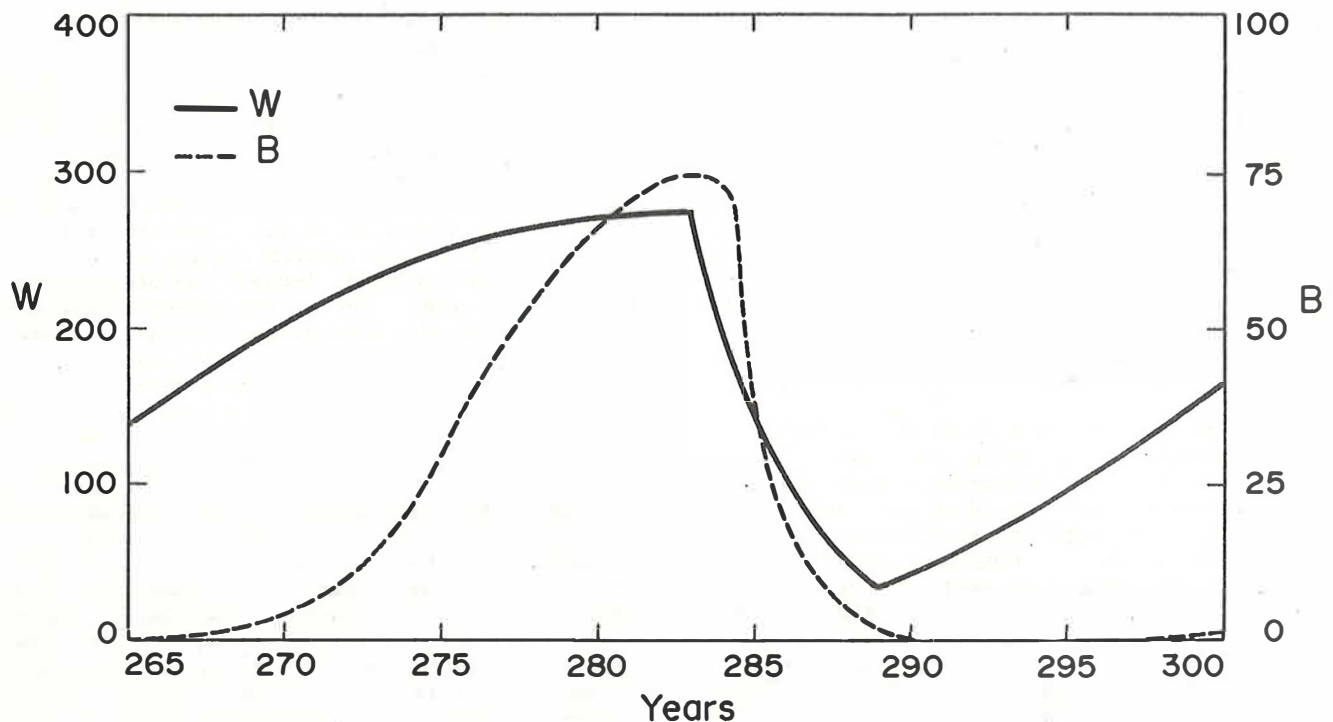


Figure 6. The 33-year outbreak cycle produced by the full model under 'natural' foliage quality conditions (i.e., $Q = .06$). Wood volume, W , and budworm density, B , are shown for years 265-300 of a numerical solution to equations (5)-(9), (11)-(14) with $n = 5$. The simulation began in year 20 with $W = 9.1 \text{ m}^3/\text{ha}$ and $B = 1.7 \times 10^{-6} \text{ egg-masses/m}^2$.

Figure 6 illustrates the behavior of the model through a typical outbreak cycle. Beginning at $t = 265$, both budworm density (B) and foliage increase with time, changes in foliage being reflected (through Fig. 2) by the wood volume (W) curve in Figure 6. Foliage increases favor the budworm population [cf. equations (12)-(14)] which grows in response. But as it grows it destroys more foliage (Fig. 4), thus reducing the foliage and volume increments. By $t = 280$ the budworm population has become so large (over 58.9 masses/m²) that current defoliation exceeds 75% [equation (8)]. Tree mortality, equation (11), begins in the fifth consecutive year ($t = 284$) of such severe defoliation and decimates the wood volume and foliage during the next six years. The budworm population crashes in response to the consequent loss of feeding and oviposition sites. By $t = 289$ most of the overstory has been destroyed (low W) and the immature, relatively less vulnerable understory trees are beginning stand regeneration.

When foliage quality, Q , is reduced 50% from its value of .06 in Figure 6, (and nothing else is changed), the model exhibits a very different behavior: the outbreak cycles are replaced by a state of apparent equilibrium with the budworm density, B , stable at 35 masses/m² and the wood volume stable at its maximum of 500 m³/ha. Curiously, this reduction of foliage quality allows both the budworm and the wood volume to maintain greater long term averages than they did in Figure 6: the budworm density does not get high enough for long enough to trigger the tree mortality process. The reduction in foliage quality acts to slow budworm increase during its population growth phase ($265 < t < 280$ in Fig. 6) and this prevents prolonged severe defoliation before the budworm population declines in response to reduced foliage levels. Hence, tree mortality seems necessary for the model to exhibit outbreak cycles; this is the basis of the tree mortality hypothesis of outbreak generation.

The foregoing analysis deserves two qualifications. First, stands don't last forever even without budworm: they deteriorate with age and become susceptible to fire, diseases, and other pests. Hence, the 'apparent equilibrium' is more properly viewed as a long-term regeneration cycle; budworm-caused tree mortality short-circuits the cycle. Second, model behavior is not independent of its starting point: for particular values of Q ($n = 5$) the model could exhibit both outbreak cycles and apparent equilibria depending on the initial conditions. These qualifications also apply to Table 2.

Table 2 summarizes the results of model simulations beginning at $t = 20$ with $W = 9.1$ m³/ha and $B = B_I = 1.7 \times 10^{-6}$ masses/m² for various values of Q . (Figs. 3 and 6 correspond to the runs for $Q = .03$ and .06, respectively.) Reducing foliage quality (Q) has a number of benefits for the forest manager: increasing peak wood

Table 2. The effect of foliage quality on model behavior.

Foliage Quality (Q)	Outbreak Cycle Period (years)	B^1 (masses/m ²)	W^1 (m ³ /ha)
.6	19	225.1	163.1
.1	27	98.46	236.6
.065	32	78.55	267.9
.06	33	75.00	274.5
.055	35	72.81	283.4
.05	37	69.79	293.3
.045	40	67.25	306.0
.04	44	64.41	322.1
.035	52	62.43	347.1
.03	55 ²	58.66	398.2
.01	55 ²	32.31	449.1
.0	55 ²	27.71	458.7
.03	55 ²	0 ³	484.6 ³

¹ B and W columns list the outbreak cycle maximums when $Q \geq .035$ and the 90-year values when $Q \leq .03$.

²Quasi steady state behavior - no outbreaks.

³No budworm immigration (i.e., $B_I = 0$).

volume, decreasing peak budworm densities, and lengthening the outbreak cycle period (realistically, steady states represent long-term regeneration cycles). Reducing foliage quality can also have detrimental effects. First, it lengthens outbreak duration (defined as the period during which $B > 25.8$ masses/m²) although this effect is usually small and not in proportion to the period lengthening. Second, tree mortality is more severe as a consequence of the greater maximum wood volumes [equation (11)]. However, further reductions of foliage quality (e.g., $Q < .03$ in Table 1) can prevent budworm outbreaks from occurring at all. Hence, the major consistent effects of reducing foliage quality in this model are increases in maximum wood volume and decreases in budworm outbreak frequency.

Other Hypotheses of Outbreak Generation

The models underlying various outbreak hypotheses are conveniently compared in terms of recruitment ratios, the ratios of budworm densities in successive years in the absence of moth immigration. For instance, according to equations (12)-(14), $B_N(t)/B(t)$ approximates the recruitment ratio for the tree mortality model. Curves a and b of Figure 7 show that this ratio increases with stand foliage and decreases with budworm density. Curve b shows that when the stand is immature ($F = 70000$ m²/ha), $B(t+1)/B(t) < 1$ so the native budworm population declines steadily. But as the stand matures (F increases) the recruitment rate rises until $B(t+1) > B(t)$ at small densities (e.g., curve a). The native population can then increase up to its equilibrium density (the density at which the recruitment curve crosses the dashed line); for curve a, 68 masses/m². At densities above and

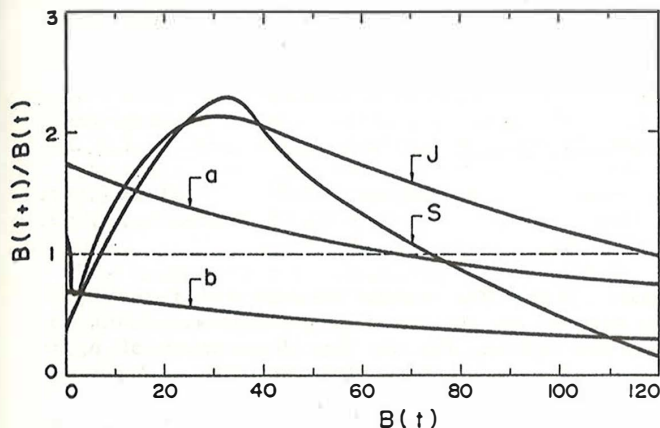


Figure 7. Budworm recruitment ratios, $B(t+1)/B(t)$, when immigration is negligible plotted against budworm density in year t , $B(t)$, in egg-masses/ m^2 . Curves a and b distinguish ratios for foliage quantities of 90000 and 70000 m^2/ha , respectively, in the model developed above. Curves J and S respectively represent ratios for Jones' (1979) and Stedinger's (1977) models. Equilibria occur wherever the curves cross the dashed line, $B(t+1) = B(t)$.

below this equilibrium the population decreases and increases, respectively. Hence, the equilibrium is stable: any slight deviation from the equilibrium density will be followed by a return to it.

Curve S in Fig. 7 typifies recruitment ratios for Stedinger's (1977) model; equilibria occur at 6 masses/ m^2 and 74 masses/ m^2 . The lower one is unstable: slightly smaller densities lead to continued decrease, slightly larger ones to continued increase. Hence, in Stedinger's model, a sparse population cannot grow of its own accord: moth invasion is needed to raise the budworm density above the unstable equilibrium density, in which case, an outbreak is inevitable.

Curve J in Figure 7 illustrates the budworm recruitment curve in a stand with moderately favorable conditions in Jones' (1979) model. Stable equilibria occur at 1 and 118 masses/ m^2 and an unstable equilibrium occurs at 5 masses/ m^2 . However, as in the tree mortality model, stand conditions determine the elevation of the entire curve. When the dip in the recruitment curve at low densities eventually clears the dashed line in response to improved stand conditions, the two lower equilibria vanish allowing the budworm to increase quickly to outbreak densities. The resulting forest destruction is reflected in the drop of the entire curve below the dashed equilibrium line and this signals the ensuing collapse of the budworm population. Subsequent stand regeneration causes the slow

elevation of the budworm recruitment curve but the next outbreak does not occur until the dip at low densities has again cleared the dashed equilibrium line.

Although stochasticities introduced by weather and moth invasion also play a role, it is clear that the low density dip, the so-called 'predator pit', dominates the behavior of Jones' model. The predator pit represents the assumed effect of a group of background natural enemies (principally birds) whose relatively small reproductive potential prevents their populations from keeping pace with budworm increases during outbreaks. This predator pit is the basis for the slow enemies hypothesis of outbreak generation attributed to Baskerville (1976) and Jones (1979) in Figure 1.

Reducing foliage quality has similar effects on the qualitative dynamics of each of the models discussed in detail above. Equation (14) shows that foliage quality, Q , determines the height of the recruitment curve, $B_N/B(t)$, at any given budworm density for the tree mortality model. Hence, for given forest conditions and budworm densities, decreasing foliage quality lowers the height of the recruitment curve and hence reduces the propensity for budworm increase. The result is a reduction of the frequency and severity of outbreaks (Table 2). Analogously, reducing foliage quality can be expected to lower recruitment curves (Fig. 7) for both Stedingers' model and Jones' model. Consequently, more immigrant moths would be needed to trigger an outbreak in Stedingers' model and greater stand maturity (larger F values) would be needed to overcome the effect of the predator pit and initiate an outbreak in Jones' model. Hence, for both these models, reducing foliage quality can be expected to reduce budworm outbreak frequencies and increase maximum wood volumes. But, since tree mortality increases with maximum wood volume, reducing foliage quality and thus extending the period between outbreaks results in greater stand destruction when outbreaks do occur (see also Casti, 1982).

The effects of reducing foliage quality are less certain for the fast enemies hypothesis of budworm outbreak generation. According to this hypothesis, certain budworm parasitoid and pathogen populations increase so fast in response to increased budworm densities during outbreaks that they subsequently decimate the budworm populations, thus ending the outbreaks. The complexity of such a system and the uncertainties regarding the attributes of the mortality factors make it particularly difficult to predict how it will respond to reductions in foliage quality. Nonetheless, given these reservations, longer intervals between outbreaks, greater wood supplies, and more severe outbreaks can be expected in the short-term. However, in the long-term, reducing foliage quality may have some undesirable effects. For instance, parasitoid and pathogen populations which lack sufficient alternate hosts and are unable to maintain their populations on low budworm populations during the

longer intervals between outbreaks may become exceedingly rare. Thus freed of these parasitoids and pathogens, the budworm might become an even greater pest than it had been before foliage quality was reduced.

Summary and Conclusions

The consequences of reducing foliage quality on spruce budworm dynamics have been discussed for four hypotheses of outbreak generation (Fig. 1). These hypotheses differed with respect to the principle biological mechanism underlying budworm outbreaks: tree mortality (Blais, 1974), slow natural enemies (Baskerville 1976; Jones 1979), fast natural enemies (adapted from Royama 1982), and moth invasion (Stedinger 1977). Despite these differences, the analysis indicated that the immediate consequences of reducing foliage quality should be similar for each hypothesis: increasing maximum wood volume, decreasing outbreak frequency, and increasing outbreak severity. The first two consequences offer benefits for forest management: increasing maximum wood volume implies an increase in the economic value of the stand at cutting time; decreasing outbreak frequency implies that a stand need be cut less often to preclude budworm-caused tree mortality, and therefore that the economic costs of harvesting could be reduced.

In the long-term it is clear that the budworm would face extinction given sufficient reduction of foliage quality. More modest and more realistic expectations for foliage quality reductions would have the budworm always present. The long-term consequences should then be similar to the short-term consequences for each hypothesis with two possible exceptions. First, if some of the fast natural enemies cannot maintain viable populations during the longer intervals between budworm outbreaks, short-term 'improvement' of the budworm problem may be followed by its long-term 'aggravation': greater outbreak frequency and smaller maximum wood volumes. Second, the possibility of genetic adaptation by the budworm to changes in foliage quality has not been considered. Suffice it to say that the budworm, with a one year generation time, appears to have the potential to adapt quickly enough to cause problems. Perhaps agriculture can suggest a solution to this potential problem: cultivar mixtures, multilines, and horizontal resistance (e.g., Fleming and Person 1978, 1982) have each been proposed as means of incorporating crop resistance against short-generation plant pathogens.

Acknowledgments

The author thanks Jacques Régnière and Karen Griffiths for helpful comments on the paper.

This research was supported in part by a grant from the Eastern CANUSA Spruce Budworm Program of the USDA Forest Service while the author

was employed at Cornell University. All interpretations and conclusions are the author's and should not be taken as the views of the Maine Forest Service, The U.S. Forest Service, or the Canadian Forestry Service.

Literature Cited

- Bakuzis, E.V.; Hansen, H.L. Balsam fir. Minneapolis: University of Minnesota; 1965. 445 p.
- Balch, R.E. The spruce budworm and forest management in the Maritime provinces. Publ. No. 60. Ottawa, Ont.: Can. Department of Agriculture, Entomology Division; 1946. 7 p.
- Baskerville, G.L. Dry-matter production in immature balsam fir stands. For. Sci. Monogr. 9:1-42; 1965.
- Baskerville, G.L. (ed.) Report of the task force for evaluation of budworm control alternatives. Fredericton, N.B.: Department of Natural Resources; 1976. 210 p.
- Baskerville, G.L.; MacLean, D.A. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Inf. Rep. M-X-102. Fredericton, N.B. Environment Canada, Canadian Forestry Service, Maritimes Forest Research Centre. 1979. 23 p.
- Blais, J.R. The policy of keeping trees alive via spray operations may hasten the recurrence of spruce budworm outbreaks. For. Chron. 50:19-21; 1974.
- Casti, J. Catastrophies, control and the inevitability of spruce budworm outbreaks. Ecol. Modelling 14:293-300; 1982.
- Devore, J.L. Probability and statistics for engineering and the sciences. Monterey, CA: Brooks/Cole; 1980. 640 p.
- Fleming, R.A.; Person, C.O. Disease control through use of multilines: a theoretical contribution. Phytopathology 68: 1230-1233; 1978.
- Fleming, R.A.; Person, C.O. Consequences of polygenic determination of resistance and aggressiveness in nonspecific host:parasite relationships. Can. J. Plant Pathol. 4:89-96; 1982.
- Fleming, R.A.; Shoemaker, C.A.; Stedinger, J.R. Analysis of the regional dynamics of unsprayed spruce budworm (*Lepidoptera: Tortricidae*) populations. Environ. Entomol. 12:707-713.
- Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. Spruce budworm (*Lepidoptera: Tortricidae*) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Mem. Entomol. Soc. Can. 110:1-49; 1980.

- Irland, L.C. Spruce budworm: economics and management for the long pull. Maine For. Rev. 13:24-26; 1980.
- Jones, D.D. The budworm site model. In: Pest management (eds. Norton, G.A.; Holling, C.S.). Laxenburg, Austria: International Institute of Applied Systems Analysis; 1979:91-155.
- Kimmins, J.P. Variations in the foliar amino acid composition of flowering and non-flowering balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* [Moench] Voss) in relation to outbreaks of the spruce budworm (*Choristoneura fumiferana* [Clem.]). Can. J. Zool. 49:1005-1011; 1971.
- Kramer, P.J.; Kozlowski, T.T. Physiology of woody plants. New York: Academic; 1979. 811 p.
- Krebs, C.J. Ecology: the experimental analysis of distribution and abundance. New York: Harper and Row; 1972. 694 p.
- MacLean, D.A. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221; 1980.
- MacLean, D.A. Impact of defoliation by spruce budworm populations on radial and volume growth of balsam fir: a review of present knowledge. Mitt der Forstlichen Bundesversuchsanstalt 142: 293-306; 1981.
- Miller, C.A. The feeding impact of spruce budworm on balsam fir. Can. J. For. Res. 7:76-84; 1977.
- Miller, C.A. An approach to measuring changes in the reproduction of spruce budworm (*Lepidoptera: Tortricidae*) field populations from survey data. Can. Ent. 111:309-316; 1979.
- Miller, C.A.; Greenbank, D.O.; Kettela, E.G. Estimated egg deposition by invading spruce budworm moths (*Lepidoptera: Tortricidae*). Can. Ent. 110: 609-615; 1978.
- Morris, R.F. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. 33:225-294; 1955.
- Morris, R.F. (ed.) The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can. 31:1-332; 1963.
- Morris, R.F.; Miller, C.A.; Greenbank, D.O.; Mott, D.G. The population dynamics of the spruce budworm in eastern Canada. In: Proceedings, 10th International Congress of Entomology; 1956 August 17-25; Montreal, P.Q. Ottawa, Ont.: Organization Committee; 1958: Vol. 4, 137-149.
- Möller, C.M.; Müller, D.; Nielsen, J. Graphic presentation of dry matter production in European beech. Det. forst. Forsog. i Danmark. 21:327-335; 1954.
- Piene, H. Effects of insect defoliation on growth and foliar nutrients of young balsam fir. Forest Sci. 26: 665-673; 1980.
- Royama, T. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.): a reanalysis of life tables from the Green River project. Manuscript. Fredericton, N.B.: Environment Canada; Canadian Forestry Service, Maritimes Forest Research Centre; 1983. 107 p.
- Seymour, R.S. Vulnerability to spruce budworm damage and 100-year development of mixed red spruce-fir stands in north central Maine. New Haven, Conn.: Yale University, Ph.D. thesis; 1980. 160 p.
- Shaw, G.G.; Little, C.H.A.; Durzan, D.J. Effect of fertilization of balsam fir trees on spruce budworm nutrition and development. Can. J. For. Res. 8:364-374; 1978.
- Smith, F.E. Population dynamics in *Daphnia magna*. Ecology 44: 651-663; 1963.
- Stedinger, J.R. Spruce budworm management models. Cambridge, MA: Harvard University, Ph.D. thesis; 1977. 260 p.
- Swenson, C.L. Jr. Spruce budworm impact on lands managed by Seven Islands Land Co. Maine For. Rev. 13:9-10; 1980.
- Thomson, A.J. Evaluation of key biological relationships of western budworm and its host trees. Inf. Rep. BC-X-186. Victoria, B.C. Environment Canada, Canadian Forest Service, Pacific Forest Research Centre. 1979. 19 p.
- White, T.C.R. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia (Berl.) 16:279-301; 1974.
- Zobel, B.J. The world's need for pest-resistant forest trees. In: Resistance to diseases and pests in forest trees (eds. Heybroek, H.M.; Stephan, B.R.; von Weissenberg, K.). Wageningen, the Netherlands: Pudoc; 1982: 1-8.