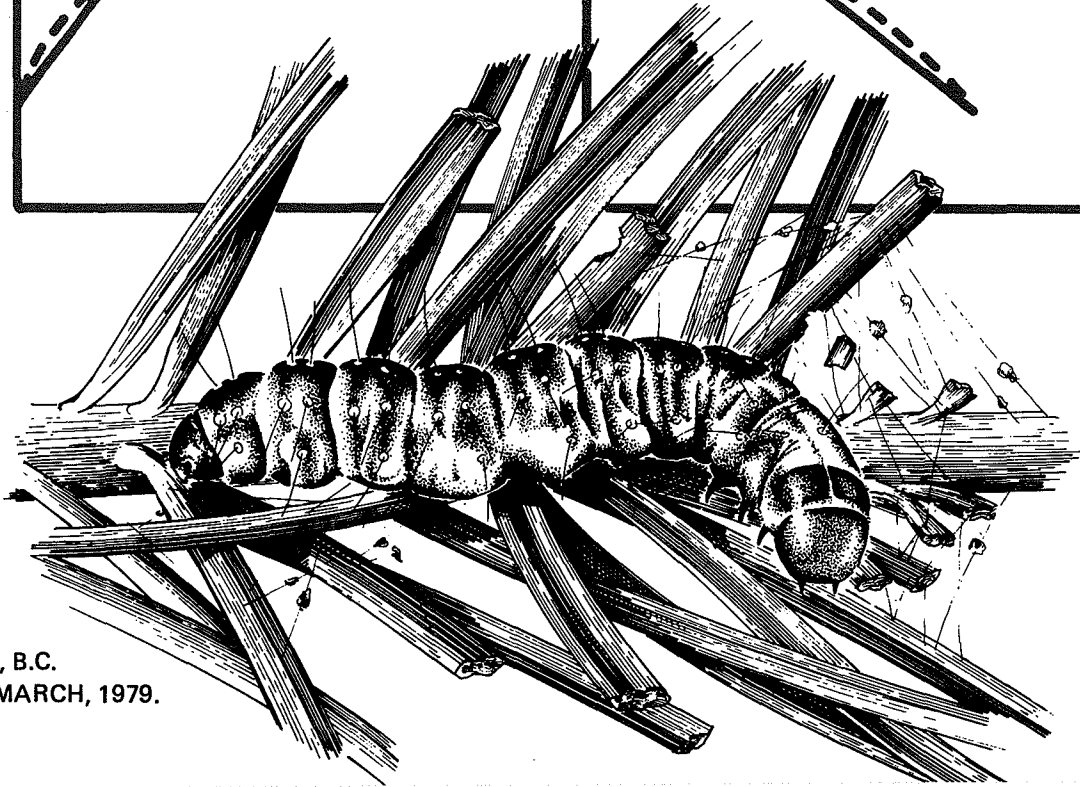
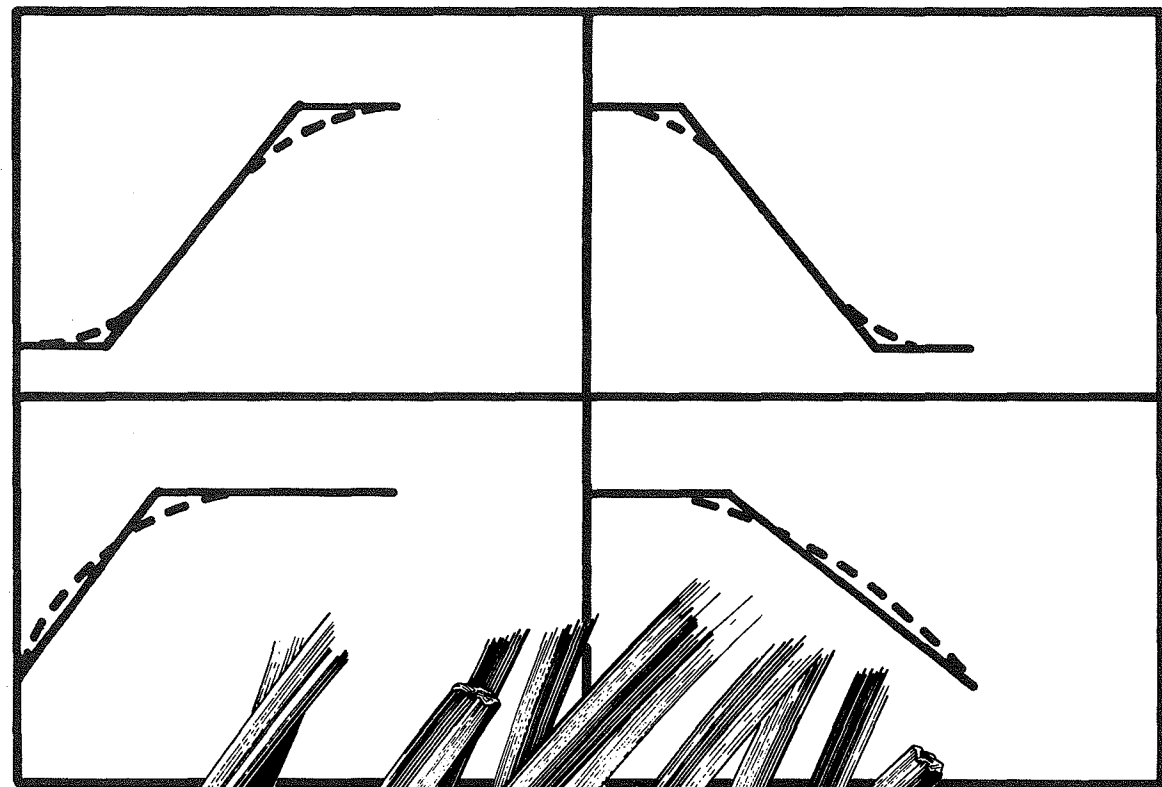


Evaluation of Key Biological Relationships of Western Budworm and its Host Trees

A.J. Thomson



ABSTRACT

Factors influencing the population dynamics of the western budworm Choristoneura occidentalis are reviewed, and the mathematical functional form of important relationships and linkage of the relationships in a simulation model are described. Each cycle of the simulation begins after the budworm eggs are laid in the fall, and is 1 year in duration. Simulation of spatial effects is accomplished by examining the population dynamics of individual cells within a grid, the cells being linked by dispersal relationships. A general method of simulating dispersal in mountainous terrain, where dispersal may be channelled by topography, is described.

In view of several presently unquantifiable relationships, no numerical analyses of the model are presented; rather, the model is used to define key relationships for further investigation and to provide a framework within which new information may be considered as it becomes available.

RÉSUMÉ

L'auteur passe en revue les facteurs qui influent sur la dynamique des populations de la Tordeuse occidentale de l'Épinette Choristoneura occidentalis et il décrit la formule mathématique fonctionnelle de rapports importants et le lien entre ces rapports dans un modèle de simulation. Chaque cycle de la simulation commence après la ponte des oeufs de la Tordeuse à l'automne et dure un an. La simulation d'effets spatiaux s'accomplit par l'examen de la dynamique des populations de cellules individuelles à l'intérieur d'une grille, les cellules étant reliées par des rapports de dispersion. L'auteur décrit une méthode générale de simulation de dispersion en terrain montagneux, où la dispersion peut être canalisée par la topographie.

Aucune analyse numérique du modèle n'est présentée à cause de nombreux rapports actuellement non quantifiables; de préférence, le modèle sert à déterminer les rapports clés en vue d'enquêtes plus poussées et de fournir un cadre au sein duquel on pourra étudier les nouveaux renseignements à mesure qu'ils deviendront disponibles.

INTRODUCTION

By 1977, the outbreak of spruce budworm, *Choristoneura occidentalis* Freeman, in British Columbia, first observed in 1969, covered 246 000 ha (603,000 acres). Tree mortality attributable to defoliation by budworm was limited, but reduced radial and height growth, dieback of previous height growth, and deformation of the main stem resulting in non-commercial future growth were observed (Shepherd et al. 1977).

A wide variety of tree and stand growth models are available to estimate the timber production of forests in the absence of budworm (Fries 1974 ; Stage 1973; Myers et al. 1976). Reduced production up to the current stage of outbreak is best estimated by damage appraisal surveys (Shepherd et al. 1977), although the final estimation of dieback of standing trees is difficult until recovery is complete, because tree tops will often produce foliage after being completely defoliated for several years.

To investigate the degree of additional damage in the absence of control of the current or future outbreaks, before the trees are harvested, a computer simulation model of budworm population dynamics can be of use.

The present study reviews the currently available information on the factors influencing the population dynamics of the budworm and develops the mathematical functional form of each relationship. As many of the key relationships cannot be quantified a fully operational simulation model is presently impractical. However, a description is given of the method of linkage of various relationships in a model in which key relationships may be defined more exactly as information becomes available, and in

which unknown relationships may easily be varied for purposes of simulation. The model is currently used to define key relationships for further investigation, and to provide a framework within which new information may be considered.

DEVELOPMENT OF THE FUNCTIONAL FORMS

The mathematical functional forms of many of the relationships in the budworm life cycle have not been defined. A general approach, however, has been used to provide a framework for discussion of the possible forms, and to facilitate alteration of the functional forms in simulations.

Consider four points A, B, C, D, with coordinates (x_A, y_A) , (x_B, y_B) , (x_C, y_C) and (x_D, y_D) , respectively. Let

$$\begin{aligned} & y_A = y_B = y_1 \\ \text{and} & y_C = y_D = y_2 \\ \text{with} & x_A \leq x_B \leq x_C \leq x_D \end{aligned}$$

Under these conditions, x_B and x_C are the inflection points of the line joining A and D, with a linear relationship of x and y being assumed between x_B and x_C (Fig. 1a). By specifying a maximum of 6 values, approximations of a wide variety of functional forms may be generated. Many of the relationships are based on relation values between $x_A = 0$ and $x_D = 1$. In such cases, only four values must be specified: x_B , x_C , y_1 and y_2 . The quantitative and qualitative nature of such relationships is established at the start of the simulation by setting the values of x_B , x_C , y_1 and y_2 . Some of the types of relationships which may be generated are indicated in Figure 1.

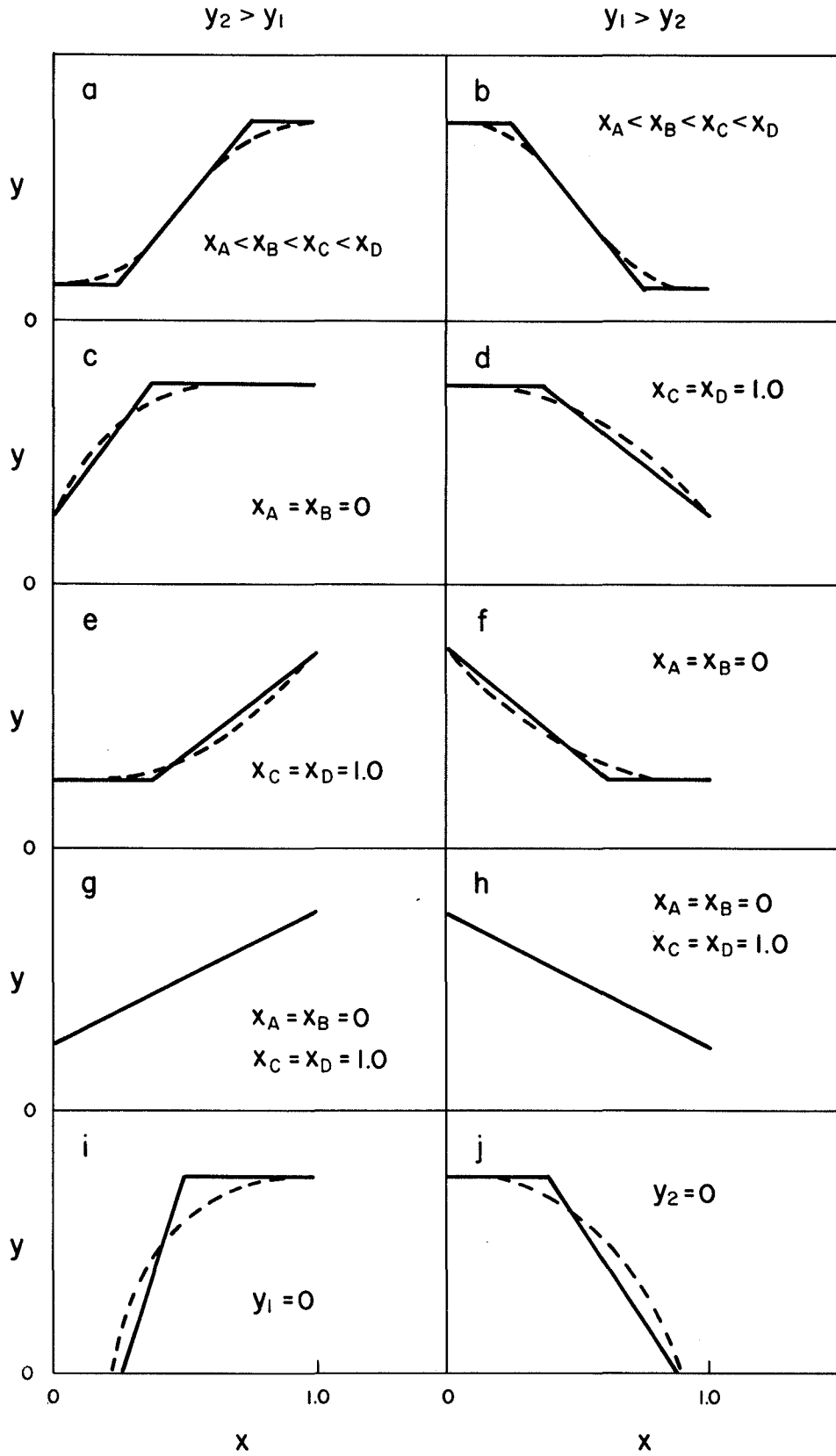


Figure 1. Examples of the different forms of relationships which can be generated by variation of the parameters x_B , x_C , y_1 and y_2 .

BIOLOGICAL RELATIONSHIPS OF THE WESTERN BUDWORM AND ITS HOST TREES

A. BUDWORM POPULATION DYNAMICS AND DEFOLIATION

Dispersal

Dispersal of the spruce budworm occurs in first instar larvae, second instar larvae, and moths. The features common to all dispersal processes are:

- (a) proportion of the population subject to dispersal
- (b) dispersal direction
- (c) dispersal distance
- (d) distribution of the dispersers along the dispersal direction
- (e) differential survival of dispersing and non-dispersing individuals.

Dispersal distance and direction and frequently the method of distribution of dispersers along the dispersal direction are influenced by local and prevailing wind patterns which, in the mountainous terrain of British Columbia, are regulated to a high degree by the underlying topography (Appendix 1).

Egg Stage

The budworm generally lays its eggs in late summer in masses on the host needles. Hatching occurs in about 10 days (Carolin and Coulter 1972). The first instar larvae disperse and form hibernacula among lichens and under bark scales on the limbs and boles of trees; they moult to the second instar and (in which form they remain in) hibernate for about 9 months. Information on the eastern budworm is used where considered relevant and information on the western budworm is lacking. Thus, for survival from egg to first instar larva, a constant 0.81 is used (Neilson 1963).

First instar larvae

Mortality of first instar larvae results principally from losses during dispersal (Morris and Mott 1963). Dispersal survival increases with increas-

ing density of the host trees and decreasing isolation of the host stand (Morris and Mott 1963). If dispersing first instar larvae land on non-host trees in a mixed stand, they will probably survive until dispersal to host foliage during the second instar in the spring; i.e., the mortality would be lower than in the second instar dispersal, where the larvae must locate host foliage to survive.

The first instar larvae are active only a few hours before forming their hibernacula (Morris et al. 1958). All the larvae emerge from an individual egg mass within 3 minutes. There is no emergence with air temperature less than 15.6°C or at RH < 50% or > 75%. Most eclosion occurs at or just before mid-day. At low air temperatures, the larvae are photopositive and move to the outside of the canopy, while at high air temperatures, or with strong solar radiation, they are photonegative and move to the interior of the canopy (Henson 1950). When moving to branch tips or to the interior of the crown, the larvae may drop on silk threads and be wind transported. The proportion of larvae available for such transport appears constant (Henson 1950).

At present, the proportion of larvae dispersing is set at a constant in the simulation. For initial development of the model, in the absence of data, 90% of the larvae are subject to dispersal. The proportion of larvae dispersing is probably related to the defoliation status of the stand, as increasing defoliation will permit increasing penetration of the wind within the canopy. The magnitude of this effect would be influenced by the proportion of non-host (non-defoliated) trees in the stand. This relationship may be included if sufficient data become available.

First instar larvae neither feed nor depend on foliage in the formation of their hibernaculum, thus survival is apparently not directly related to the defoliation status of the trees. However, loss of foliage may reduce the survival of dispersers indirectly by reducing the ability of the canopy to intercept dispersing larvae, resulting in more larvae landing on substrates where their survival is low. Survival of non-dispersing larvae is set at 1.0. Survival of dispersers includes effects of defoliation, and of

stand density and isolation.

Maximum first instar larval survival is determined by stand density and isolation. This survival will decrease with increasing defoliation expressed as the ratio of the present host foliage biomass relative to the undefoliated host needle biomass (discussed in a later section). The relationship of survival to defoliation is assumed initially to be of the form indicated in Figure 1g (x = foliage ratio, y = first instar larval survival), y_2 being the maximum survival rate in undefoliated stands with endemic budworm populations. Increasing the difference between y_1 and y_2 reflects increases in the defoliation effect assumed to be exerted on survival. The magnitude of y_2 will increase in higher density and less isolated stands. Until the relationship of survival to these stand parameters is quantified, y_2 is set as a constant at the start of the simulation.

Second Instar larvae

On emerging from hibernacula, the second instar larvae undergo dispersal from which, like first instar, survival depends upon stand isolation (Morris and Mott 1963). The second instar larvae are photopositive at normal spring temperatures, locating on the terminal twigs. During movement toward the terminals, they may drop on silk threads and may be blown away, as with the first instar larvae (Henson 1950). If staminate flowers are available, the larvae rapidly establish feeding sites on the flowers; otherwise, the larvae may wander for days (Blais 1952). Extended wandering enhances the probability of larvae being transported by wind. The proportion of second instar larvae dispersing is therefore likely to be greater than that of the first instars and will have a much higher variability. There will be direct and indirect effects of foliage on the proportion dispersing; with limited new growth, the larvae will have to search longer for feeding sites, and with increasing defoliation there will be increased wind effect within the canopy. Winds during the first instar dispersal tend to be convective, while those during the second instar tend to be turbulent (Henson 1950). The patterns of dispersal and the survival values for the two dispersal phases may be quite different. Long distance dispersal of second instars has been indicated (Henson 1950; Morris and Mott 1963), but its occurrence at a sufficiently high rate to initiate an outbreak has not been demonstrated. Indirect effects of defoliation may be expected as in the first instar dispersal.

As with the first instar larvae a constant proportion, 95% in this case, of larvae are assumed to disperse, the non-dispersers having a survival rate of 1.0. The dispersers have a maximum survival rate determined by stand density and isolation, reduced by defoliation as in Figure 1g (x = foliage ratio, y = second instar survival). Presently, there are insufficient data to formulate a method of simulating the variability in behavior indicated above.

This maximum survival rate (y_2) will probably be lower than that for first instar larvae because, unlike the latter, the larvae must locate host foliage to survive. The value of y_1 , the minimum survival rate, will also be lower than that for the first instar larvae. In the model, the dispersal is implemented before the foliage is incremented. If dispersal occurred after foliage incrementation, it would result in higher survival and would reflect a less likely phenological relationship of bud flush and larval emergence from the hibernacula.

When the second instar larvae begin to feed survival will decrease with decreasing foliage and increasing competition for the buds available. The ability of larvae to mine old needles, and buds at different stages of development will be of importance here, but lacks any quantitative basis.

Two weather phenomena influence the overall second instar survival. The nutritional reserves contained in the egg are used for (a) development of the embryo, (b) eclosion, (c) dispersal of first instar larvae, (d) formation of the hibernacula, (e) moulting to second instar, (f) hibernation for up to 9 months, (g) emergence from the hibernacula, (h) second instar larval dispersal, and (i) final location and penetration of needle or bud. McMorran (1973) indicates that a long period of warm weather in the fall, after formation of the hibernacula, results in depletion of these nutritional reserves to the extent that after emergence from the hibernacula in spring, there remains insufficient nutritional reserves to permit the larvae to locate and penetrate needles or buds. This effect would be enhanced if the nutritional reserves passed to the eggs decreased with increasing starvation of the previous generation.

Once the larvae emerge from the hibernacula, they become vulnerable to the weather. In spring, warm weather initiating bud flush and larval emergence, followed by cold weather and frost, can result in high larval mortality (Johnson and Denton 1975; Ives 1974). Whether adverse weather would also damage the new foliage or kill the larvae before they

do much bud damage through their mining activity would depend on the precise phenology and the magnitude of the weather effect.

Post dispersal survival is therefore modified to reflect the failure of larvae to successfully mine needles or buds. In the absence of data, a simple relationship of survival to bud availability is assumed, as in Figure 1g (x = foliage ratio, y = survival). The foliage ratio here is the actual new foliage after incrementation (described in a later section) relative to the maximum new foliage carried by the stand. A value of $y_1 > 0$ reflects survival by mining old needles.

An alternative formulation is to assume that each bud may be attacked only by a single larva. A relationship as in Figure 1f would result (x = buds available per larva, y = second instar survival). A value of $y_1 < 1$ reflects the fact that some larvae will always fail to find buds. The value of y_2 must be less than $1/x_C$. This formulation assumes that mining old needles does not contribute significantly to survival.

The possible low survival when the larvae emerge while the buds are too undeveloped to penetrate may be simulated by reducing y_1 and y_2 in either of the methods discussed.

Entry points for inclusion of the two weather effects, discussed above, have been included in the simulation, but presently there are no data to guide formulation of the required relationships. Also, an entry point has been included for implementation of control measures against the second instar larvae.

Bud destruction by second instar larvae

The effect of larvae on foliage will also depend on the phenology of bud flush and larval emergence. If the larvae mine the buds, they may destroy all or part of the potential foliage production of that bud while, if feeding starts after bud flush, the damage will be negligible. The proportion of the bud destroyed by the second instar appears to be critical as it determines the availability of foliage for the later instars and may also influence bud development for the following year, as lateral bud initiation occurs around this time (Allen and Owens 1972). The proportion destroyed of each attacked bud is a constant established at the start of the simulation.

Survival from third to sixth instar

Surviving second instar larvae moult to third instars. In the absence of detailed population records, survival values from third to fourth, fourth to fifth and fifth to sixth instar are all set at 1.0 all remaining larval mortality being implemented in the sixth instar. This may be revised as information becomes available.

An entry point is provided for control measures against the fourth instar. Control at this point acts prior to any significant defoliation.

Sixth instar survival

(a) Defoliation and starvation mortality

Miller (1977) indicates that the second, third and fourth instar larvae consume only 4% of the total amount of food eaten throughout the larval stage. Fifth instar larvae consume 9% and sixth instars consume 87%. The timing of the spray will therefore influence the amount of defoliation that has already occurred. Defoliation, at present, is implemented in the model only during the sixth instar, apart from the foliage loss owing to bud mining by the second instars. As the survival of fifth instar to sixth instar is set at 1.0 the sixth instars in the model are effectively fifth and sixth instars of field populations.

The first mortality effect, if no spraying is implemented, is from starvation. In calculating this effect, the extent of defoliation is also calculated. If spraying is implemented at the start of the instar, the larvae are killed before they consume a significant quantity of foliage; thus, they do not compete with the larvae which will survive the spray. If, on the other hand, spraying is implemented toward the end of the instar, the larvae, before dying, consume a significant quantity of foliage and compete with those that survive the spray.

The effect of different timings of control measures in relation to the larval development is expressed in the simulation by a parameter representing the proportion of the instar completed by a larva before it is killed. A low value of this parameter implies control measures carried out primarily on the fifth instars. The effective number of larvae is thus

effective number = (number of larvae surviving the spray) + [(number of killed larvae) x (proportion of development completed)]

The total feeding per sixth instar larvae is related to foliage availability, modified by the suitability of the foliage for larval feeding. Larvae feed on old foliage only after they have wandered considerably without finding new needles (Heron 1965). There are chemical differences between staminate flowers, new vegetative shoots, and old needles that affect their palatability for budworm larvae. Both physical and chemical changes occur in needles as they mature and influence budworm feeding. The relationship of feeding to foliage availability was determined from unpublished data of R. Shepherd. The total feeding describes the total foliage destruction as distinct from foliage consumption, as larvae destroy considerably more foliage than they consume (Graham and Orr 1940). It is assumed that consumption is a constant proportion of foliage destruction under all conditions.

Only the larger instars appear able to utilize older foliage, a certain minimum total consumption of new foliage being required to allow survival of the earlier instars. If this minimum cannot be met, as a result of extensive bud destruction by the second instars because of early larval emergence in relation to flushing, or of high competition for available foliage, high mortality results. Morris *et al.* (1958) indicate that the increased mortality owing to larval competition for food is due to starvation and also to an increase in the rate at which larvae drop out of trees while attempting to find new food sources.

There may also be an upper limit of new foliage consumption, above which no attempt is made to feed on old foliage, which results in premature pupation, small adults, and lower fecundity. At present, the last two effects have not been incorporated explicitly in the simulation.

The optimal nutritional status of the larvae is achieved by consumption of a maximum quantity of new needles. The relative nutritional status declines if they do not achieve this maximum consumption, or if part of the consumption is of old foliage. Heron (1965) shows that although the later instars will survive well on old foliage, they produce undersized adults, indicating that the nutritional quality of older needles is less than that of new foliage.

The nutritional status determines the sixth instar larval survival and the final fecundity of the adults. Although starvation mortality is common, the relationship of the mortality to the degree of starvation has not been established (Johnson and Denton 1975).

Unpublished data of R. Shepherd indicate that the maximum total feeding (foliage destruction) is 1.8 g dry weight of needles per larva. To determine the actual feeding rate, the quantity of new foliage per larva is determined. If this is in excess of 1.8 g/larva, each larva is assumed to eat 1.8 g new foliage. If there is less than 1.8 g/larva, all new foliage is consumed with each larva consuming the foliage available, and the deficit between the actual and maximum consumption is determined. All new foliage must be consumed before the larvae will feed on old needles.

The larvae may attempt to make up any deficit by feeding on old needles. A factor (≤ 1.0) is used to account for the lower palatability of old needles, and determines the proportion of the deficit that the larvae may attempt to fill by old foliage consumption. The actual consumption of old foliage is determined by (deficit) x (proportion of deficit which can be filled) in place of the maximum feeding rate of 1.8 g. An alternative approach would be to allow the proportion of the deficit, filled by old-foliage consumption, to increase with increasing feeding deficit.

The relative nutritional status of the larval population is determined as follows: new foliage is assigned a relative nutritional value of 1.0, the relative nutritional value of old foliage is determined at the start of the simulation. The relative nutritional status is obtained from

$$\frac{[(\text{feeding rate on new foliage}) + (\text{feeding rate on old foliage}) \times (\text{relative nutritional value of old foliage})]}{(\text{maximum feeding rate})}$$

The relationship of starvation survival to relative nutritional status is assumed to be of the same form as Figure 1a or 1c (x = relative nutritional status; y = survival from starvation). A value of $y_2 = 1.0$ is assigned, assuming that larvae can withstand some starvation without dying. A value of $y_1 \approx 0$ and $x_B > x_A$ implies a minimal nutritional level required for survival. This would not result in complete extinction of the population, as

a few individuals always get enough food to survive. This is reflected by the non-zero value of y_1 .

(b) Fecundity

Fecundity will also be determined by the relative nutritional status of the larvae, discussed above. Even under extreme conditions of defoliation and population starvation, some larvae will get enough food to survive. It is postulated that if a larva survives, it can produce, as an adult, a minimum number of eggs. There will also be a maximum fecundity attained if the larvae feed at their maximum rate on new foliage. McKight (1971) indicates that 256 and 154 are the maximum fecundity and average maximum of the western budworm.

The relationship of fecundity to nutritional status is of the form indicated in Figure 1e (x = relative nutritional status; y = fecundity). The value of x_B represents the survival of a few individuals under high starvation conditions, and corresponds to the value of x_B in the relationship of starvation survival to nutritional status. These few survivors are assumed to develop a basal number of eggs. The value of y_2 (average maximum fecundity) is presently set at 154, with $y_1 \geq 40$, where 40 is the approximate number of eggs in an egg mass. Any starvation results in reduced fecundity, although it may not reduce survival, as indicated above.

(c) Parasitism and Predation

The primary importance of parasites and predators is in maintaining the budworm population at low levels until such population is able to expand at a rate exceeding the ability of the parasites and predators to contain it (Morris *et al.* 1958; Ludwig *et al.* 1978). This release results from increased survival owing to good weather, and with the eastern budworm, from changes in forest composition (Ives 1974). During an outbreak, parasites and predators exert little effect (Graham and Orr 1940; Morris *et al.* 1958), but may be important in eliminating the outbreak when the budworm population has been severely depleted by starvation.

Survival from parasites and predators is evaluated from relationships of the form in Figure 1a (x = larval density; y = survival). Parasitism and pre-

dation are evaluated separately. In both cases, the greatest effect is at low budworm population densities, where the budworm survival is minimal (y_1). At high larval densities, the budworms vastly outnumber the predators and parasites; thus survival approaches 1.0 (y_2). Increasing the value of x_B determines the budworm density at which the population begins escaping control by parasites or predators. Decreasing the value of x_C restricts the range of population densities over which the parasites or predators exert their effect.

Budworm density is expressed as budworm/kg needles, where the normal needle biomass (of the undefoliated stand) is used. Although parasite mortality occurs mainly in the late instars, attacks by the parasite actually occur in the early instars. The number of third instar larvae/kg foliage is used to determine the parasitism rate, although the mortality occurs in the sixth instar. Sixth instar larvae/kg foliage are used to determine the predation rate. Parasitism apparently has an effect over a wider range of densities than predation, as the invertebrate parasite populations can increase more rapidly than the predator (principally avian) populations, in response to budworm population increases.

In the absence of data, parasitism and predation are assumed to have a fixed rate; i.e., the relationship of survival to larval density does not change over the course of an outbreak. A dynamic relationship could readily be incorporated by making the values of y_1 , x_B and x_C fluctuate in relation to budworm density in the previous year. This would be most applicable to parasites, as the numerical response of vertebrate predators to prey increases is slow.

At low prey densities, vertebrate predators (e.g., birds) may switch to alternate hosts. This possibility may be incorporated by using an alternative relationship of survival (y) to density (x), similar to Figure 1h, when budworm density falls below a specified level.

In the model, parasite and predator mortality are computed after defoliation has been calculated, although there is some indication of an alternative mechanism for parasites; i.e., parasitism results in the larvae stopping feeding some time before mortality occurs; alternatively, the parasite mortality could be computed before defoliation is calculated.

d) Weather effects on survival

No data are available to evaluate the effect of weather on sixth instar larval survival; thus, some simple formulation must be postulated. The relationships used to describe the effects of these various factors on sixth instar larval survival are presumably for average weather conditions. When weather is good, survival will be better than average and the opposite when weather is poor.

Each year of the simulation is assigned a weather index: 1 (poor), 2 (average) or 3 (good). The overall sixth instar survival is modified by a factor determined from the index, with a value of 1.0 in average years. Factor values of 0.75 and 2.0, for example, could be used in poor and good years, respectively.

Pupal survival

As many of the mortality factors acting on the sixth instar larvae also act on the pupae, pupal survival (y) is a function of sixth instar survival (x), of the form in Figure 1g. The exact relationship, from Macdonald (1963), is

$$(\text{pupal survival}) = 0.3495 + 0.828 (\text{sixth instar survival})$$

Proportion female

The total number of eggs produced in a unit area depends on the number of adults, the proportion of females, and on the relative fecundity. Determination of the fecundity and the mortality effects acting during the development of the egg through to the adult stage has already been described. The remaining relationship, the proportion female, has been defined by Miller (1963) as a function of the pupal survival, of the form in Figure 1g with

$$(\text{proportion female}) = .289 + .237 (\text{pupal survival})$$

Adult dispersal and oviposition

The adult population is not determined *per se* in the simulation; rather, the potential number of eggs produced by the population is determined. This procedure facilitates simulation of the dispersal procedure; eggs are divided into those laid before dispersal and those subjected to the dispersal process.

Pre-oviposition mortality of adults as a result of insecticide application may be simulated by reduction of the total eggs produced. Similarly, the effects of pheromone confusion control measures, which result in non-insemination of many females, effectively removes the egg complement of these females from the total produced. A low rate of successful matings also occurs in years with wet conditions at the time of moth flight, resulting in low activity (Greenbank 1963).

It is widely believed (Greenbank 1973; Harvey 1977) that the females must lay some eggs before making an exodus flight from the stand. However, Blais (1953) indicates that females developing from starved larvae, with a low initial egg complement, can fly before ovipositing; the proportion increases with increasing larval starvation (Greenbank 1973). A female makes only one exodus flight in its life; i.e., it does not continue to disperse night after night (Greenbank 1973).

The exodus flight of the female exposes it to passive transport by convective and turbulent winds. In the absence of wind, the dispersal distance is small because of the short flight time (Greenbank 1963). Turbulent transport results in a gradual downwind spread of the population. Long-range transport is generally associated with the convective processes occurring with the passage of cold fronts and pre-frontal thunder storms (Greenbank 1973). At endemic levels, however, wind dispersal is unlikely to result in sufficient concentration of the budworm population to affect its release from natural controls (Greenbank 1957).

Although the proportion of females making an exodus flight is determined principally by the larval starvation, this activity may be enhanced or suppressed by weather conditions at the time of moth flight, flight being eliminated by continuous rain and stimulated by strong gusts of wind, respectively (Greenbank 1963).

The final factor in generation survival is the oviposition success rate. Miller (1963) found that more eggs were laid on non-defoliated twigs when caged ovipositing females were exposed to a defoliated and non-defoliated twig; however, it is not known how this might affect field populations because, if no new foliage is available, oviposition may occur readily on old foliage. The experiments of Miller (1963) are analogous to the feeding preference-aversion experiments described by Dethier (1976).

That defoliation does not inhibit oviposition is indicated by Morris (1955), who found extremely high egg mass counts on severely defoliated trees.

Dispersal is a response to adverse conditions, which also results in reduced fecundity. The proportion of eggs being laid before dispersal is related to fecundity, as indicated in Figure 1a or 1g

(x' = relative fecundity, y = proportion of eggs laid in cell of origin)

Relative fecundity is defined as

$$(\text{relative fecundity}) = \frac{(\text{Actual fecundity}) - (\text{minimum fecundity})}{(\text{maximum fecundity}) - (\text{minimum fecundity})}$$

i.e., the fecundity is scaled between 0 and 1.

Assigning $y_1 > 0$ implies that some eggs are always laid before dispersal, regardless of the predisposition to disperse. The dispersal occurring even under optimal conditions is reflected by having $y_2 < 1.0$.

The weather index of the year discussed above is used to modify the dispersal which is reduced by wet conditions. The proportion of eggs being laid in the site of origin is modified by a factor set at the start of the simulation for poor, average and good years, the factor being > 1 in poor years and < 1 in good years. In the model, oviposition success is not reduced by the defoliation status of the stand, nor has the possible effect of poor weather on mating success been incorporated.

Survival of non-dispersed eggs is set at 1.0. Survival of dispersed eggs depends on the dispersing moths being deposited in a host stand. Assuming the dispersal process distributes moths evenly over an area, survival will depend on the proportion of the area covered by host stands. The effect of mixed stands on survival depends on the ability of moths to locate host trees in stands of decreasing proportion of hosts.

If dispersers are not deposited evenly over an area, as might be expected if the cells are large and contain several mountain ranges and major valleys, use of the total cell area in determining the survival rate is inaccurate. This situation is simulated by setting the proportion of the total cell area in which dispersers are deposited at a constant value.

The simulation can be carried out on a single cell. Dispersal in this case is presently treated as follows: (a) dispersal out of the cell is exactly balanced by dispersal into the cell, or (b) dispersers out of the cell are lost from the system, there being no dispersal into the cell.

B. THE HOST FOLIAGE

General hypothesis

The basic unit of foliage selected for the simulation was kg oven-dry weight of needles per hectare. This unit has a number of important advantages, primarily that of being common to the disciplines and studies which must be brought together in a model of this scope; e.g., available dry weight of needles per larva is an index of larval starvation; defoliation effects are easily incorporated, and needle biomass may provide a link with mensurational studies on radial and height growth increments, since dry matter production is closely related to the amount of foliage (Möller 1946, 1947; Baskerville 1965). Use of dry weight of needles permits comparison of different host species, and also intraspecific comparisons of different growth forms under different site conditions.

Needle dry weight does not provide an easily-sampled unit for the expression of egg and larval density. By comparison, branch surface area (foliated length \times 0.5 maximum foliated width), the established basis of budworm density measurements (Carolin and Coulter 1972), is readily measured in the field, but lacks the wide applicability of the dry weight unit. Branch surface area also fails to indicate large differences in foliage availability (due to previous defoliation or different rates of lateral branching or needle production or both) on branches of similar surface area. Comparisons of different host species and intraspecific comparisons under different growth conditions are therefore impractical.

As the budworm feeds preferentially on new foliage (Johnson and Denton 1975), the method of classifying foliage with respect to needle age must be established. Separation into at least new- and old-foliage components is required. Old needles, however, vary in photosynthetic efficiency and rate of drop-off with age (Mitchell 1975; Silver 1962; Smith 1972). In early versions of the model, each year's growth of needles was considered separately, to allow for possible complete loss of foliage after several years'

removal of current flush in conjunction with the normal loss rate of needles. Current research (A. Van Sickle, pers. comm.) indicates that old needles are retained much longer when trees are under defoliation stress. In addition, with removal of the younger (outer) foliage, the photosynthetic efficiency of remaining older needles may be increased. As a compromise, to account for the overall effect of these interacting processes, only two classes of needles are used: new and old. For the old foliage, a retention rate is assigned, dependent on defoliation status. Normally, this rate represents the average between high and low rates over the range of foliage ages. During defoliation, the rate represents improved retention of the oldest foliage. This is true especially if budworm feeding preference for old foliage decreases with increasing foliage age, as is apparently the case.

Möller (1946, 1947) observed that the amount of foliage in coniferous stands appeared constant across a range of stand densities once full occupancy of the site was achieved. The quantity of foliage per unit area will thus increase rapidly with age to a constant level. For example, in *Pinus sylvestris* (Madgwick 1974), foliage weight becomes constant at age 15-20 years. Evidently, as stands mature, there is a transition from many small trees with a small quantity of foliage per tree to fewer, larger trees with more foliage per tree; thus, the overall quantity of foliage per unit area remains constant.

Baskerville (1965) examined the applicability of Möller's observations to balsam fir and found that there was a slight tendency toward increasing amounts of foliage with increasing density. This exception to Möller's generalization appeared to result from the high shade tolerance of balsam fir (*Abies balsamea* (L.) Mill.). Douglas-fir is much less shade tolerant than balsam fir (Fowells 1965). The model therefore assumes conformity with Möller's hypothesis; i.e., a constant foliage weight per hectare for all stands aged 20 years or more. This constant, which has an average of 2000 kg/ha, based on data provided by H. Brix (pers. comm.), varies with site conditions. In mixed stands, this will be reduced in proportion to other species in the stand.

As *C. occidentalis* has one generation per year, each cycle of the simulation is designed to correspond to this time frame. Each year the foliage must be incremented. Firstly, the previous year's new foliage becomes old. Since the total weight of needles remains constant within a unit area, in an undefoliated stand,

this must be balanced by an equal reduction of the previous old foliage.

Silver (1962) found that current needles comprised 28% of the total foliage of Douglas-fir; thus 38.89%; i.e., $(28 \times 100)/(100-28)$, of the old foliage must be lost to allow for the aging of this old foliage, and 61.11% of the old foliage is retained. This retention rate increases with increasing defoliation.

After aging the previous year's new growth, the current year's new foliage must be determined. The maximum quantity of new foliage produced by a stand is established as 28% of the constant total foliage per unit area discussed above. Little information is available as to how this potential new foliage production is reduced by defoliation. Douglas-fir can apparently withstand some defoliation without reducing the next year's growth and can respond to severe defoliation by adventitious budding (A. Van Sickle, pers. comm.). Even so, the tree's response to long-term defoliation and how this varies among host species is not known.

Addition of new foliage

The effect of defoliation on new foliage added in a given year is simulated in the following manner. The maximum current flush is $0.28x$ (average undefoliated biomass). The proportion of this maximum which is actually achieved will be determined by some index of the defoliation status of the tree. A relationship of the form indicated in Figure 1a or 1c (x = defoliation; y = proportion of the maximum new foliage) is expected, with $y_2 = 1.0$, under the assumption that trees can withstand some defoliation. The lower limit to the current flush ($y_1 > 0$) is the result of adventitious budding.

The foliage parameter which determines the biomass of new foliage added is not known. There are several possibilities.

- (i) New foliage biomass addition depends on the total old and new foliage remaining after all defoliation is complete in the previous year. This implies some effect of the old foliage on bud initiation, growth and development.
- (ii) The new foliage biomass addition is determined by the new foliage remaining after defoliation in the previous year.

- (iii) The buds producing the current flush in any year are established at the time of bud flush in the previous year. The phenology of bud destruction may influence the following year's bud development.
- (iv) New foliage addition depends only on the old foliage in the previous year.

At present, the new foliage remaining at the end of the year is used to establish the current flush in the following year, as it is known that defoliation of new foliage reduces the subsequent year's flush, but it is not known what effect, if any, defoliation of old needles might have on subsequent flush.

Use of a constant value of γ_1 , the minimum rate of new foliage production, implies an unlimited capacity of Douglas-fir to withstand defoliation. Possibly the value of γ_1 will decline over the course of an outbreak, resulting ultimately in death of the tree when it can no longer produce foliage. Such a reduction also results in a decline in the foliage available for budworm feeding, provides a time-limit to the maintenance of high population levels, and increases the recovery time of the tree and the possibility of tree mortality. No data are available to shed light on these possibilities; thus, these phenomena are not incorporated into the model, a constant γ_1 being used.

When using a relationship of the form of Figure 1a, care must be taken in selecting a combination of γ_1 and x_B values to ensure that the inflection point does not result in a given quantity of new foliage producing no increase of foliage in the following year (Fig. 2). This possibility may be achieved by keeping $\gamma_1 > x_B$ in numerical value.

With a value of γ_1 which declines with increasing defoliation, death of the tree could be assumed once such a condition resulted.

Retention of old foliage

In the undefoliated tree, to maintain the average needle biomass, a proportion .6111 of old needles must be retained. As indicated above, defoliation results in abnormally high retention rates of old needles. The retention rate is determined from the total foliage at the start of the year, using a relationship of the form in Figure 1f (x = total foliage relative to maximum, y = retention rate).

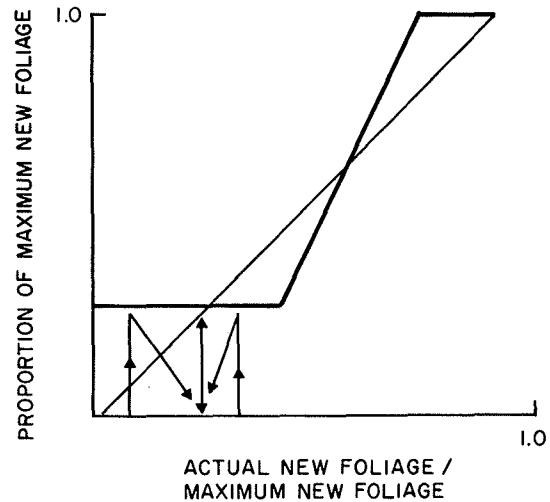


Figure 2. With certain combinations of new foliage production rate in relation to post-defoliation foliage, the stand would never recover its full complement of foliage. This condition should either be prohibited in the simulation, or assumed to result in tree mortality.

This assumes that a certain amount of defoliation is necessary to produce the abnormal retention rates. Values of minimum retention $\gamma_2 = 0.6111$ and maximum retention $\gamma_1 < 1.0$ are used, assuming that some old foliage is always lost. The relationship must be used with the constraint that the total weight of old needles retained cannot exceed 0.72 x (average non-defoliated biomass).

Number of buds

As the average dry weight of needles per shoot is approximately 0.6 g in undefoliated trees (H. Brix, pers. comm.), the number of buds are estimated from the biomass of new needles added. Defoliation results in small shoots being produced in the subsequent year, but this effect has not been quantified.

Forest aging

Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir) is the principal host of C. occidentalis in B.C. and the western United States. Through the action of fire, clearcutting and pest effects, Douglas-fir tends to form even-aged stands (Fowells 1965). The principal data base for the study, the B.C. Forest Inventory, uses 9 age classes of trees. However, the budworm outbreak area in B.C. contains very few stands of age class 9, thus classes 8 and 9 are combined. This facilitates simulation of forest aging by

making the interval between each class 20 years. The areas of host-tree-containing stands of each class may be extracted from the inventory data to characterize each cell of the grid within which simulation takes place.

Forest aging is accomplished by moving all areas of age classes 1 to 7 to the next highest age class every 20 years of simulation. Age class 8 accumulates all mature and overmature timber until reduced by logging, and provision could also be made for a random reduction attributable to fire effects. The reduced area is replaced by an equivalent area of age class 1.

Death of individual trees results in filling in of the vacated space by the remaining crowns (Mitchell 1975). Effects of individual tree mortality are therefore considered in the foliage relationships of the model.

STRUCTURE OF THE MODEL

The general structure of the model is illustrated in Figure 3. Each iteration starts with the state of the host and insect life cycle in the fall, after all defoliation and oviposition are complete. Spatial effects in the model are simulated by examining the population dynamics within each cell of a grid, then linking the cells by dispersal relationships. The status of each cell is defined at the start of the iteration as number of eggs, kilograms dry weight of old and new needles, and the current age structure of the forest. The foliage biomass and larval population dynamics are evaluated contemporaneously interacting by the bud destruction and defoliation relationships.

The survival rates of eggs, each of the 6 larval instars, the pupae, and adults are assigned individually in the simulation. Developmental stages are discrete and proceed stepwise within the model; i.e., all individuals of the population are considered to be of the same developmental stage. Although information on the survival of several instars is lacking, this construction facilitates modification as data become available. Survival rates in such cases are currently set at 1.0.

For each cell, the survival from eggs to first instar larvae and the proportion of larvae dispersing are determined, and the dispersing larvae redistributed. After the dispersal has been completed, each cell has

a population of first instar larvae distinguishable as to whether they originated within the cell or dispersed in from another cell. The survival of the dispersed and non-dispersed individuals is then calculated and the number of second instar larvae entering hibernation derived.

At the point in the iteration representing spring conditions, the foliage is incremented: some of the old foliage dies and the number of buds prior to flushing is estimated. Simultaneously, the second instar larvae are redistributed by the dispersal routines and the survival of dispersed and non-dispersed larvae is determined, as with the first instar larvae. Additionally, the larval survival is modified by the availability of buds and the implementation of any simulated control procedures. The surviving larvae penetrate buds and destroy a proportion of the potential foliage production by the buds.

After the bud-mining stage, the survival to the sixth instar is determined. In the sixth instar, a number of mortality effects, from starvation, predators and parasites, and weather are computed and the survival to pupae is evaluated. From the relationships used to define the feeding process, the loss of new and old foliage is calculated. This loss, averaged over the larvae, established the larval survival rate and the fecundity of the adults.

The pupal survival rate also determines the proportion of adults which are female. From this proportion, and from the number of surviving pupae and the fecundity, the number of eggs produced within the cell is calculated. These eggs are subdivided into those laid within the cell and those carried to other cells by dispersal of adults, the proportion laid before dispersal being determined by the degree of larval starvation. Similarly to the two larval dispersals, survival of the dispersed and non-dispersed eggs determines the total egg population at the start of the next iteration.

The age class structure used to define the forest is based on the 20-year increments of the B.C. Forest Inventory (cf. section B). Every 20 iterations, the age class of each hectare of host timber, within each cell, is incremented by 1, to accumulate in age class 8 until logged.

DISCUSSION

The model described here addresses the more

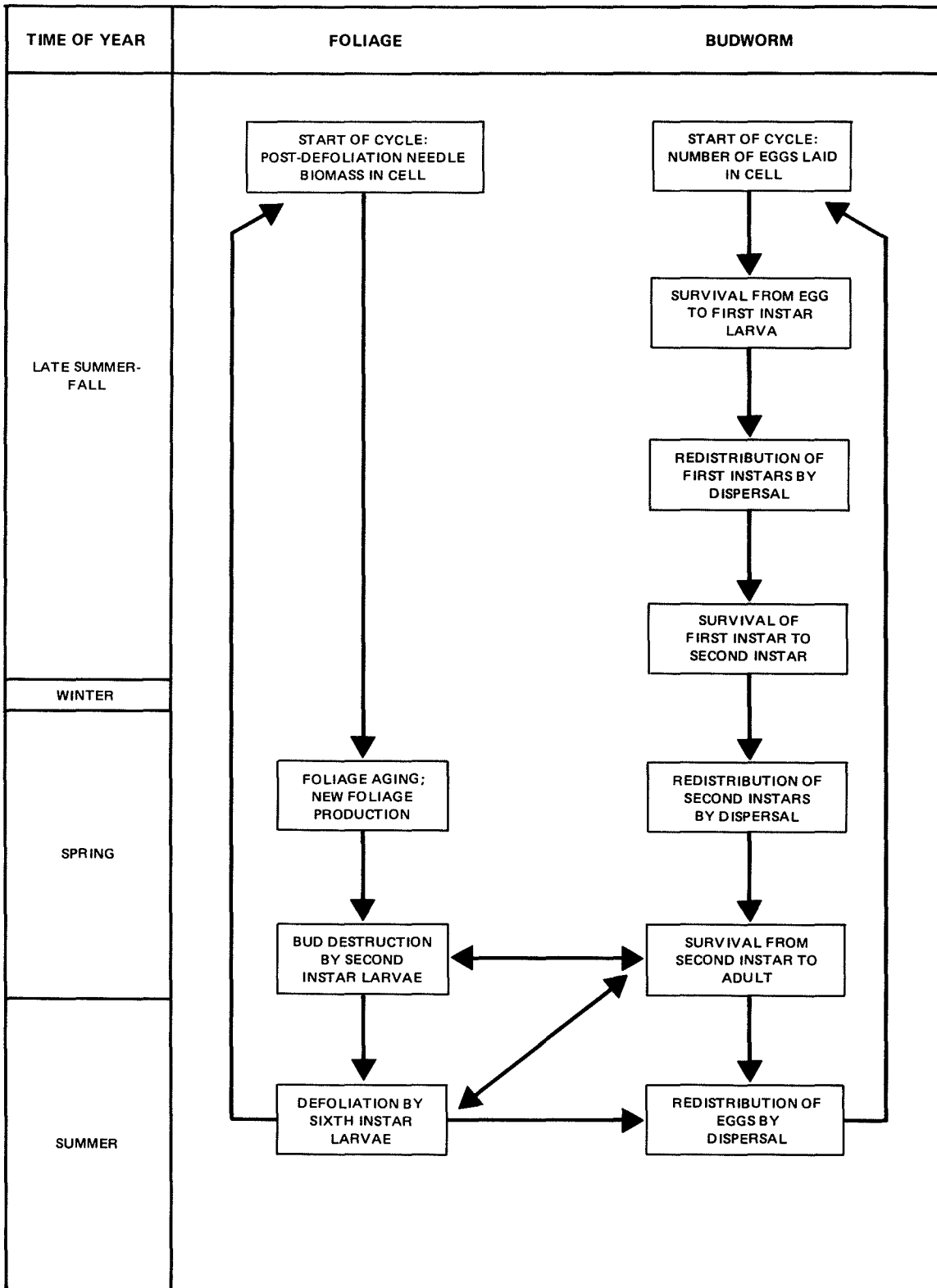


Figure 3. The general cyclical structure of the model, with the foliage and budworm dynamics being considered in parallel, is illustrated. The budworm interacts with the foliage through the feeding process.

direct influences on the budworm population dynamics. Many subtle relationships are indicated in the budworm literature, but no attempt has been made to evaluate their effect. For example, Harvey (1977) indicates that egg size declines as oviposition proceeds. Larvae from these later, smaller eggs have slower emergence from the hibernacula, higher survival, and a smaller proportion of male pupae. No explanation for this phenomenon was found, and its significance to the population dynamics is unknown.

The Forest Insect and Disease Survey records for 1978 indicate that the spruce budworm outbreak in B.C. has collapsed over much of its range. As the collapse has occurred equally in stands over the whole range of defoliation histories and intensities, the collapse is apparently not related to starvation of the population. The geographic scale of the population collapse seems to implicate some weather-related mortality as the causative factor. Timing of the survey, however, precluded identification of the stage of the life cycle at which mortality occurred.

Apart from its general influence on the overall survival rate, several specific weather effects have been identified as having possible major impact on budworm survival. For example, a long period of warm weather in the fall may result in increased mortality of the second instar larvae through exhaustion of larval food reserves. Some weather effects appear to influence the mortality by altering the phenological relationships of larval emergence and bud flush. If the larvae emerge before the buds begin to swell, the larvae may not be able to mine the buds. High larval mortality may also result from low temperatures following the larval emergence period.

The pattern of visible defoliation by the western budworm in B.C. has the appearance of bands along the hillside. Visible defoliation was low or absent in the valley bottoms during the current outbreak, although this may not occur in other parts of its range. This banding pattern may also reflect some weather-related mortality effect. Until the underlying causes of this banding of the population are understood, a realistic population model may not be developed. To facilitate the evaluation of this phenomenon, current development of the model described herein is being carried out on small cells, within individual valley systems, where effects of aspect and elevation may be examined. This scale of simulation also facilitates examination of the

effects of stand composition on the population dynamics.

Lack of information on basic tree growth processes, such as the regulation of the bud setting and development rates, inhibits not only understanding of the outbreak dynamics itself, but evaluation of the impact of the outbreak and potential recovery from the outbreak.

The form and values of individual relationships can be easily altered for purposes of the simulation. The limits of the equations and the form of the relationships will become more definitive as information accumulates. The model will therefore never be a final entity; it guides the research to critical areas of the budworm-tree interaction and is, in turn, modified by results of the investigations. Further reports will be made on specific processes within the model and on the dynamics of the simulation under different conditions.

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APPENDIX A

Dispersal

Spatial effects of dispersal are simulated by examining the population dynamics within cells of a grid and linking the cells to allow population transfer between them. The relative effects of different forms of dispersal are determined by the grid scale; e.g., with large cells, larval dispersal effects and the effects of stand isolation and density will be masked. In the model, cell size is easily varied since the dynamics within each cell is independent of grid scale.

The dispersal direction of both larvae and adults is determined by local winds, except in the case of long-distance dispersal by pre-frontal convective winds. In mountainous terrain, local winds are determined by the topography, the airflow being guided into the principal drainage channels (Schroeder and Buck 1970). As the larvae and adults are more active at certain times of the day (Henson 1950), the prevailing wind direction (up or down valley, or up or down slope) determines the direction of dispersal. The method of simulating dispersal, for both larvae and adults, is as follows:

Assume a rectangular grid, containing $N = i \times j$ cells, where cell C_{ij} is the j^{th} cell on the i^{th} row. Each cell is assigned a unique identifier number (I) from 1-N. Excluding the grid edge, each cell has

8 neighbours. The identifier of the adjacent cell into which dispersers will pass can be specified. A maximum number of cells over which dispersal can occur (n) is assumed. For each cell (I) of the grid, therefore, it is possible to specify the ordered sequence of cells entered by individuals dispersing from cell (I). The actual number of cells over which dispersal actually occurs (n' ; $n' \leq n$) is set as a constant, but is probably determined by the weather at the time of dispersal.

The distribution of the dispersers among the cells is computed using a matrix D , in which the value of $D(n', k)$, $n' = 1, \dots, n$; $k = 1, \dots, n'$; defines the proportion of dispersers which lands in the k^{th} cell away from the cell of origin when dispersal is occurring over n' cells.

Table 1 illustrates the values of the matrix for a maximum dispersal distance (n) of 5 cells if (a) the proportion of dispersers decreases with distance from source, or (b) there is a modal dispersal distance. The method may be adapted for multiple dispersal directions and different matrices would be used with the first and second instar larvae and the adults.

TABLE 1

Construction of dispersal matrix (D) of proportion of dispersers landing in each cell, assuming maximum dispersal distance of 5 cells, for 2 contingencies: (a) decrease in proportion of dispersers with distance from source; (b) dispersal over modal distance with fewer dispersers on either side of mode (for further description see text).

Case	Max. dispersal distance (no. of cells n')	No. of cells away from cell of origin (K)				
		1	2	3	4	5
Decrease with distance	1	1.00	0.00	0.00	0.00	0.00
	2	0.60	0.40	0.00	0.00	0.00
	3	0.50	0.30	0.20	0.00	0.00
	4	0.45	0.25	0.15	0.15	0.00
	5	0.43	0.23	0.13	0.11	0.10
Modal dispersal	1	1.00	0.00	0.00	0.00	0.00
	2	0.60	0.40	0.00	0.00	0.00
	3	0.20	0.60	0.20	0.00	0.00
	4	0.00	0.20	0.60	0.20	0.00
	5	0.00	0.00	0.20	0.60	0.20

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