United States
Department of
Agriculture

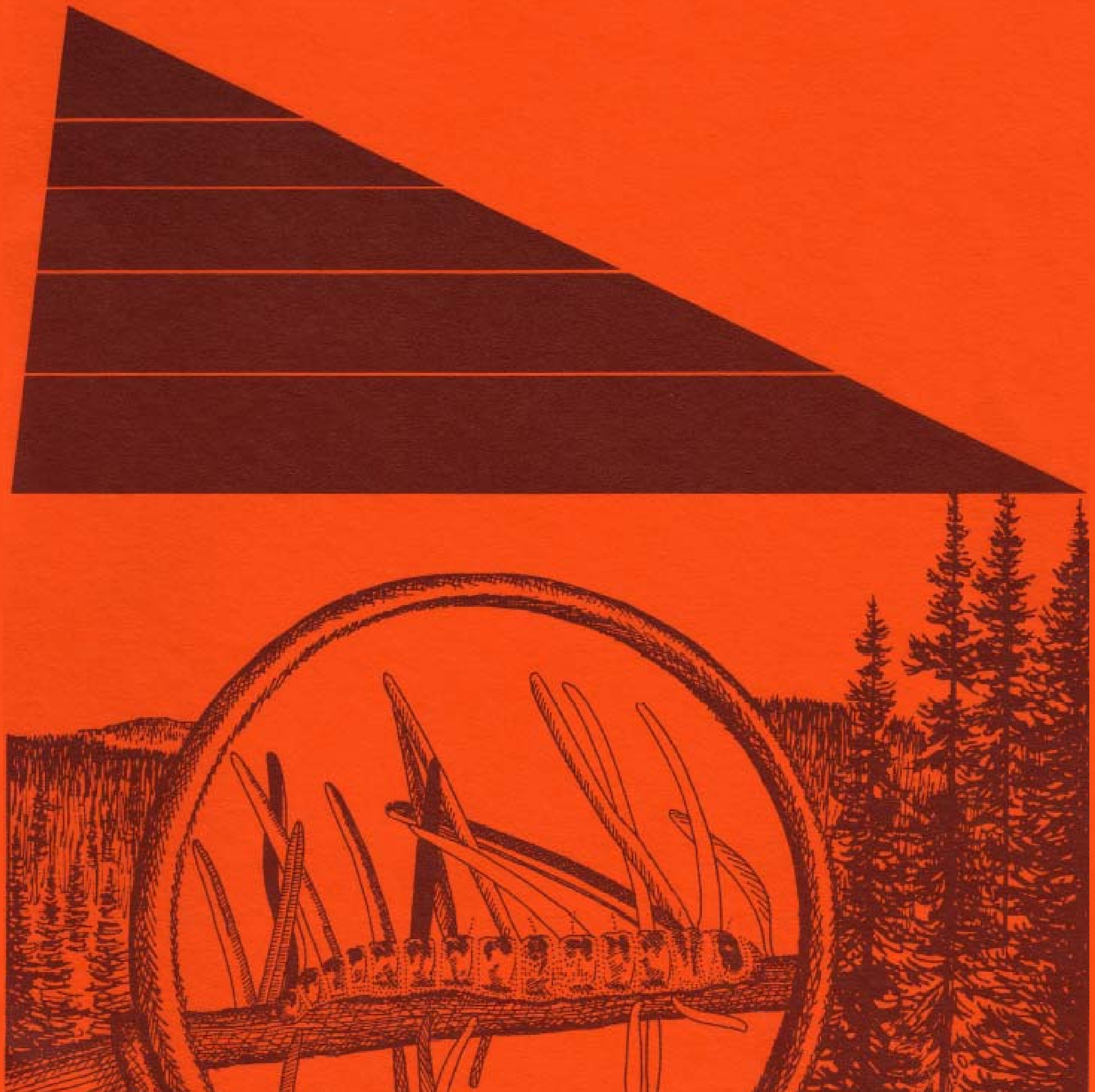
Forest Service

Pacific Northwest
Research Station

General Technical
Report
PNW-GTR-241
July 1989

The Western Spruce Budworm Model: Structure and Content

Katherine A. Sheehan, William P. Kemp, J.J. Colbert, and
Nicholas L. Crookston



In 1977, the United States Department of Agriculture and the Canada Department of the Environment agreed to cooperate in an expanded and accelerated research and development effort, the Canada/United States Spruce Budworms Program (CANUSA), aimed at the spruce budworm in the East and the western spruce budworm in the West. The objective of CANUSA was to design and evaluate strategies for controlling the spruce budworms and managing budworm-susceptible forests, to help forest managers attain their objectives in an economically and environmentally acceptable manner. The work reported in this publication was wholly funded by the Program. This manual is one in a series on the western spruce budworm.

July 1989

Authors

KATHERINE A. SHEEHAN is with the USDA Forest Service, Pacific Northwest Region, Forest Pest Management, Portland, OR; WILLIAM P. KEMP is with the USDA Agricultural Research Service, Rangeland Insect Laboratory, Bozeman, MT; J.J. COLBERT and NICHOLAS L. CROOKSTON are USDA Forest Service employees based at the Northeastern Forest Experiment Station and Intermountain Research Station in Morgantown, WV, and Moscow, ID, respectively.

Contents

Abstract

Sheehan, Katharine A.; Kemp, William P.; Colbert, J.J.; Crookston, Nicholas L. 1989. The western spruce budworm model: structure and content. Gen. Tech. Rep. PNW-GTR-241. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 70 p.

The Budworm Model predicts the amounts of foliage destroyed annually by the western spruce budworm, *Choristoneura occidentalis* Freeman, in a forest stand. The model may be used independently, or it may be linked to the Stand Prognosis Model to simulate the dynamics of forest stands. Many processes that affect budworm population dynamics are simulated in detail, including budworm and host phenology, larval growth and feeding, larval and adult dispersal, and the effects of natural enemies. This publication describes the structure, assumptions, and default parameter values of the Budworm Model.

Keywords: Model, population dynamics, insect populations, defoliation, stand growth and yield, western spruce budworm, *Choristoneura occidentalis,* Tortricidae.

Summary

The Budworm Model simulates the population dynamics of the western spruce budworm *(Choristoneura occidentalis* Freeman) to predict defoliation caused by budworms. This model was designed for scientists to identify critical factors that affect budworm population dynamics and for managers to evaluate the effects of budworm defoliation on stand growth and yield. While the computer code has been thoroughly tested for accuracy and some components of the model have been evaluated, the Budworm Model as a whole has not been rigorously evaluated. This publication is intended to document the structure and content of the model and to facilitate its further evaluation by scientists and managers. A user's guide is being developed for the Budworm Model that will include information needed to run the model, such as stand characteristics, weather data, and budworm density at the start of the simulation. Default values for many parameters can be changed by users.

The Budworm Model can be used as an independent, stand-alone model, or it can be linked to the Prognosis Model for simulating the effect budworm-caused damage has on forest growth and yield. In either case, budworm populations may be simulated for 1 to 30 stands.

For each stand, budworm populations are simulated on three model trees, one for each size class (0-7 m, 7-14 m, and 14+ m), for each host species. Each model tree is further divided into crown thirds. Budworm populations are modeled separately, but not independently, for each '10liage cell" (crown third of a tree size class of a host species).

The Budworm Model follows the life cycle of the budworm. The net effects of processes that occur from egg hatch to larval emergence from hibernacula are simulated without much detail. Processes involved during the period from larval emergence to adult emergence-larval dispersal, budworm and host foliage growth, defoliation, and budworm mortality-are modeled in detail.

During the latter period, a series of steps is executed every 20 degree-days (°D) Celsius. First, in early spring, a portion of larvae in hibernacula may emerge and search for feeding sites. Second, host shoots expand and grow. Third, budworm larvae grow and consume foliage. Fourth, larvae disperse if there is a shortage of foliage. Finally, mortality sources—natural enemies, insecticides, or the effects of foliage quality—act on budworm populations. The 20 °0 time step counter is incremented, and this series of steps is repeated until all budworms have become adults.

All budworms are assumed to have the same developmental rates—that is, all budworms require the same number of degree-days to complete a given life stage. Emergence times from hibernacula vary, however, and those larvae that emerge during one 20 °D interval are considered a cohort. Growth, feeding, dispersal, and mortality of each cohort are modeled separately. During a given 20 °D interval, budworms of a range of ages-corresponding to the range in emergence times—may be present.

After surviving members of the youngest cohort have emerged as adults, adult dispersal and oviposition are simulated. Users may specify either a net dispersal rate or a simple process model for adult dispersal and mortality.

A number of output options exist and range from virtually no output (useful when the Budworm Model is linked to the Prognosis Model) to detailed descriptions of budworm and foliage status for every 20°D interval during spring and summer.

Introduction

Development of the Budworm Model was a key objective of the western component of the Canada/United States Spruce Budworms Program (CAN USA-West), a 6-year research and development program of the USDA Forest Service and the Canadian Forestry Service. By integrating results of many CAN USA-sponsored studies, the Budworm Model assisted CANUSA-West's program management in identifying critical areas deserving additional research, in fostering communication among research disciplines, and in promoting common units for field measurements (Colbert and others 1983).

The Budworm Model was designed to be a tool for forest or pest managers and for researchers. Scientists can analyze results of this model (particularly the stand-alone version) to identify variables and relationships that are most important in determining the model's prediction; those subjects that are critical to the model's predictions and that are poorly understood at present deserve consideration for additional research. The model may thus assist in identifying and justifying future research.

The Prognosis Model (Stage 1973) projects stand growth and yield on the basis of individual trees from inventories. It 'simulates stands through rotations. The combined Prognosis-Budworm Model allows forest managers to predict the effects of the western spruce budworm on stand yields. Treatments designed to mitigate the impact of budworm defoliation on stand growth and yield may also be evaluated through use of the combined model. Treatments that can be easily simulated include a range of thinning options, regeneration methods, and insecticide applications. When appropriate weather data are available, pest managers can use the stand-alone Budworm Model to estimate budworm phenology during a season and, thus, time sampling or spray operations.

The initial version of the Budworm Model was based on information gathered at a CAN USA-West workshop held in early 1980. Approximately 30 researchers and potential users brainstormed to produce a model that was sometimes based on educated guesses. McNamee, and others (1980 unpubl.)[1] led that workshop and wrote the computer model.

A second workshop that revised the Budworm Model and connected it to the Prognosis Model was developed by Nicholas L. Crookston and Peter J. McNamee.[2]

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[1] An "unpubl." following a reference indicates that the material is from an unpublished source. Such references are located in "Literature Cited- Unpublished," which follows "Literature Cited."

[2] Personal communication. FORTRAN computer code on file, Nicholas L Crookston, Forestry Sciences laboratory, 1221 South Main Street, Moscow, ID 83843.

Based on preliminary results from CANUSA-sponsored projects and intensive reviews of the existing model, a third version (the current one) of the Budworm Model was proposed by Colbert and others (1981 unpubl.). This version has been extensively reviewed by most CAN USA-West investigators and users and by a panel of non-CANUSA experts. We caution potential users that the behavior of this model has not been thoroughly tested. In this paper we describe this third version of the Budworm Model-its assumptions, structure, parameters, options, and some of the known weaknesses.

Framework for Using the Budworm Model

Overview of the Budworm Model

Spatial scale and resolution—Budworm populations in 1 to 30 stands may be simulated using the Budworm Model. Within a stand, characteristics, such as species composition, density, and structure, are assumed to be homogeneous. The Budworm Model simulates the period from egg hatch to adult emergence independently for each stand. Adult dispersal and oviposition may be simulated either among stands or independently for each stand. Thus, interactions among budworm populations in different stands can occur in the model only during adult flight and oviposition.

Within a stand, three Budworm Model trees, one for each height class (0-7 m, 7-14 m, and 14+ m), are simulated for each host species. Another set of three trees represents all nonhost species in the stand. The Budworm Model simulates five host species:

Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco);
grand fir *(Abies grandis* Dougl. ex D. Don) Lindl.);
white fir *(Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.);
subalpine fir *(Abies lasiocarpa* (Hook.) Nutt.); and
Engelmann spruce *(Picea Engelmannii* Parry ex Engelm.).

Although western larch *(Larix occidentalis* Nutt.) is sometimes considered a host species, many biological details about this species have not been quantified; examples include larch phenology and growth pattern, and budworm feeding rates on larch. The Budworm Model is designed to include larch as a host species; however, larch is not currently simulated as a host species in the Budworm Model.

Each Budworm Model tree is divided into crown thirds. Budworm populations and the damage they cause are modeled separately for each "foliage cell" (species, tree size class, and crown third). Four foliage age classes are modeled within each foliage cell: current, 1-year-old, 2-year-old, and 3-year-old and older. The numbering of the nine crown levels modeled per host species is shown in figure 1.

Temporal scale and resolution,- and relation to budworm life cycle—The Budworm Model may be used independently to simulate budworm populations for 1 to 15 years. For longer simulations, the Budworm Model should be used in combination with the Prognosis Model, as described later.

For each year of a simulation, stand characteristics, defoliation, and budworm populations are estimated. Within a year, a smaller time-step—20 °D—is used to simulate the portion of the budworm life cycle from emergence of larvae in the spring to adult emergence in the late summer.

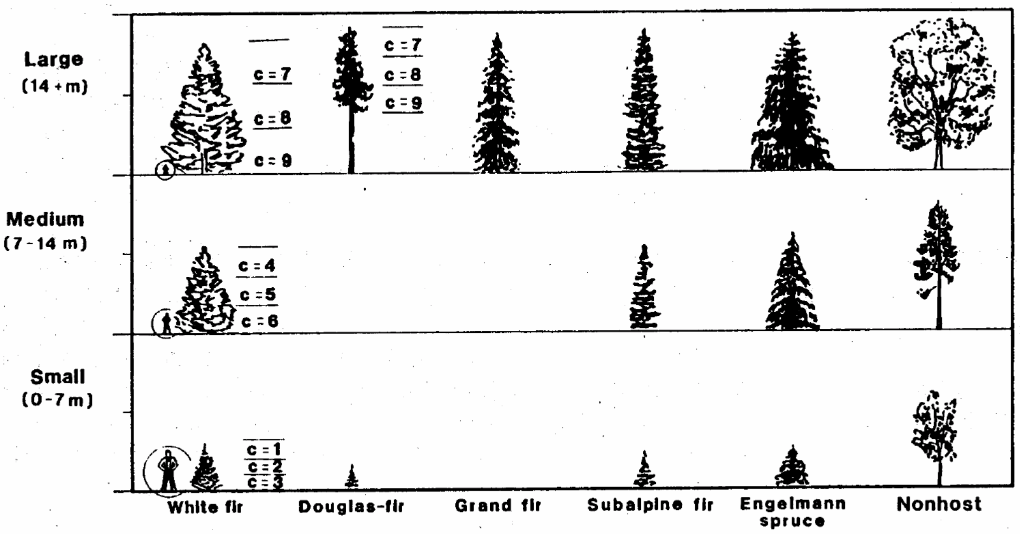

Figure 1—The Budworm Model trees for an example stand, labeled to show the three size classes (z) and nine crown levels (c) per species (after Sheehan and others 1987). In this stand, there were no small grand firs and no medium grand firs or Douglas-firs.

In the Budworm Model, the budworm life cycle is separated into three components (fig. 2). The net effects of events during the period from egg hatch to larval emergence from hibernacula are simulated in BWMOO-Part I. BWMOO-Part II covers the period from establishment of second instars within foliage cells to emergence of adults; the processes involved-larval dispersal, budworm and host growth, defoliation, and budworm mortality—are modeled in detail during each 20° D period. BWFLY uses either a process model to simulate adult dispersal among stands or a net dispersal rate to simulate adult dispersal independently for each stand.

Indicator variables and management actions—For each stand, the Budworm Model predicts annual values of the following variables:

- Stand characteristics: amounts of new, 1-year-old, 2-year-old, and older foliage in each foliage cell (that is, by host, tree size class, and crown third); and defoliation by foliage cell and by model tree (host and tree size class).

- Budworm characteristics (for each foliage cell): egg-mass and fourth-instar density (per square meter and per 100 buds); percentage of shoot expansion at fourth instar; number of adults; and proportion of budworm mortality during the period from larval emergence from hibernacula to adult emergence that was caused by birds, ants, parasites, insecticides, dispersal, or foliage quality.

- Budworm characteristics (for each stand): number of potential eggs produced by adults from that stand; percentage of mortality before and during adult dispersal; number of eggs actually laid in each stand; and final egg-mass density.

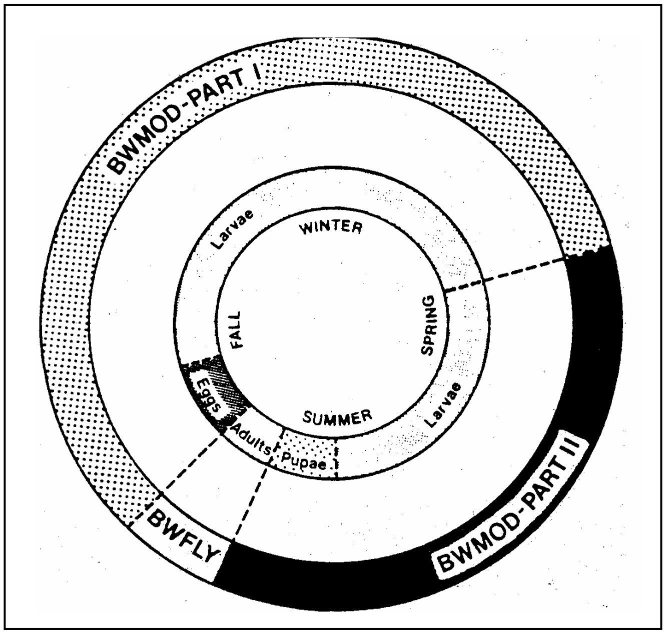

Figure 2—The two components of the Budworm Model—
BWMOO and BWFLY (after Sheehan and others 1987).

In addition, tree growth and mortality relative to that which would occur in the absence of budworms are calculated for 5-year periods. If a stand is simulated for less than 5 years, then growth and mortality are estimated for the entire simulation.

Management actions that can be simulated include insecticide application, pheromone application for mating disruption, and augmentation of birds, ants, or parasites. When the Budworm Model is combined with the Prognosis Model (as described later), the full range of management actions supported by the Prognosis Model—such as thinning to reach a target basal area or diameter distribution (Wykoff and others 1982)—may be used.

Information needed to run the Budworm Model—The Budworm Model requires information on initial stand conditions, initial budworm populations, weather, and any user options such as management actions or parameter specifications.

Users must supply the initial site and stand information that is listed in table 1. Most users of the stand-alone Budworm Model will use a Budworm extension of the Prognosis Model (WRITEFOL keyword[3])_ to generate a file for each stand in the required format, and then use those files as input to the Budworm Model. When the Budworm Model is used in combination with the Prognosis Model, the necessary site and stand information are automatically supplied to the Budworm Model.

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[3] "User's Guide to the Western Spruce Budworm Modeling System." Review draft manuscript on file, Nicholas L. Crookston_ Forestry Sciences Laboratory, 1221 South Main Street, Moscow, ID 83843.

Table 1—Initial site and stand information required by the Budworm

Variable name	Description
For each site:	
BAMAX	Maximum basal area (square feet per acre) for site (carrying capacity)
BASALA	Current basal area (square feet per acre) of the stand
IELEV	Stand elevation (meters above sea level)
IHABIT	Habitat type number (Pfister and others 1977)
For each Budworm Model tree (that is, by tree size class [z] and host [h]):	
BWTPHA_{hz}	Number of trees per hectare that each Budworm Model tree represents
For each crown level [c]:	
FOLNH_{c}	Amount (grams) of nonhost foliage
For each foliage cell (that is, by crown level [c] and host [h]):	
BUDSGch	Potential foliage (grams) that would be produced during the current season given no budworm defoliation
CLEN_{ch}	Length of foliage cell (meters)
CLHT_{ch}	Height at foliage cell midpoint (meters)
$\mathrm{FOLD1}_{ch}$	Amount (grams) of 1-year-old foliage
$\mathrm{FOLD2}_{ch}$	Amount (grams) of 2-year-old foliage
FREM_{ch}	Amount (grams) of 3-year-old and older foliage

Budworm densities at the start of an outbreak may be specified by the user. Carolin and Coulter (1972) predict that 3.5 egg masses per 1,000 in^2 (5.43 masses per m^2) at midcrowns of large trees will result in approximately 25-percent defoliation—the minimum defoliation detectable during aerial surveys. Assuming 41.7 eggs per egg mass (table 2), the model sets egg densities at the start of an outbreak to 266 eggs per m^2 in midcrowns of medium-size trees by default. Rather than use this default value, users may specify initial egg-mass densities for midcrowns of medium-size trees (by host). Users may also specify the egg-mass densities of each foliage cell relative to the egg-mass density at midcrowns of medium-size trees.

In addition, users may change the default values of most parameters by use of keywords (see footnote 3). These options allow users to tailor the Budworm Model to local conditions and to explore the sensitivity of the model to those parameters. Examples of parameters that users may wish to specify include dates that hosts and budworms start to develop in the spring (which affect synchrony of hosts and budworm) and bird densities within stands.

Table 2—Mean number of eggs per egg mass reported for western spruce budworm

	Mean number of eggs per mass	Number of plot-years observed	Source
	44.9	25[1]	Campbell and others (1984b)
	36.2	2	Eldridge and Egan (1983b unpubl.)
	42.5	2	Washburn and Brickell (1973)
	26.8	7	McKnight (1969b)
	35.1	3	Harris and Dawson (1982)
	37.6	3	Waters and Volney (1982 unpubl.)
Mean[2]	41.7		

[1] Number of plot-years is specified in Campbell and others (1983 unpubl.).

[2] Average of means weighted by the number of plot-years. This is the default value used in the model, EPMASS = 41.7.

The Prognosis-Budworm Model

The Budworm Model may be run in combination with either the base Prognosis Model (used to simulate one stand) or the Parallel Processing Extension (used to simulate several stands in parallel). Wykoff and others (1982) describe in detail the structure and applications of the former, and Crookston will document the latter.[4] Simulation of adult budworm dispersal among stands requires parallel processing of stands; when only one stand is simulated at a time (serial processing), the Budworm Model uses a net adult dispersal rate. All other aspects of the Budworm Model are unaffected by the choice of serial or parallel simulation of stands. Modifications of the Prognosis Model necessary to simulate effects of budworm defoliation are described by Crookston (1985)[5][6] and are briefly reviewed here.

Figure 3 shows the steps that occur during a simulation of one stand by the combined Prognosis-Budworm Model. The Prognosis Model first calibrates its growth equations to account for local conditions and accepts options (such as thinning or harvesting) as specified by the user. A series of steps is then performed during each growth period (usually 10 years) in the simulation. After simulating any harvests that were scheduled for the current growth period, the Prognosis Model predicts growth and mortality for each Prognosis Model tree in the absence of budworms. The initial

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[4] "User's Guide to the Parallel Processing Extension of the Prognosis Model." Draft on file, Nicholas L. Crookston, Forestry Sciences Laboratory, 1221 South Main Street, Moscow, ID 83843.

[5] "Foliage Dynamics Component of the Western Spruce Budworm Model." Draft on file, Nicholas L. Crookston, Forestry Sciences Laboratory, 1221 South Main Street, Moscow, ID 83843.

[6] "Damage Component of the Western Spruce Budworm Model." Draft on file, Nicholas L. Crookston, Forestry Sciences Laboratory, 1221 South Main Street, Moscow, ID 83843.

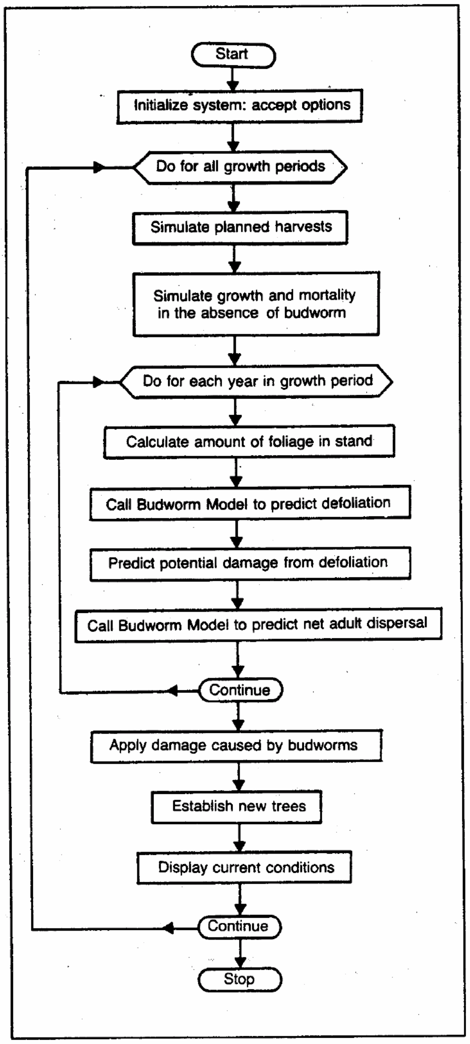

Figure 3—Schedule of events during the simulation of one stand by the Prognosis-Budworm Model (after Sheehan and others 1987). This model can process stands singly or serially without interactions.

amounts of foliage that would be present given no budworm defoliation are also predicted. During each year (in growth periods when budworms are active), the Budworm Model determines the amount of foliage present at the start of the year (as a function of foliage at the start of the growth period and defoliation history), predicts budworm population levels and the resulting defoliation, calculates the potential damage that results from that defoliation, and simulates the adult dispersal. At the end of each growth period, actual damage caused by defoliation by budworm is applied to the Prognosis Model trees, regeneration may occur, and the current stand conditions are displayed.

The sequence of steps that occurs when several stands are simulated at once by the Parallel Processing Extension is shown in figure 4. The Prognosis Model begins by calibrating itself for each stand and accepting the user's options for each stand. The following steps are then performed during each growth period. For each stand, the Prognosis Model simulates harvests scheduled for the current growth period and growth and mortality in the absence of budworms. For each year when budworms are active, foliage amounts, defoliation, and potential damage are predicted for each stand as described for the base Prognosis-Budworm Model. After all stands have been defoliated for the current year, the Budworm Model predicts adult dispersal among stands during that year. At the end of a growth period, actual damage, regeneration, and current stand conditions are updated for each stand as described for the base Prognosis Model.

The start of a budworm outbreak during a certain growth cycle may be scheduled by the user or be scheduled by the Prognosis Model using a normally distributed random variable with mean and variance set to the regional outbreak frequency as observed by Kemp (1983) and by Kemp and others (1985).

The Stand-Alone Budworm Model

The Budworm Model may also be used independently of the Prognosis Model to simulate annual budworm population dynamics and defoliation. A set of master programs, referred to as the "stand-alone driver," provide instructions and information that would otherwise be provided by the Prognosis Model (see footnote 3). The Budworm Model; whether it is independent or combined with the Prognosis Model, does not change.

The structure of the stand-alone model is illustrated in figure 5. To begin, the program accepts initial stand and budworm conditions plus any options specified by the user. During each year of the simulation, the Budworm Model calculates the amount of foliage present at the start of the year, simulates budworm populations and resulting defoliation, and (as an option) predicts potential damage caused by budworm defoliation. At the end of the year, the Budworm Model predicts the effects of adult dispersal.

We do not recommend using the stand-alone version of the Budworm Model for simulations longer than 10 years because of potential errors in estimating foliage present for those longer runs. The Budworm Model updates the initial amounts of foliage each year as a function of the previous year's defoliation. Changes in foliage amounts that are a result of changes in tree size or mortality of individual trees are not accounted for by the stand-alone Budworm Model. In the Prognosis-Budworm Model, foliage estimates that include changes in tree dimensions and mortality are recalculated at the start of each growth cycle.

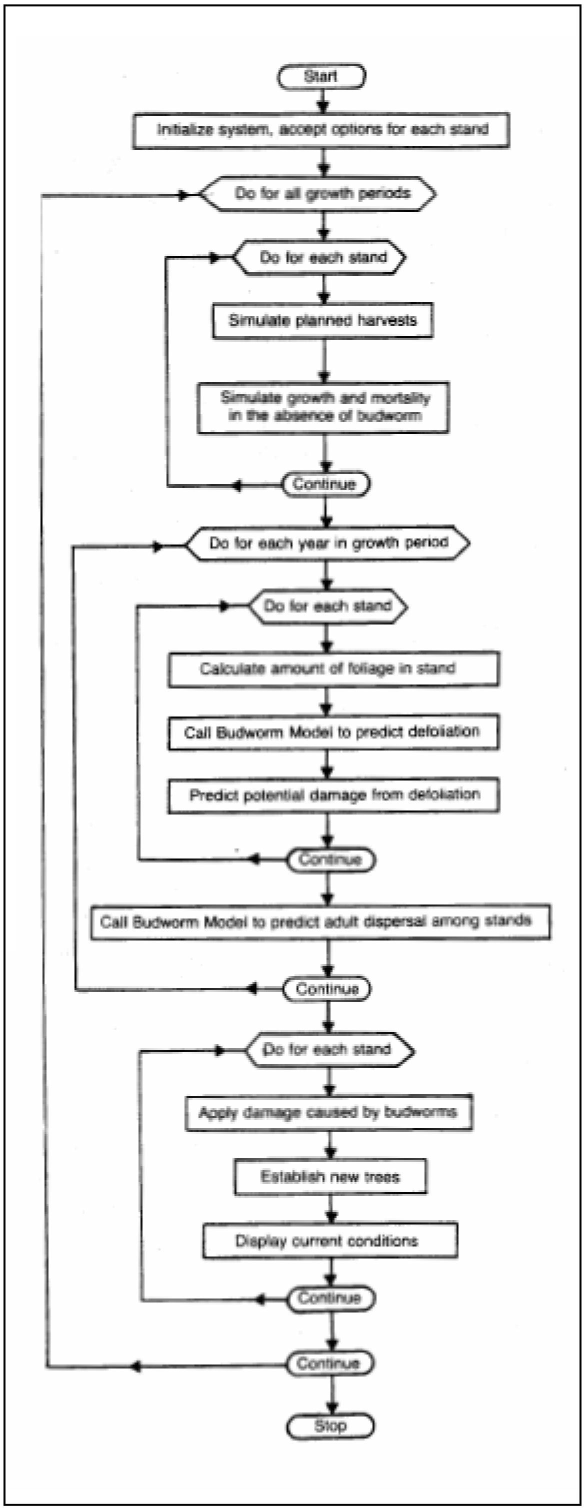

Figure 4—Schedule of events during the simulation of several stands in parallel by the Prognosis-Budworm Model (taken from Sheehan and others 1987).

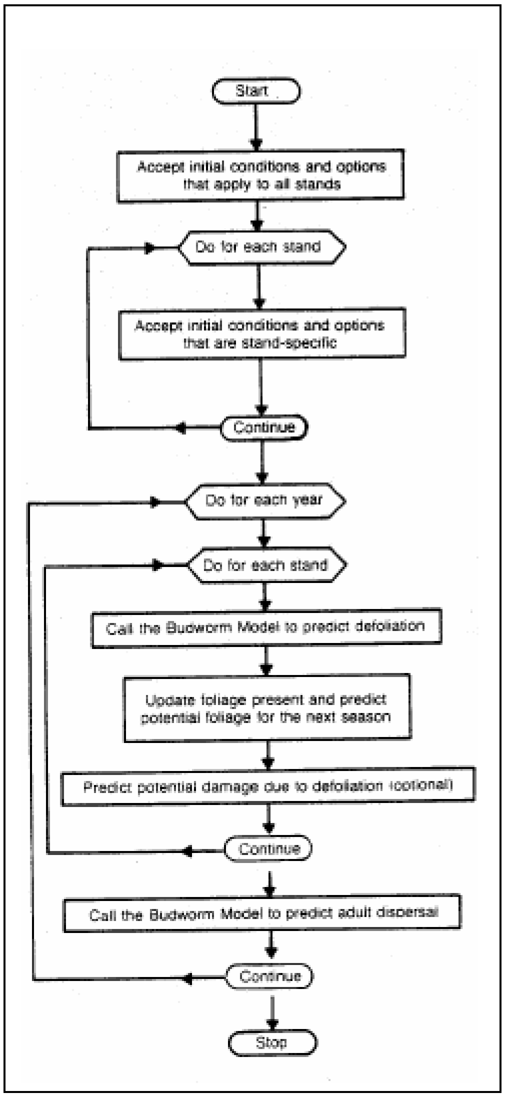

Figure 5—Sequence of events during the simulation of several stands by the stand-alone Budworm Model.

The Weather Model

The Weather Model is called from either Prognosis (Prognosis-Budworm Model) or the stand-alone driver (stand-alone Budworm Model) to generate daily weather for each year in the simulation. The Weather Model is described by Kemp and others[7] and Sheehan and others (1987) and is briefly reviewed here.

The Weather Model provides three options for predicting daily temperatures (maximum and minimum) and precipitation. Two options use weather records from a particular location to create a set of climatic parameters specific to that location. The Weather Model then uses these parameters to simulate daily weather. A third option allows a user to specify actual daily weather.

Simulating weather data—The stochastic features of the Weather Model are based on work by Bruhn (1980) and Bruhn and others (1979). A long, consecutive record of weather data from a particular location is used to derive a much smaller set of statistical parameters that characterize the climatic features of. that location. Climatic parameters from four weather stations in the Pacific Northwest have been stored in the Weather Model: (1) McCall, 10; (2) Priest River Experiment Station, 10; (3) Kalispell, MT; and (4) Baker, OR. A user may specify the set that is most appropriate for a given stand. Climatic parameters for additional weather stations are available in Kemp and others (see footnote 8). Alternatively, the user may develop and use climatic parameters from other weather stations as described in Kemp and others (see footnote 7).

The Weather Model uses these climatic parameters to predict maximum and minimum temperature and precipitation following methods developed by Bruhn and others (1979).

Actual weather data—The Weather Model will also accept daily maximum and minimum temperatures and precipitation amounts as an alternative to stochastic weather generation. The model assumes no data are missing. Under this option, when the Weather Model is called for a given year, the actual weather data supplied for that year are returned for later use by the Budworm Model.

Onsite weather adjustments—Weather measured at a weather station may be very different from that occurring at a particular forest stand. To improve the accuracy of local temperature predictions, base station temperatures are modified to account for differences in elevation using the standard lapse rate of 6.3 °C per 1,000 m (Barry 1981). The additional use of potential solar radiation to account for difference in latitude, azimuth, slope, and date, as used in other temperature extrapolation studies (Running 1981, Running and Hungerford 1983), failed to improve test data set predictions to any significant degree (see footnote 7).

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[7] "User's guide to the Weather Model: A Component of the Western Spruce Budworm Modeling System." Kemp, William P.; Crookston, Nicholas L.; Thomas, Paul W. Manuscript in review; copy on file, William P. Kemp, USDA-ARS Rangeland Insect Laboratory, Bozeman, MT 59717-0001.

The Budworm Model

During each year of a simulation, the Budworm Model updates foliage present in each stand, simulates budworm populations and the defoliation they cause, and calculates potential damage that results from defoliation. Crookston (see footnote 5) will describe both the calculation of initial foliage at the start of a Prognosis Model growth period (or when requested via the WRITEFOL keyword for use by the stand-alone Budworm Model) and the annual updating of foliage amounts by the Budworm Model to account for the previous year's defoliation. Crookston (1985 and see footnote 6) gives details about how the Budworm Model calculates relative damage (that is, height growth, diameter growth, and mortality compared to expected values when budworm is absent) at the end of each year and how the Prognosis Model translates relative damage into actual damage at the end of each growth period.

The remainder of this paper describes the assumptions, functions, and default parameter values for the portion of the Budworm Model that simulates the budworm life cycle. See the Key to Subscripts for conventions used in this document.

Eggs to Larvae Emerging in the Spring, BWMOD-Part I

Initial foliage conditions—At the start of each year in a simulation, the Budworm Model calculates potential new foliage for the year. These calculations are based on the foliage present at the start of the Prognosis growth period and on defoliation history.

The potential new foliage for the current year is converted to the number of vegetative buds in equation 1:

$$BUDS_{ch} = \frac{BUDSG_{ch}}{BUDMAS_{ch}} \qquad (1)$$

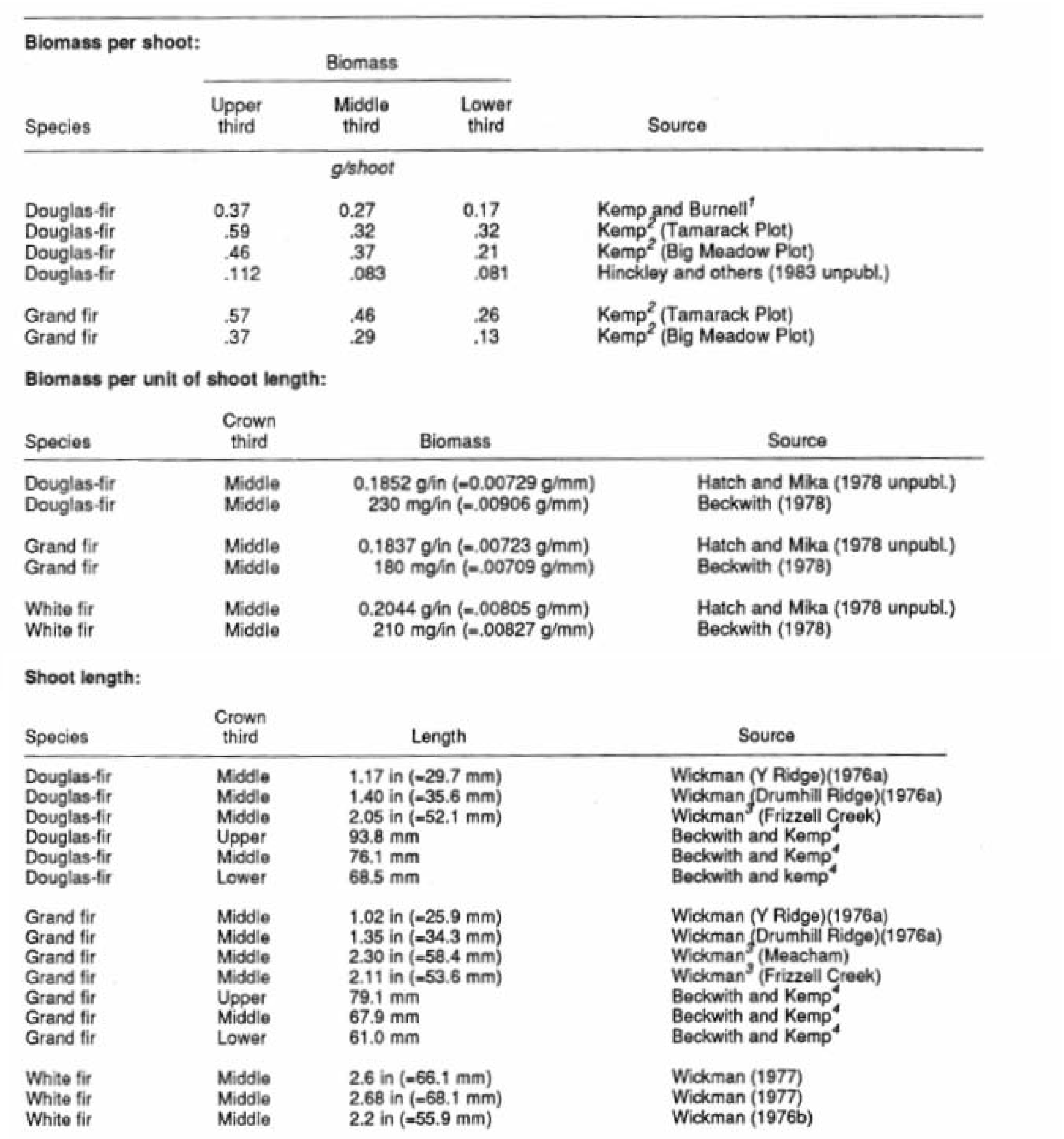
where: $BUDS_{ch}$ = total number of live buds in crown level c of host h,

$BUDSG_{ch}$ = total grams of potential new foliage for the current year in crown level c of host h, and

$BUDMAS_{ch}$ = average potential biomass produced per shoot for crown level c of host h.

The average biomass produced on a given shoot may vary greatly from year to year (Silver 1962); weather and cone crop production are highly variable factors known to influence biomass produced per year (Morris 1951). Because these effects have not been quantified, mean values reflecting several years and sites have been used. Measurements of mean biomass per shoot, mean biomasss per unit of shoot length, and mean shoot lengths (summarized in table 3) were used to calculate mean biomass per shoot at midcrown. Values for Douglas-fir were used for Engelmann spruce, and grand fir values were used for subalpine fir. Relative differences among crown thirds (table 4) were used to adjust mean potential biomass per shoot for crown thirds; relative differences noted for Douglas-fir were used for Engelmann spruce, and grand fir differences were used for white fir and subalpine fir. Default values for $BUDMAS_{ch}$ are listed in table 5. At the start of the season, the number of vegetative buds not previously mined by budworms ($BUDSAV_{ch}$) is set equal to the number of vegetative buds present ($BUDS_{ch}$).

Table 3—Sources of mean biomass per shoot, mean biomass per unit of shoot length, and mean shoot lengths, used to calculate mean potential biomass per shoot



Biomass per shoot:

Species	Biomass Upper third	 Middle third	 Lower third	Source
		g/shoot		
Douglas-fir	0.37	0.27	0.17	Kemp and Burnell[1]
Douglas-fir	.59	.32	.32	Kemp[2] (Tamarack Plot)
Douglas-fir	.46	.37	.21	Kemp[2] (Big Meadow Plot)
Douglas-fir	.112	.083	.081	Hinckley and others (1983 unpubl.)
Grand fir	.57	.46	.26	Kemp[2] (Tamarack Plot)
Grand fir	.37	.29	.13	Kemp[2] (Big Meadow Plot)

Biomass per unit of shoot length:

Species	Crown third	Biomass	Source
Douglas-fir	Middle	0.1852 g/in (=0.00729 g/mm)	Hatch and Mika (1978 unpubl.)
Douglas-fir	Middle	230 mg/in (=.00906 g/mm)	Beckwith (1978)
Grand fir	Middle	0.1837 g/in (=.00723 g/mm)	Hatch and Mika (1978 unpubl.)
Grand fir	Middle	180 mg/in (=.00709 g/mm)	Beckwith (1978)
White fir	Middle	0.2044 g/in (=.00805 g/mm)	Hatch and Mika (1978 unpubl.)
White fir	Middle	210 mg/in (=.00827 g/mm)	Beckwith (1978)

Shoot length:

Species	Crown third	Length	Source
Douglas-fir	Middle	1.17 in (=29.7 mm)	Wickman (Y Ridge)(1976a)
Douglas-fir	Middle	1.40 in (=35.6 mm)	Wickman (Drumhill Ridge)(1976a)
Douglas-fir	Middle	2.05 in (=52.1 mm)	Wickman[3] (Frizzell Creek)
Douglas-fir	Upper	93.8 mm	Beckwith and Kemp[4]
Douglas-fir	Middle	76.1 mm	Beckwith and Kemp[4]
Douglas-fir	Lower	68.5 mm	Beckwith and kemp[4]
Grand fir	Middle	1.02 in (=25.9 mm)	Wickman (Y Ridge)(1976a)
Grand fir	Middle	1.35 in (=34.3 mm)	Wickman (Drumhill Ridge)(1976a)
Grand fir	Middle	2.30 in (=58.4 mm)	Wickman[3] (Meacham)
Grand fir	Middle	2.11 in (=53.6 mm)	Wickman[3] (Frizzell Creek)
Grand fir	Upper	79.1 mm	Beckwith and Kemp[4]
Grand fir	Middle	67.9 mm	Beckwith and Kemp[4]
Grand fir	Lower	61.0 mm	Beckwith and Kemp[4]
White fir	Middle	2.6 in (=66.1 mm)	Wickman (1977)
White fir	Middle	2.68 in (=68.1 mm)	Wickman (1977)
White fir	Middle	2.2 in (=55.9 mm)	Wickman (1976b)

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[1] Unpublished work by Kemp and Burnell; personal communication, William P. Kemp, USDA-ARS, Rangeland Insect Laboratory, Bozeman, MT 59717-0001.

[2] Personal communication, William P. Kemp.

[3] Personal communication, Boyd E. Wickman, USDA Forest Service, Forestry and Range Sciences Laboratory, Route 3, Box 2315, La Grande, OR 97850.

[4] Unpublished work by Beckwith and Kemp; personal communication, William P. Kemp.

Table 4—Relative differences in biomass per shoot among crown-thirds

Species	Relative differences in biomass Upper third	 Middle third	 Lower third	Source
		g/shoot		
Douglas-fir	1.37	1.00	0.63	Kemp and Burnell[1]
Douglas-fir	1.84	1.00	1.00	Kemp[2] (Tamarack Plot)
Douglas-fir	1.24	1.00	.57	Kemp[2] (Big Meadow Plot)
Douglas-fir	1.35	1.00	.98	Hinckley and others (1983 unpubl.)
Mean	1.45	1.00	.80	
Grand fir	1.24	1.00	.57	Kemp[2] (Tamarack Plot)
Grand fir	1.28	1.00	.45	Kemp[2] (Big Meadow Plot)
Mean	1.26	1.00	.51	

[1] Unpublished work by Kemp and Burnell; personal communication, William P. Kemp, USDA-ARS, Rangeland Insect Laboratory I Bozeman, MT 59717-0001.

[2] Personal communication, William P. Kemp.

Table 5—Potential biomass per shoot ($BUDMAS_{ch}$), by crown level and host (grams/shoot), calculated from sources listed in tables 3 and 4

Tree size (z)	Crown level (c)	Host (h) Douglas-fir	 Grand fir	 White fir	 Subalpine fir	 Engelmann spruce
Small (1)	Top (1)	0.493	0.420	0.628	0.420	0.493
	Middle (2)	.352	.344	.515	.344	.352
	Bottom (3)	.215	.217	.448	.217	.215
Medium (2)	Top (4)	.493	.420	.628	.420	.493
	Middle (5)	.352	.344	.515	.344	.352
	Bottom (6)	.215	.217	.448	.217	.215
Large (3)	Top (7)	.493	.420	.628	.420	.493
	Middle (8)	.352	.344	.515	.344	.352
	Bottom (9)	.215	.217	.448	.217	.215

The number of reproductive buds present is calculated with equation 2:

$$RBUDS_{ch} = BUDS_{ch} \times BRATIO_{ch} \times CONES_{h} \qquad (2)$$

where: $RBUDS_{ch}$ = number of reproductive buds in crown level c of host h,
$BRATIO_{ch}$ = proportion of reproductive to vegetative buds in crown level c of host h,
$BUDS_{ch}$ = total number of vegetative buds calculated in equation 1, and
$CONES_{h}$ = 0 if a bad (no) cone year, or 1 if a good cone year.

$BRATIO_{ch}$ is based on unpublished data from Ray *Shearers*[8] that includes the ratio of female:vegetative and male:vegetative buds for the cone-bearing portion of Douglas-fir, grand fir, and subalpine fir trees (table 6). The $CONES_{h}$ variable is controlled by the keyword, CONES. Because little is known about what controls the initiation of cone production, the user must activate this, if desired, for specific hosts and years in each stand being simulated. These ratios were assumed to be maximums and to represent the reproductive cones present in the tops of medium and large trees. By default, ratios in the middle thirds of these trees were assumed to be one-half of the maximum, and ratios in the bottom thirds of medium and large trees and the tops of small trees were assumed to be one-quarter of the maximum. The ratios assumed by default are shown in table 7; the values of Douglas-fir were used for all species because of the small sample size for the other species.

Foliage parameters that do not change during a season, such as the position of each foliage cell relative to other foliage cells, are then calculated for the stand. For all possible pairs of foliage cells, the position of a foliage cell (c', hi) relative to another foliage cell (c, h) is stored in $IPOSIT_{chc'h'}$ (position indicated by value of IPOSIT-equals 1 if below, 2 if lateral, and 3 if above). The heights at midpoint ($CLHT_{ch}$) and length ($CLEN_{ch}$) of each foliage cell was passed to the Budworm Model by the Prognosis Model or the stand-alone driver. If a foliage cell (c,h) has a midpoint ($CLHT_{ch}$) that is in the interval, $CLHT_{c'h'} + O.5*CLEN_{c'h}'$, then foliage cell (c,h) is considered lateral to foliage cell (c',h'). For each foliage cell (c,h), $LEVELS_{chq}$ stores the number of foliage cells by direction (q) (q equals 1 if below, equals 2 if lateral, and equals 3 if above) relative to that crown level. $IPOSIT_{chc'h'}$ and $LEVELS_{chq}$ are used by the Budworm Model to predict larval dispersal (see p. 42).

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[8] Personal communication, Ray Shearer, Missoula Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807_

Table 6—Ratios of female to vegetative buds and male to vegetative buds for undefoliated trees by host species

Species and statistics	Bud ratio Female: vegetative	 Male: vegetative
Douglas-fir:		
Mean	0.85:1.00	1.25:1.00
Number of observations	22	21
Standard deviation	0.77	0.73
Grand fir:		
Mean	0.33:1.00	—
Number of observations	1	—
Subalpine fir:		
Mean	0.59:1.00	—
Number of observations	2	—
Standard deviation	0.02	

Source: Based on unpublished data from Raymond C. Shearer, USDA Forest Service, Intermountain Forest Range Experiment Station, Missoula, MT 59807.

Table 7—Ratios of reproductive to vegetative buds by foliage cell ($BRATIO_{ch}$) assumed by default (arbitrarily

Tree size (z)	Crown level (c)	Host (h) Douglas-fir	 Grand fir	 White fir	 Subalpine fir	 Engelmann spruce
Small (1)	Top (1)	0.53	0.53	0.53	0.53	0.53
	Middle (2)	0	0	0	0	0
	Bottom (3)	0	0	0	0	0
Medium (2)	Top (4)	2.10	2.10	2.10	2.10	2.10
	Middle (5)	1.05	1.05	1.05	1.05	1.05
	Bottom(6)	.53	.53	.53	.53	.53
Large (3)	Top (7)	2.10	2.10	2.10	2.10	2.10
	Middle (8)	1.05	1.05	1.05	1.05	1.05
	Bottom (9)	.53	.53	.53	.53	.53

Finally, subroutine BWFOL is called to summarize the amounts and proportions of foliage present in the stand. Table 8 shows the variables that are calculated by BWFOL

Table 8—Foliage variables calculated by Subroutine BWFOL

Variable	Description
$CLPROP_{ch}$	Proportion of a Budworm Model tree's foliage in each crown level c of host h.
$CLSUM_{zh}$	Total foliage per model tree.
$FOLCEL_{ch}$	Grams of foliage present in a given crown level c of host h.
$IFPRES_{ch}$	For crown level c of host h, set to I if current foliage is present; otherwise set to 0.
$PROBNH_{c}$	Proportion of total amount of foliage in crown level c ($TFOLCL_{c}$) that is nonhost.
$SPECPR_{ch}$	Proportion of total amount of foliage in crown level c ($TFOLCL_{c}$) by host h.
$TCLPR_{c}$	Proportion of total foliage per hectare in crown level c.
$TFOLCL_{c}$	Total amount of foliage (grams/ha) in crown level c, summed across all tress species.
TFOLSA	Total host foliage surface area (m^2) per hectare.

Distribute eggs within the stand—The number of eggs present in each foliage cell at the start of a budworm generation may be passed to the Budworm Model using either of two options:

1. Mean egg-mass density (egg masses per square meter) at midcrowns of medium-sized trees, by host ($AVEGGD_h$).
2. Total number of eggs per hectare (TOTEGG).

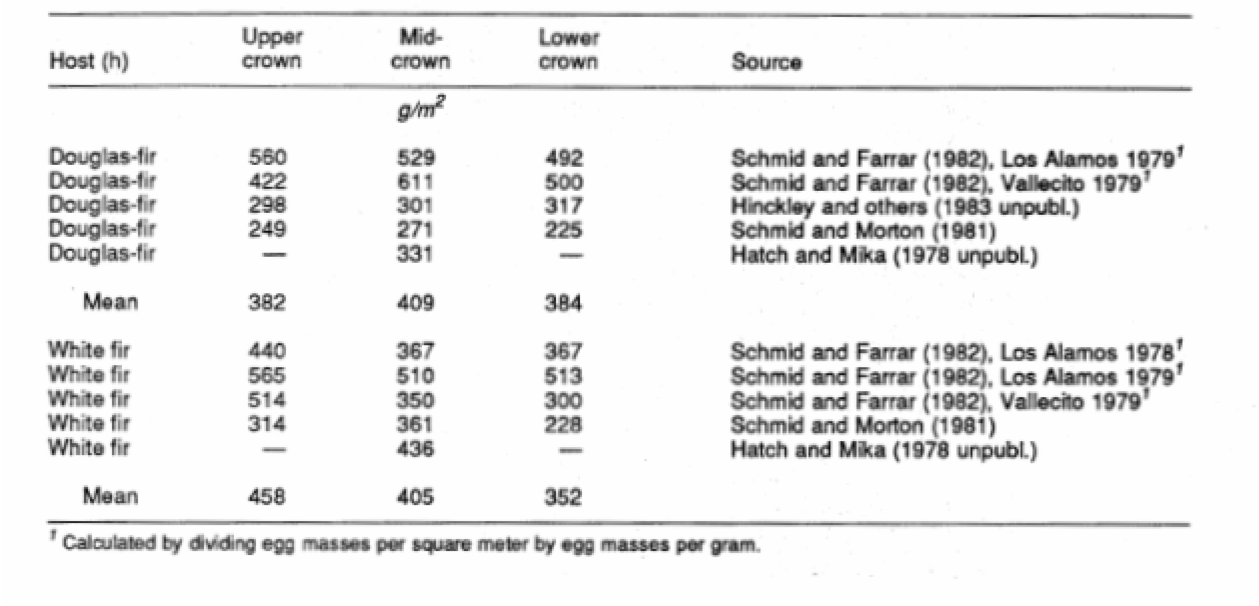
Users wishing to specify budworm densities at the start of an outbreak would generally use the first option; BWFL V, the adult dispersal subroutine, provides the egg information using the latter option.

The BWMOD begins by determining the number of eggs present in each foliage cell ($TEGGS_{ch}$) of the model trees. If the first option is used, TEGGS is calculated from the following equation:

$$TEGGS_{ch} = (AVEGGD_h \times EPMASS \times REGDEN_{ch}) \times \frac{FOLCEL_{ch}}{GPERM2_{ch}} \tag{3}$$

where:
$TEGGS_{ch}$ = total number of eggs in crown level c of host h,
$AVEGGD_h$ = mean egg-mass density at the midcrown of medium-sized trees of host h,
EPMASS = constant for average number of eggs per egg mass,
$REGDEN_{ch}$ = ratio of egg-mass density in crown level c to host h relative to the egg-mass density of midcrowns of medium-size trees,
$FOLCEL_{ch}$ = grams of foliage in crown level c of host h, and
$GPERM2_{ch}$ = constant for grams of foliage per square meter of foliated branch for each crown level c of host h.

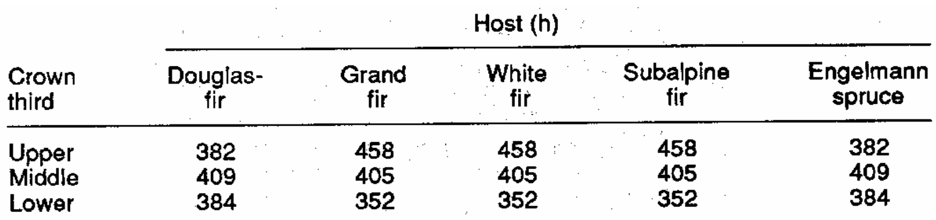
Table 9A—Relation between foliage weight (g) and foliage surface area (m^2), by host



Host (h)	Upper crown	Mid-crown	Lower crown	Source
		g/m²		
Douglas-fir	560	529	492	Schmid and Farrar (1982), Los Alamos 1979[1]
Douglas-fir	422	611	500	Schmid and Farrar (1982), Vallecito 1979[1]
Douglas-fir	298	301	317	Hinckley and others (1983 unpubl.)
Douglas-fir	249	271	225	Schmid and Morton (1981)
Douglas-fir	—	331	—	Hatch and Mika (1978 unpubl.)
Mean	382	409	384	
White fir	440	367	367	Schmid and Farrar (1982), Los Alamos 1978[1]
White fir	565	510	513	Schmid and Farrar (1982), Los Alamos 1979[1]
White fir	514	350	300	Schmid and Farrar (1982), Vallecito 1979[1]
White fir	314	361	228	Schmid and Morton (1981)
White fir	—	436	—	Hatch and Mika (1978 unpubl.)
Mean	458	405	352	

[1] Calculated by dividing egg masses per square meter by egg masses per gram.

Table 9B—Grams of foliage per square meter ($GPERM2_{ch}$): default values calculated from data shown in table 9A by assuming white fir values for grand fir and subalpine fir, and Douglas-fir values for Engelmann spruce [1]



	Host (h)				
Crown third	Douglas-fir	Grand fir	White fir	Subalpine fir	Engelmann spruce
Upper	382	458	458	458	382
Middle	409	405	405	405	409
Lower	384	352	352	352	384

[1] For a given host and crown third, the same values are used for each tree size class.

The default value for the average number of eggs per egg mass is 41.7 (see table 1) and may be altered by the user. Default values for the biomass of foliage per square meter of foliage in each foliage cell are found in table 9 and can also be changed by the user.

When the total number of eggs per hectare is provided (option 2), the Budworm Model first calculates (using equation 4) the proportion that is laid in each foliage cell ($EGPROP_{ch}$) based on relative egg-mass density ($REGDEN_{ch}$) and weighted by foliage in the cell ($HCLPR_{ch}$) relative to all host foliage in the stand:

$$EGPROP_{ch} = \frac{REGDEN_{ch} \times HCLPR_{ch}}{\sum_{c'=1}^{C} \sum_{h'=1}^{H} (REGDEN_{c'h'} \times HCLPR_{c'h'})} \qquad (4)$$

where:

$EGPROP_{ch}$ = proportion of eggs to be laid in each crown level c of . host h,

$REGDEN_{ch}$ = ratio of egg-mass density in crown level c of host h relative to the egg-mass density of midcrowns of medium-size trees, and.

$HCLPR_{ch}$ = proportion of total host foliage per hectare in crown level c of host h.

Egg-mass densities for specific crown thirds, relative to midcrown densities of medium-size trees, observed for western spruce budworm are summarized in table 10; default values for $REGDEN_{ch}$ are also shown. For the spruce budworm *(Choristoneura fumiferana* (Clemens)), Regniere (1983) and Wilson and Bean (1963) also reported highest egg-mass densities in the tops of trees and lowest densities in the lower crowns. Regniere employed methods similar to equation 4 (using actual egg densities instead of relative ones) to estimate crown level preference of ovipositing spruce budworm females.

The total number of eggs in each foliage cell ($TEGGS_{ch}$) of the model trees is calculated in equation 5:

$$TEGGS_{ch} = \frac{TOTEGG \times EGPROP_{ch}}{BWTPHA_{hz}} \qquad (5)$$

where:

$TEGGS_{ch}$ = total number of eggs in crown level c of host h,

$EGPROP_{ch}$ = proportion of total eggs to be laid in crown level c of host h, calculated in equation 4, above

$BWTPHA_{hz}$ = number of trees represented per hectare for host h and tree size z that contains crown level c (see figure 1), and

TOTEGG = eggs per hectare (supplied by user for first year of simulation and thereafter by BWFLY [see below]).

The Budworm Model assumes that eggs are laid randomly on hosts within a crown level. The Budworm Model further assumes that if no eggs are present (TOTEGG = 0 or under option 1, $AVEGGD_h = 0$ for all hosts h), no budworms will be present to feed in the spring. Therefore, in a year when this is true, the spring and summer section of the Budworm Model (BWMOD-Part II) is bypassed and defoliation does not occur.

Table 10A—Egg-mass densities (all hosts combined) relative to the density in midcrowns of 7- to 14-meter trees

Tree size	Relative density Upper crown	 Mid-crown	 Lower crown	Number of plot-years	Source
0-7 m	1.73	1.20	0.60	20	Campbell and others (1984c)
7-14 m	1.54	1.0	.55	30	Campbell and others (1984c)
Mixed	1.33	1.0	.54	5	Waters and Volney (1981 unpubl.)
Mixed	1.21	1.0	.60	2	Waters and Volney (1981 unpubl.)
[1]	2.00	1.0	.35	2	Carolin and Coulter (1975)
[1]	1.30	1.0	.85	6	Schmid and Farrar (1982)
Mean[2]	1.49	1.0	.55		
14+ m	4.58	2.61	1.94	14	Campbell and others (1984c)
14+ m	3.21	2.75	1.94[3]	6	Carolin and Coulter (1972)
Mean[2]	4.17	2.65	1.94		

[1] These references did not give tree sizes.

[2] Average of means weighted by number of plot-years.

[3] Carolin and Coulter (1972) sampled large trees only; therefore, densities relative to midcrowns of medium-size trees cannot be calculated directly. To compare the relative densities observed among crown thirds of large trees by Carolin and Coulter (1972) with those observed by Campbell and others (1984c), the relative density at lower crowns for Carolin and Coulter (1972) was set equal to that of Campbell and others (1984c), and the densities for the midcrown and upper crown thirds were calculated relative to the lower crown thirds.

Table 10B—Relative egg-mass densities ($REGDEN_{ch}$) used by default In the Budworm Model [1]

Tree size	Upper crown	Mid-crown	Lower crown
0-7 m	1.73	1.20	0.60
7-14 m	1.49	1.00	.55
14^+ m	4.17	2.65	1.94

[1] For a given crown level, the same values are assigned to all hosts.

Calculate egg mortality—Some eggs laid in a foliage cell are nonviable eggs (the proportion is stored in parameter PNV) and some are parasitized eggs (the proportion is stored in parameter PEP). Table 11 summarizes egg-mortality data used to calculate the default values of PNV and PEP (0.054 and 0.012, respectively). Users may specify other values. PNV and PEP do not vary among hosts or crown levels. The model assumes no interaction among parasitized eggs and nonviable eggs. After egg mortality is simulated, the values of $TEGGS_{ch}$ are changed from total eggs per foliage cell to total surviving eggs per foliage cell.

Table 11—Egg mortality rates

	Proportion parasitized	Proportion nonviable	Number of plot-years	Source
	0.012	0.054	18	Campbell and Torgersen (1983 unpubl.) and Torgersen and others (1984)
	.12	—	3	Harris and Dawson (1979)
	.005	—	3	Wilkes (1948)
Mean[1]	0.025	0.054		

[1] Average of means weighted by number of plot-years.

Apply dispersal and overwintering mortality—After fall dispersal, most larvae are found on the bole and inner branches of the lower crown (Eldridge and Egan 1983a unpubl., McKnight 1969a, Terrell 1959). Therefore, all of the newly hatched larvae that occur on each Budworm Model tree are summed (in $BUGT_{hz}$), and mortality rates during fall dispersal and overwintering (FALLOW) and spring dispersal to feeding sites (SPRNGD) are applied to the entire population on a model tree. The number of surviving eggs per foliage cell ($TEGGS_{ch}$) is summed by model tree using the following equations:

$$BUGT_{h1} = \sum_{c=1}^{3} TEGGS_{ch}$$

$$BUGT_{h2} = \sum_{c=4}^{6} TEGGS_{ch}$$

$$BUGT_{h3} = \sum_{c=7}^{9} TEGGS_{ch} \qquad (6)$$

where: $BUGTh_z$ = number of larvae that emerge on tree size z of host h, and

$TEGGS_{ch}$ = total number of surviving eggs in crown level c of host h.

Mortality during fall dispersal has bee.n estimated at 23 and 61 percent (mean = 42 percent, two observations) by Eldridge and Egan (1983b unpubl.). By comparison, Miller (1958) recorded 48 to 82 percent mortality (mean = 64.1 percent, s = 10.0) for eastern spruce budworm over 13 plot-years. Eldridge and Egan (1983a unpubl., 1983b unpubl.) also reported that mortality within hibernacula during the winter averaged 21.5 percent (four observations), while V.M. Caroling observed 24.3 percent. (four observations). Miller (1958) reported 15.7 percent overwintering mortality (nine

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[9] Unpublished data on file. Research Work Unit 4501. Forestry and Range Sciences Laboratory. Route 2. Box 2315, La Grande. OR 97850.

observations) for eastern spruce budworm. The observations of Eldridge and Egan (1983a unpubl., 1983b unpubl.) were used to calculate the default mortality rate for fall dispersal and overwintering mortality (FALLOW = 1 - [1 - 0.42)(1 - 0.22)] = 0.55) that is applied to the entire population on a Budworm Model tree ($BUGT_{hz}$).

The Budworm Model separates spring-dispersal mortality into two parts: the base mortality that occurs as larvae leave their hibernacula and move out to the foliage, and additional mortality that may occur as larvae search for buds or needles to mine. This additional mortality is highly variable and is affected by both the timing of host bud flush relative to budworm emergence and by stand structure; it is modeled in detail in BWMOD-Part II. The base mortality rate during spring dispersal (SPRNGD) has not been quantified through research and is set to 0.30 by default. Eldridge and Egan (t983a unpubl., 1983b unpubl.) noted that total spring mortality averaged 60 percent (3 observations); Miller (1958) reported 40.5 percent (11 observations). By default, the maximum survival rate is 0.29 after egg mortality, fall dispersal, overwintering, and initial spring dispersal have been simulated. Because the model includes additional mortality, such as larvae searching for feeding sites, this rate compares favorably to the range in egg-to-fourth-instar survival rates (0.30-0.02) found by Campbell (1987) for the Pacific Northwest. The number of larvae on each budworm model tree by host is reduced to account for overwintering mortality and base spring dispersal through equation 7:

$$BUGT_{hz(t+1)} = BUGT_{hzt} \times (1.0 - FALLOW) \times (1.0 - SPRNGD) \qquad (7)$$

where: $BUGT_{hzt}$ = number of larvae that are on tree size z of host h at time t (before overwintering and base spring-dispersal mortality has occurred),

$BUGT_{hz}(t+1)$ = number of larvae that are on budworm model tree size z of host h at time t+1 (after overwintering and base spring-dispersal mortality has occurred),

FALLOW = constant for proportion of budworm that die during the fall and overwintering period (default = 0.55), and

SPRGND = constant for proportion of budworm that die during base spring dispersal (default = 0.30).

Just prior to the iterative portion of the model (fig. 6), the model determines where larvae that have successfully overwintered will begin to search for food. The Budworm Model assumes that larvae overwintering on a model tree of host h. and size. class z will initially search for foliage in one of the crown thirds associated with that tree (that is, crown levels 1-3 for size class 1, crown levels 4-6 for size class 2, or crown levels 7-9 for size class 3; see fig. 1). The proportion of larvae that begin to search for foliage in each crown third of a given model tree is assumed to be a function of both the relative amounts of foliage in each crown third of the tree and observed patterns of relative densities of second instars, as follows:

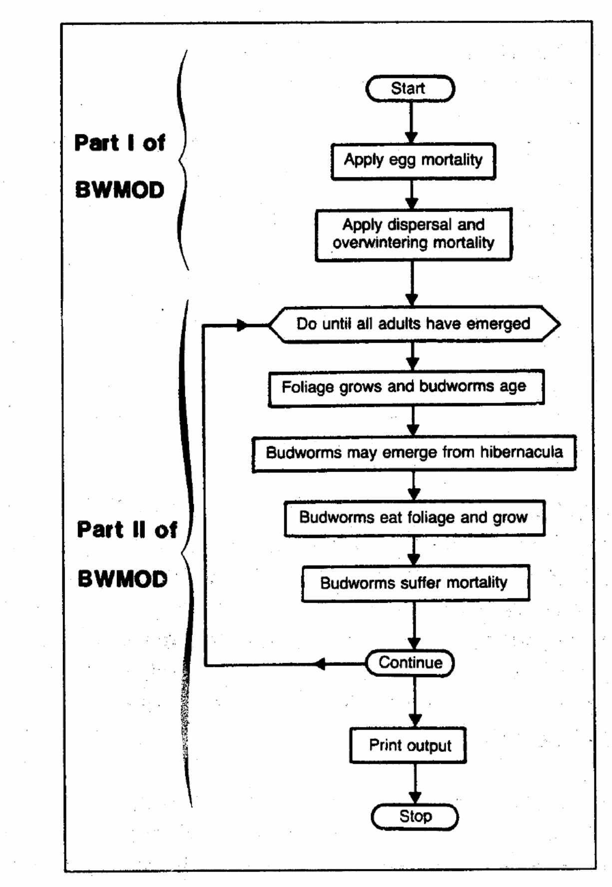

Figure 6—Sequence of events simulated by BWMOD (taken from Sheehan and others 1987).

$$BWPROP_{ch} = \frac{BWRLDN_c \times CLPROP_{ch}}{TPROP2_{zh}} \qquad (8)$$

where:

$TPROP2_{zh}$ = $\sum_{c'=3z-2}^{3z} BWRLDN_{c'} \times CLPROP_{c'h}$,

$BWPROP_{ch}$ = proportion of surviving larvae that overwinter on model tree of host h and size class z that will begin to search for foliage in crown level c,

$BWRLDN_c$ = relative densities of second instars by crown level c for all hosts, and

$CLPROP_{ch}$ = proportion of the foliage of the model tree of host h and size z that is in crown level c.

Note that both the amounts of foliage present and the observed patterns of second-instar densities are weighted equally in equation 8. For a given host, the values of $BWPROP_{ch}$ for the three crown levels that correspond to a given tree size class (see fig. 1) will sum to 1.0.

Table 12 shows relative densities of second instars by crown third (summed across tree size classes). By default, $BWRLDN_c$ uses these values for all hosts and all height classes. $BWPROP_{ch}$ will be used during the following spring to simulate the initial spatial distribution of newly emerged larvae.

Table 12—Proportion by crown-third of early instars in needles and buds (weighted mean values are used as default values in the model)

Height class	Upper crown	Mid-crown	Lower crown	Number of plot-years	Source
Mixed	0.454	0.341	0.204	1	Waters and Volney (1981 unpubl.)
Mixed	.379	.312	.309	3	Waters and Volney (1982 unpubl.)
14^{+}m	.583	.254	.163	1	Carolin and Coulter (1972)
Mean[1]	0.440	0.316	0.243		

[1] Average of means weighted by number of plot-years.

Emerging Larvae Through Pupae, BWMOD-Part II

The budworm life cycle from the time of emergence in the spring through the pupal period has been divided into intervals that are based on budworm development. The budworm's rate of development is modeled as a linear function of temperature, with higher temperatures (above a threshold) leading to faster budworm development. Each interval is 20 °D long and is calculated using the budworm's temperature thresholds as described in the next section. The number of degree days that occur for a particular calendar day depends on maximum and minimum temperatures as supplied by the Weather Model.

In some ways, the methods described here for simulating budworm phenology are simplistic. Developmental thresholds have been shown to vary among western spruce budworm populations (Volney and others 1983), and development of most insects is not linear near upper and. lower thresholds (Logan and Hilbert 1983, Stinner and others 1974, Wang 1960). Additionally, local topography can cause frost pockets or cold air drainage down a canyon. These problems are far outweighed, however, by the difficulty in predicting temperatures for the specific microsites occupied by larvae. Larvae developing in buds or in webs may experience temperatures that differ from ambient air temperatures by -3 °C to +8 °C (Shepherd 1958, Wellington 1950). Because of the difficulty in modeling these processes, they are simplified in the Budworm Model, and temperatures are adjusted for elevation only, with constant temperature thresholds affecting budworm development.

Host phenology (the timing of bud break and shoot elongation) is also a function of daily weather (Campbell and Sugano 1979, Libby and others 1980, Thomson and Moncrieff 1982, Wareing and Saunders 1971). Although Cleary and Waring (1969) and Sorensen and Campbell (1978) demonstrated that both air and soil temperatures affect host phenology, the latter authors found that air temperatures (which control developmental rates) have a greater influence on bud-break timing than do soil temperatures (which determine when development starts). Air temperatures are used in the Budworm Model to calculate host phenology. Degree-days are calculated separately for each host using host-specific development thresholds.

During each 20 °D interval, several events are modeled: foliage growth, emergence of larvae from hiberacula, larval growth, destruction of foliage, and budworm mortality (fig. 6). These steps are repeated every 20 °D until all surviving budworms have emerged as adults. After all adults have emerged, the total number of potential eggs produced per stand is calculated and stored.

Host and budworm phenology

Calculate degree-days—At the start of each Budworm Model time step, the number of degree-days that accumulate during each new Julian day is calculated. Julian days are accumulated until the associated degree-days total at least 20. The first calendar day when a degree-day may begin to accumulate is set by BSTART (for budworms) and $HSTART_h$ (for hosts); by default, BSTART is set to April 1 (Julian day 91) and $HSTART_h$ is set to May 1 (Julian day 121) for all hosts.

Daily maximum ($TMAX_d$) and minimum ($TMIN_d$) temperatures supplied by the Weather Model are used to calculate the number of degree-days that occur each calendar day. Equations 9 and 10 (after Everson and others 1976) are used to calculate degree-days for budworm and hosts, respectively:

$$DDNOW_d = \left(\frac{TMAXX_d + TMIN_d}{2.0}\right) - BWLOW \qquad (9)$$

$$DDAYH_{hd} = \left(\frac{TMAXX_d + TMIN_d}{2.0}\right) - HOSTLO_h \qquad (10)$$

where: $DDNOW_d$ = the number of degree-days accumulated on Julian day d for budworm,
$DDAYH_{hd}$ = the number of degree-days accumulated for host h on Julian day d,
$TMAXX_d$ = minimum of $TMAX_d$ and BWHI for equation 9,
$TMAXX_d$ = minimum of $TMAX_d$ and $HOSTHI_h$ for equation 10,
BWHI = upper development threshold for budworm (°C),
$HOSTHI_h$ = upper development threshold for host h (°C),
$TMAX_d$ = maximum temperature on Julian day d (°C),
$TMIN_d$ = minimum temperature on Julian day d (°C),
BWLOW = lower temperature threshold for budworm (°C), and
$HOSTLO_h$ = lower temperature threshold for host h (°C).

Negative values for $DDNOW_d$ and $DDAYH_{hd}$ are reset to zero. Note that these equations do not allow any development on relatively warm spring days with cold nights when the average temperature is less than the threshold. On the last calendar day of a 20 °D interval, any additional degree-days beyond the 20 °D are credited to the next 20 °D interval. Only one 20 °D interval is permitted per calendar day; in the unlikely event that 40 °D or more occurs on one day (for example, if the threshold were 5.5 °C and the mean daily temperature was 45 °C or greater), then the second 20 °D interval would not be simulated until the next calendar day.

The model equations assume that the upper thresholds for both budworm and host signify developmental plateaus. Temperatures above the threshold do not affect developmental rates for either the budworm or hosts.

By default, the lower developmental thresholds are set to 5.5 °C for budworm (BWLOW) and for all hosts ($HOSTLO_h$). Other researchers have used 5.5 °C as the threshold for western spruce budworm and hosts (Beckwith and Kemp 1984, Shepherd 1961, Wagg 1958), eastern spruce budworm (Henson 1948, Miller and others 1971), and other forest insects (Embree 1965, Ives 1973, Wickman 1981). Volney and others (1983), however, reported other thresholds for western spruce budworm ranging from 6.5 to 8.5 °C. Thomson and Moncrieff (1982) reported that 2.8 °C was the most accurate lower threshold temperature for coastal Douglas-fir; 5.5 °C has commonly been adopted as the threshold temperature for other phenological studies of western conifers (Wickman 1976a, 1976b, 1977, 1981).

The upper development threshold for budworm (BWHI) is set to 37.8 °C by default. Wellington (1949) noted that eastern spruce budworms (fourth through sixth instars) avoid temperatures above 37-38 °C, and Wellington and Henson (1947) reported that above 100 °F (37.8 °C) sixth-instar eastern spruce budworm react photonegatively (usually dropping from their feeding sites or moving in toward the trunk).

The upper development threshold for all hosts ($HOSTHI_h$) has been arbitrarily set to 35 °C. Brix (1967) noted that the growth of Douglas-fir seedlings is greatly reduced above 30 °C

The model also assumes that a minimum number of degree-days must occur before budworm larvae emerge from their hibernacula (TREQ). Results of field and laboratory studies (summarized in table 13) were used to calculate the default minimum degree-days required for larval emergence (68 °D). Although Thomson and Moncrieff (1982) reported that 247-340 °D above 2.78 °C are required for first bud flush (depending on the date that degree-days begin to accumulate), the onset of bud swelling may occur several weeks before bud flushing (Allen and Owens 1972). In the model, the minimum degree-days required for bud development is set to zero by default. Upper and lower thresholds, first date when degree-days may begin to accumulate for both budworm and hosts, and minimum degree-days required for larval emergence can be specified by the user.

Extremely low temperatures that occur after larvae emerge from hibernacula sometimes cause extensive budworm mortality (Buchanan 1945,1947; McKnight unpubl.). Fellin and Schmidt (1973) reported a 90-percent (or more) reduction in budworm populations following a late spring frost (temperatures reached -6 °C). Blais (1981) observed much higher foliage mortality (mean shoots frozen, 46 percent; range, 18 to 99 percent) than eastern spruce budworm mortality (mean budworm mortality, 17 percent; range, 0 to 48 percent) following temperatures of -2 to -3 °C.

Table 13—Minimum degree days above 5.5 °C required for second instars to emerge from hibernacula (TREQ)

Field or laboratory study	Number of plot-years	Mean degree days required	Source
Field	5	62.4	Fellin and Theroux[1]
Field	2	49	Beckwith[2]
Field	1	121	Wagg (1958)[3]
Lab	1	95.6	Volney and others (1983)[4]
Mean[5]		69.6	

[1] Unpublished report by Fellin and Theroux; personal communication, David G. Fellin, USDA Forest Service, Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807.

[2] Personal communication, unpublished data from Roy Beckwith, USDA Forest Service, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331.

[3] Computed from equation fitted to all data (Wagg 1958, p. 14).

[4] Weighted means of three Dry Lakes Flat (b) populations-from *C. occidentialis* (female) x *C. retiniana* (male) cross.

[5] Average of means weighted by number of plot-years.

Blais (1957) reported that an unusually cool wet summer in 1956 in the Gaspé Peninsula of Quebec caused a significant reduction in eastern spruce budworm populations. The date of 50-percent adult emergence was delayed from mid-July in 1956 to the end of August in 1957, and then only 37 percent of the egg masses were totally hatched while 53 percent were unhatched. Prebble (1945) reported that late frosts were ". . . undoubtedly responsible, directly through freezing of larvae, or indirectly through the destruction of favored food. . ." for the decline in eastern spruce budworm populations in Ontario in 1945.

The model assumes that temperatures lower than a specified threshold (COLDT, set to -6 °C by default) cause immediate mortality to proportions of both budworms (COLDBK, set to 0.05 by default) and host buds ($COLOHK_h$, set to 0.01 for each host by default).

Grow new foliage—Foliage variables are updated every 20 °D time step. First shoot elongation is predicted for each host, and then foliage biomass production is calculated. Only shoot elongation, and not bud flushing, is explicitly modeled.

The Budworm Model uses a logistic growth equation (Beckwith and Kemp 1984) to predict host shoot elongation during a 20 °D step:

$$TOTLN_{chs} = \left(\frac{A1_{ch}}{1.0 + e^{(A2_{ch} + A3_{ch} \times HDDAY_{hs})}} \right) + A4_{ch} \qquad (11)$$

where: $TOTLN_{chs}$ = total shoot length (millimeters) for crown level c of host h at current 20 °D step s,

$HDDAY_{hs}$ = total degree-days accumulated for host h from Julian day $HSTART_h$ to the current 20 °D step s, and

$A1_{ch}$, $A2_{ch}$, $A3_{ch}$, $A4_{ch}$ = constants for crown level c on host h, and e denotes the exponential function.

Table 14—Parameters for Douglas-fir and grand fir growth equations
(A1-A4), maximum shoot length (GMAX), and minimum shoot

	Douglas-fir			Grand fir		
Parameters	Upper crown	Mid-crown	Lower crown	Upper crown	Mid-crown	Lower crown
A1	–58.365	–53.299	–46.916	–71.584	–64.840	–48.380
A2	–6.925	–5.817	–6.233	–4.990	–4.901	–4.963
A3	.0292	.0248	.0279	.0219	.0226	.0257
A4	66.556	60.379	53.270	75.244	67.628	50.759
GMAX(mm)	66.6	60.4	53.3	75.2	67.6	50.8
GMIN(mm)	8.2	7.2	6.4	4.2	3.2	2.7

Source: Beckwith and Kemp (1984).

Table 14 lists the default values of parameters $A1_{ch}$-$A4_{ch}$ and $GMAX_{ch}$ and $GMIN_{ch}$ (maximum and minimum shoot growth by crown level c of host h) for Douglas-fir and grand fir. The Budworm Model uses the same crown-specific parameters for all three tree height classes; also, the grand fir parameters are used for white fir and subalpine fir, and the Douglas-fir parameters are used for Engelmann spruce.

The amount of new foliage grown in a 20 °D interval is determined by the following equation:

$$ADDLN_{chs} = TOTLN_{chs} - TOTLN_{ch(s-1)} \qquad (12)$$

where: $ADDLN_{chs}$ = shoot growth (millimeters) for crown level c of host h during 20 °D step s, and
$TOTLN_{chs}$ = total shoot length (millimeters) for crown level c of host h during 20 °D step s (equation 11).

Next, the proportion of total potential shoot length for each crown level and host that . was grown during this 20 °D step is calculated:

$$PROPTF_{chs} = \frac{ADDLN_{chs}}{GMAX_{ch}} \qquad (13)$$

where: $PROPTF_{chs}$ = proportion of total shoot length grown in crown level c of host h during 20 °D step s,
$ADDLN_{chs}$ = shoot growth (millimeters) as calculated in equation 12, and
$GMAX_{ch}$ = total possible shoot growth (millimeters) for crown level c of host h.

The Budworm Model assumes that biomass production parallels shoot elongation. Total live foliage (g) grown during the current step is calculated from the equation:

$$ADDFOL_{chs} = BUDS_{chs} \times BUDMAS_{ch} \times PROPTF_{chs} \qquad (14)$$

where: $ADDFOL_{chs}$ = total live foliage (grams) grown in crown level c of host h during 20 °D step s,

$BUDS_{chs}$ = total number of vegetative buds present in crown level c of host h during 20 °D step s, and

$BUDMAS_{ch}$ = average potential biomass produced per shoot for crown level c of host h (table 5), and

$PROPTF_{chs}$ = calculated in equation 13, above.

Total dead foliage ($ADDFD_{chs}$) that would have grown during the current step in the absence of budworm is calculated similarly to $ADDFOL_{chs}$, except dead buds ($BUDSK_{chs}$ + $BUDSD_{chs}$) are used instead of live buds ($BUDS_{chs}$). $BUDSK_{chs}$ stores the number of dead buds (killed by budworm feeding early in the season), and $BUDSD_{chs}$ stores the number of damaged buds (representing potential foliage killed by budworms-see p. 41 for details). The biomass of newly grown live foliage ($ADDFOL_{chs}$) is then added to three state variables: $FOLIVE_{chs}$, $FNEW_{chs}$, and $POTFOL_{chs}$.

$FOLIVE_{chs}$ is the accumulated total biomass of new foliage produced in crown level c of host h through 20 °D steps 1,...,s. $FNEW_{chs}$ is the same as $FOLIVE_{chs}$, except that $FNEW_{chs}$ is decreased by subsequent budworm defoliation. $FOLIVE_{chs}$ is therefore the amount of new foliage produced by live buds in the absence of budworm defoliation, and $FNEW_{chs}$ is the amount of new foliage that remains after budworm defoliation has occurred in step s. $POTFOL_{chs}$ is similar to $FOLIVE_{chs}$, except $POTFOL_{chs}$ also accumulates the biomass of foliage that would have been grown by buds killed or damaged by defoliation during this 20 °D step ($ADDFD_{chs}$). At the end of the growing season, $POTFOL_{chs}$ is equal to the biomass of foliage that would have been present if no defoliation had occurred during that season. FNEWchs, $FOLIVE_{chs}$, and $POTFOL_{chs}$ are used to calculate defoliation at the end of each 20 °D interval (see p. 40 for details).

Percentage of shoot expansion ($PEXPAN_{chs}$) is calculated using the average length of all shoots in each crown third as follows:

$$PEXPAN_{chs} = 100.0 \times \left(\frac{TOTLN_{chs} - GMIN_{chs}}{GMAX_{ch} - GMIN_{ch}} \right) \qquad (15)$$

where: $PEXPAN_{chs}$ = average percentage of shoot expansion of all shoots in crown level c of host h during 20 °D step s,

$TOTLN_{chs}$ = total shoot length (millimeters) calculated from equation 11 in crown level c of host h during 20 °D step s,

$GMIN_{ch}$ = average minimum shoot length (millimeters) in crown level c of host h, and

$GMAX_{ch}$ = maximum shoot length (millimeters) in crown level c of host h.

Very little information exists concerning exactly when buds have developed enough to become suitable for mining by budworms. Reproductive buds of coastal Douglas-fir burst approximately 1 month before vegetative buds (Allen and Owens 1972; Owens and Smith 1964, 1965); Franklin and Ritchie (1970) reported that for both grand fir and subalpine fir in the Cascade Range (Linn County, OR), reproductive buds burst several weeks earlier than vegetative buds.

The proportions of buds developed enough to be suitable for mining are calculated using equations 16 and 17:

$$VBUDEV_{chs} = (PEXPAN_{chs} \times VBSLOP) + VBINT \tag{16}$$

$$RBUDEV_{chs} = (PEXPAN_{chs} \times RBSLOP) + RBINT \tag{17}$$

where: $VBUDEV_{chs}$ = proportion of vegetative buds that are suitable for mining in crown level c of host h during 20 °D step s,

$RBUDEV_{chs}$ = proportion of reproductive buds that are suitable for mining in crown level c of host h during 20 °D step s,

$PEXPAN_{chs}$ = average percentage shoot expansion of all shoots in crown level c of host h through 20 °D step s, calculated in equation 15,

$VBSLOP$ = slope for proportion of vegetative buds suitable for mining,

$VBINT$ = intercept for proportion of vegetative buds suitable for mining,

$RBSLOP$ = slope for proportion of reproductive buds suitable for mining, and

$RBINT$ = intercept for proportion of reproductive buds suitable for mining.

Figure 7 shows the relationships between $PEXPAN_{chs}$ and both $RBUDEV_{chs}$ and $VBUDEV_{chs}$ that are assumed; values for VBSLOP, VBINT, RBSLOP, and RBINT were arbitrarily selected.

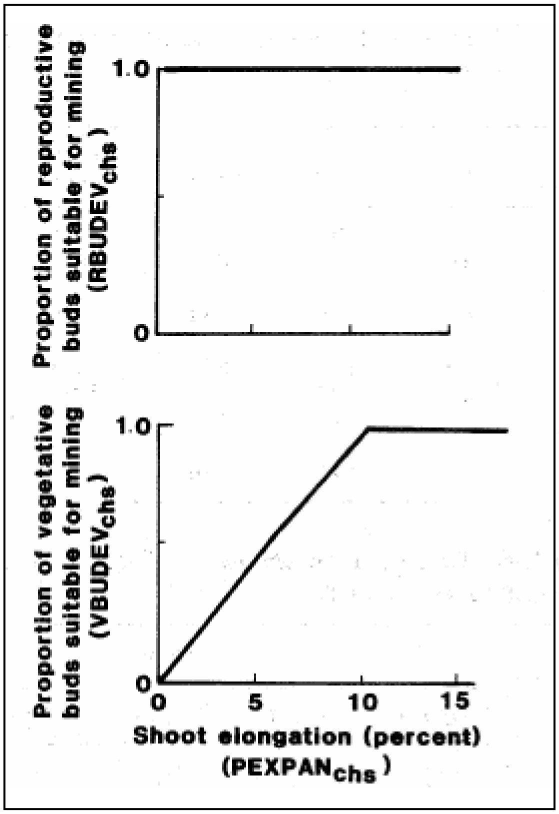

Figure 7—The percentage of shoot elongation is used to predict proportion of reproductive buds and vegetative buds suitable for mining (default values).

Aging the budworms —During each 20 °D interval, budworms that have already emerged from hibernacula are aged by 20 °D. Table 15A summarizes degree-day requirements (above 5.5 °C) for western spruce budworm by life stage (males and females combined). Beckwith. (1983a unpubl.)found that the mean pupal periods for males and females reared at several different temperatures were nearly identical; Sanders (1975) found similar results for eastern spruce budworm reared at constant temperatures. Other researchers found that during the larval-pupal period, male budworms developed 56 °D (Blake and Wagner 1984) to 71 °D (Beckwith 1983a unpubl.) faster than females. A similar trend was also reported for eastern spruce budworm (McGugan 1954). Regniere (1982) reported unpublished data from Eidt and Cameron for eastern spruce budworm that, when averaged for several rearing temperatures, showed that female larvae spend a greater proportion of their total larval development time as sixth instars (and to a lesser degree, as fifth instars), compared with male larvae. In the Budworm Model, a mean difference of 64 °D (the average of 56 °D and 71 °D) between females and males was assumed, and the extra degrees were added to female fifth instars (25 percent) and sixth instars (75 percent). Table 15B shows the resulting values rounded to the nearest 20 °D.

Table 15A—Degree-days above 5.5 °C required by life stage (data from literature)

	Instar							
Sex	Second	Third	Fourth	Fifth	Sixth	Pupae	Field or laboratory study	Source
F + M	73	82	105	46	130	167	Field	Beckwith and Kemp (1984)
F + M	138	46	59	129	114	228	Field	Beckwith (1983a unpubl.) Bear Springs Plot
F + M	128	47	78	84	174	180	Field	Beckwith (1983a unpubl.), Meadow Creek Plot
F + M	48	69	95	130	186	216	Field	Wagg (1958)
F + M	125	57	89	59	99	131	Lab	Lyon and others (1972)
F + M	—	—	—	—	—	151	Lab	Beckwith (1983a unpubl.)
Mean	102	60	85	90	141	186		

Table 15B—Degree-days above 5.5 °C required by life stage (default

	Instar					
Sex	Second	Third	Fourth	Fifth	Sixth	Pupae
M	100	60	80	80	120	180
F	100	60	80	100	160	180

[1] Modified as described in text to account for longer female development time, and rounded to nearest 20 °D.

$BUGSF_{chrs}$ and $BUGSM_{chrs}$ store the number of female and male budworms in each 20 °D cohort r, by foliage cell. IYOUNG and IOLD store the ages (in number of 20 °D intervals since emergence from hibernacula) of the youngest and oldest budworm cohorts. Budworms are aged during each 20 °D interval by incrementing IOLD (and IYOUNG if larval emergence is completed). For a given 20 °D step s, the age of the youngest budworm cohort is IYOUNG, the age of the next older cohort is IYOUNG +1, and so on. Arrays $LIMITF_a$ and $LIMITM_a$ store the life stage of female and male budworms at age a.

Larval emergence—If all larvae have emerged, the Budworm Model skips this section.

The proportion of larvae that emerge in a given 20 °D step s is set by $PEMERG_s$. The default $PEMERG_s$ function, shown in figure 8, was calculated for the Dry Lakes Flat (b) population from southern Oregon that was studied in the lab at 25 °C by Volney and others (1983). All the larvae that emerge during one 20 °D interval form one cohort (r) and are stored separately in $BUGSF_{chrs}$ (for females) and $BUGSM_{chrs}$ (for males).

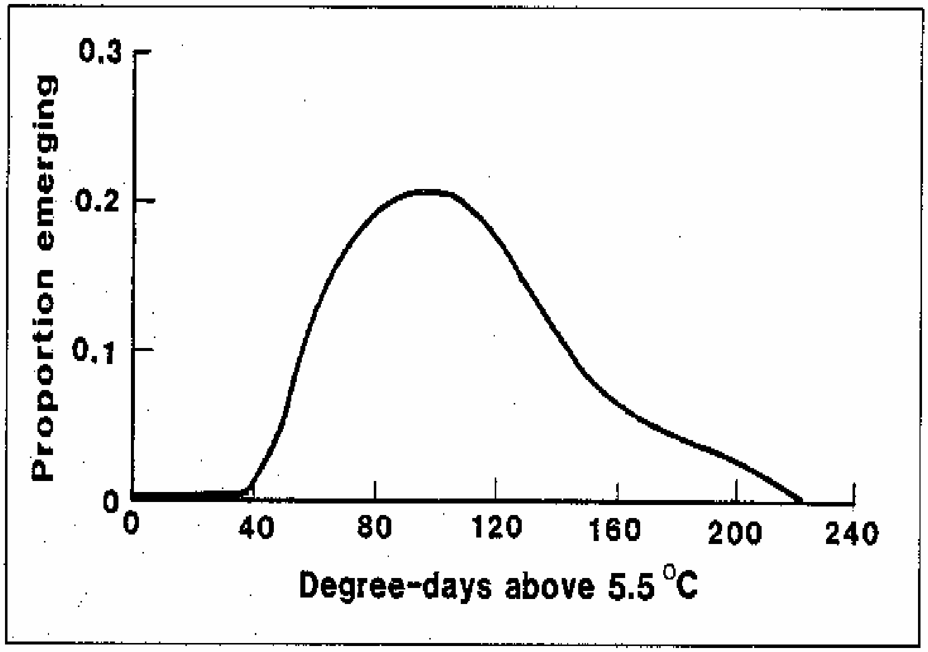

Figure 8—Pattern of budworm emergence from hibernacula (default values, taken from Sheehan and others 1987; data from Volney and others 1983).

The number of newly emerged larvae that search for feeding sites in a given foliage cell during a 20 °D interval is calculated using equation 18;

$$BUGSEM_{chrs} = BUGT_{hz} \times BWPROP_{ch} \times PEMERG_{s} \qquad (18)$$

where: $BUGSEM_{chrs}$ = total number of budworms of cohort r emerging from hibernacula in crown level c of host h during 20 °D step s,

$BUGT_{hz}$ = total number of budworm larvae on budworm model tree size z (corresponding to crown level c) of host h after overwintering and springtime base mortality has occurred as calculated in equation 7,

$BWPROP_{ch}$ = proportion, of larvae that will begin to search for foliage in crown level c of host h as calculated in equation 8, and

$PEMERG_{s}$ = proportion of larvae emerging from hibernacula at 20 °D step s to form cohort r.

Male and female larvae have been found to have similar emergence patterns (Schmidt 1977). Half of $BUGSEM_{chrs}$ is therefore added to $BUGSF_{chrs}$ (which stores the number of emerged female larvae by cohort r) and also to $BUGSM_{chrs}$ (which stores the number of emerged male larvae).

The model assumes that a proportion (SPDISP, default arbitrarily set to 0.05) of these newly emerged larvae will disperse immediately, even if buds suitable for mining are present; these dispersing larvae are stored in $DISPBW_{chr}$. The rest of the newly emerged larvae, and larvae that emerge from needles they had mined because no buds were available when they first emerged (stored earlier in $BMINE_{chs}$), search for buds to mine. The number of available buds is equal to those vegetative buds that are expanded enough for mining (proportion stored in $VBUDEV_{chs}$; see fig. 7), not previously mined by another budworm (stored in $BUDSAV_{chs}$), and not part of the foliage that is effectively hidden (a proportion [HIDBUD] of the total number of buds, default arbitrarily set to 0.1), plus those reproductive buds ($RBDUS_{chs}$) that are expanded enough for mining (proportion stored in $RBUDEV_{chs}$; see fig. 7) and are not effectively hidden (HIDBUD). Larvae are partitioned between vegetative and reproductive buds according to the proportion of total available buds represented by the two types of buds. Note that in the model, reproductive buds can be mined by more than one larva, but only one larva may mine a vegetative bud. If there are enough suitable buds, the Budworm Model reduces $BUDSAV_{chs}$ by the total number of mined buds multiplied by the proportion of mined buds that are vegetative ($VBPROP_s$), and budworms begin feeding.

If there are more larvae than suitable buds, the model calculates how many larvae (if any) were able to find buds ($WBUDS_{chs}$) and decreases the number of available vegetative buds ($BUDSAV_{chs}$) by total mined buds multiplied by $VBPROP_s$.

Older larvae that had been mining needles and still have not found new foliage die. Newly emerged larvae that have not found buds to mine will either disperse (a pro portion, SPRING, default arbitrarily set to 0.5) or mine needles. The model assumes that larvae mine needles for one instar (two to three 20 °D intervals) before resuming their search for new foliage. Half of these larvae will therefore emerge from the needles after two intervals (40 °D) and half will emerge after three intervals (60 °D); these larvae are stored in $BMINE_{ch(s+2)}$ and $BMINE_{ch(s+3)}$, respectively. Needle-mining larvae are assumed to mine one needle per larva on all hosts. McGugan (1954) noted that most eastern spruce budworm larvae mine one balsam fir needle or from two to six white spruce needles per larva. The amount of older foliage remaining is decreased by the number of mined needles. multiplied by the mean biomass per needle. Biomass per needle (WTN_{ch}) was estimated for 1- to 3-year-old foliage by Beckwith (1978) for Douglas-fir (0.005 g/needle), grand fir (0.009 g/needle), and white fir (0.013 g/needle); by default, grand fir values are used for subalpine fir and Douglas-fir values are applied to Engelmann spruce. One-year-old foliage ($FOLD1_{ch}$) is mined if available; 2-year-old ($FOLD2_{ch}$) and older foliage ($FREM_{ch}$) is used if needed. McGugan (1954) reported that 87 to 95 percent of eastern spruce budworm larvae that mine needles are found on 1-year-old foliage.

Larval feeding and foliage destruction

Amount destroyed —The potential amount of foliage destroyed ($DESTRY_{chs}$) per foliage cell (ch) in a given 20 °D interval (s) if all larvae fed on new foliage is a function of the amount actually consumed and the proportion of total amount destroyed that is clipped but not eaten ("wasted"); this is calculated in equation 19:

$$DESTRY_{chs} = \sum_{r=1}^{R} \left[\left(\frac{BUGSF_{chrs} \times EATF_{fh}}{1.0 - WASTEF_{fh}} \right) + \left(\frac{BUGSM_{chrs} \times EATM_{fh}}{1.0 - WASTEM_{fh}} \right) \right] \quad (19)$$

where: $DESTRY_{chs}$ = potential grams of foliage destroyed by feeding larvae in crown level c of host h during 20 °D step s,

$BUGSF_{chrs}$ = number of female budworm larvae of cohort r in crown level c of host h during 20 °D step s,

$EATF_{fh}$ = grams of new foliage eaten by a single female budworm of the life stage f corresponding to females in cohort r on host h per 20 °D step,

$WASTEF_{fh}$ = proportion of new foliage clipped but not eaten by female budworms of life stage f corresponding to females in cohort r on host h per 20 °D step,

$BUGSM_{chrs}$ = number of male budworm larvae of cohort r in crown level c of host h during 20 °D step s,

$EATM_{fh}$ = grams of new foliage eaten by a single male budworm of the life stage f corresponding to males in cohort r on host h per 20 °D step, and

$WASTEM_{fh}$ = proportion of new foliage clipped, but not eaten, by male budworms of the life stage f corresponding to males in cohort r on host h during 20 °D step.

Blake and Wagner[10] and Roy C. Beckwith[11] measured total amount consumed by older larvae for both females and males (table 16). Miller (1977) reported that 96 percent of the total biomass consumed by eastern spruce budworm was eaten by fifth and sixth instars; Beckwith (1978) showed that approximately 90 to 93 percent was consumed by the last two Douglas-fir tussock moth instars. In the Budworm Model, fifth and sixth instars were assumed to consume 90 percent of the total amount consummed, fourth instars consume 5 percent, third instars consume 3 percent, and second instars consume 2 percent. Blake and Wagner (1984) reported that of the amount of foliage ingested by fifth and sixth instars, fifth instars consumed 35 percent (or 32 percent of total if fifth and sixth instars are assumed to eat 90 percent of the total amount consumed) and sixths consumed 65 percent (or 58 percent of the total). The amount consumed per instar was divided by the number of 20 °D intervals per instar (see table 15) to determine the amount consumed per 20 °D by instar.

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[10] Personal communication, Michael R. Wagner, School of Forestry, Box 4098, Northern Arizona University, Flagstaff, AZ 86011.

[11] Personal communication, Roy C. Beckwith, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331.

Table 16—Foliage consumed (milligrams per larva) by fourth through sixth Instars

Host (h)	Males	Females	Source
Douglas-fir	172	205	Blake and Wagner[1]
Douglas-fir	149	279	Beckwith[2]
Mean:	161	242	
Grand fir	167	262	Beckwith[2]
Subalpine fir	197	248	Blake and Wagner[1]
White fir	197	315	Blake and Wagner[1]

[1] Unpublished work by Blake and Wagner; personal communication, Michael R. Wagner, School of Forestry, Box 4098, Northem Arizona University, Flagstaff, AZ 86011.

[2] Unpublished work by Beckwith; personal communication, Roy C. Beckwith, USDA Forest SerVice, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331. Beckwith actually measured consumption by third through sixth instars. In the model, third instars are assumed to consume 3.03 percent of the total amount eaten by third through sixth instars. The values observed by Beckwith were therefore decreased by 3.03 percent for inclusion in this table.

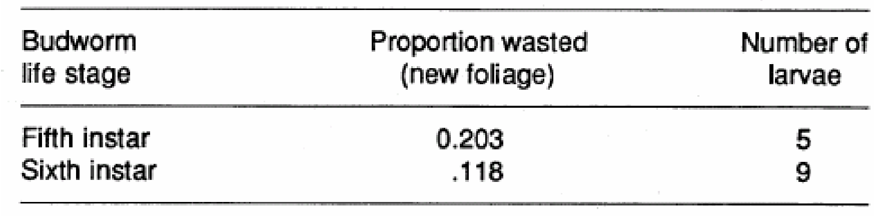
Table 17—Default values for grams of new foliage of host h consumed by one budworm per instar f and per 20 °D step by sex ($EATF_{fh}$ for females and $EATM_{fh}$ for males)

	Second instar		Third instar		Fourth instar		Fifth instar		Sixth instar	
Host and sex	Total grams	Grams per 20 °D	Total grams	Grams per 20 °D	Total grams	Grams per 20 °D	Total grams	Grams per 20 °D	Total grams	Grams per 20 °D
Douglas-fir:										
M	0.0034	0.0007	0.0051	0.0017	0.0085	0.0021	0.0541	0.0135	0.0980	0.0163
F	.0051	.0010	.0077	.0026	.0128	.0032	.0816	.0163	.1479	.0185
Grand fir:										
M	.0035	.0006	.0053	.0018	.0088	.0022	.0563	.0141	.1021	.0170
F	.0055	.0011	.0083	.0028	.0138	.0035	.0883	.0178	.1601	.0200
White fir:										
M	.0041	.0008	.0062	.0021	.0104	.0026	.0662	.0166	.1201	.0200
F	.0066	.0013	.0100	.0026	.0166	.0042	.1062	.0212	.1926	.0241
Subalpine fir:										
M	.0041	.0008	.0062	.0021	.0104	.0026	.0662	.0166	.1201	.0200
F	.0052	.0010	.0078	.0026	.0131	.0033	.0835	.0167	.1514	.0189

Table 17 shows the default values for mean amount consumed per instar and per 20 °D per instar. Because variation in amounts consumed has been noted among instars, hosts, and sexes (Blake and Wagner 1984, Wagner and Blake 1983), the Budworm Model has been designed to handle this variation. By default, Douglas-fir values are used for Engelmann spruce.

The proportion of total destroyed foliage that is clipped but not actually consumed ($WASTEF_{fh}$ and $WASTEM_{fh}$) was measured in laboratory studies by Blake and Wagner (1984) for fifth and sixth instars (table 18A). Beckwith and

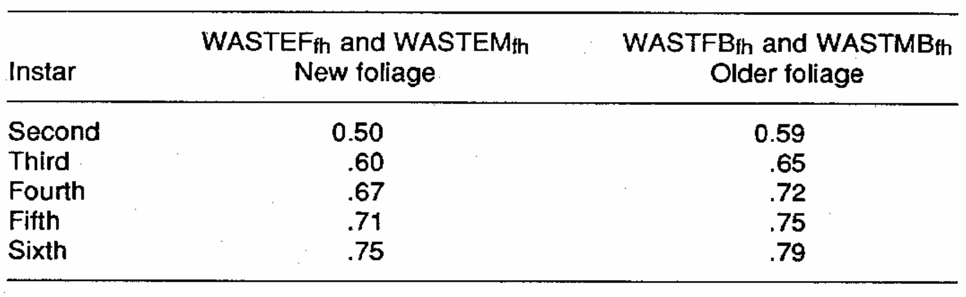
Table 18A—Proportion of total amount of foliage destroyed by budworms that was not consumed



Budworm life stage	Proportion wasted (new foliage)	Number of larvae
Fifth instar	0.203	5
Sixth instar	.118	9

Source: Blake and Wagner (1984).

Table 18B—Default values used by the Budworm Model for all hosts



Instar	$WASTEF_{fh}$ and $WASTEM_{fh}$ New foliage	$WASTFB_{fh}$ and $WASTMB_{fh}$ Older foliage
Second	0.50	0.59
Third	.60	.65
Fourth	.67	.72
Fifth	.71	.75
Sixth	.75	.79

Kemp[12] observed that older larvae waste far more foliage in the field than they do in the laboratory because of their habit of webbing one or two developing shoots and then feeding on the portions of the needles accessible from their webs; Miller (1977) reports similar observations for eastern spruce budworm. Beckwith[12] further noted that disturbance may force larvae to abandon webbing, leaving unused food behind. The default values for proportions wasted (table 18B) therefore were set arbitrarily higher than the laboratory observations. The model allows the user to vary these proportions by host and sex, but the default values are the same for larvae on all hosts and of both sexes.

If enough new foliage is present (that is, the amount of current foliage present ($FNEW_{chs}$) minus the proportion effectively hidden from larvae (HIDFOL, set to 0.1 by default) is greater than $DESTRY_{chs}$), then the model assumes that all larvae feed on new foliage. If not enough new foliage is available, the model assumes that some larvae will feed on older foliage (the proportion is set by $BACKFD_{fh}$) and the rest will disperse. Dispersing larvae are stored in $DISPBW_{chr}$.

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[12] Personal communication, Roy C. Beckwith, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331.

Table 19—Survival rates for larvae reared on older foliage

Species	Instar when rearing on older foliage was initiated	Proportion surviving to adult stage
Douglas-fir	3	0.16
	4	.16
	5	.12
	6	.88
Grand fir	3	.44
	4	.44
	5	.68
	6	.83
Subalpine fir	3	.28
	4	.24
	5	.60
	6	.64

Source: Beckwith (1983b unpubl.).

Beckwith (1983b unpubl.) reported larval survival rates in the laboratory as a function of host and instar when reared on older foliage. By default, the model assumes that the proportion of larvae that feed on older foliage ($BACKFD_{fh}$) rather than disperse, when there is insufficient new foliage, is equal to the survival rates of larvae that feed on older foliage (table 19). Default rates for second instars are set to 50 percent of the third-instar rate; Douglas-fir rates are used for Engelmann spruce and grand fir rates are used for white fir. These backfeeding larvae are temporarily stored in $BACKLV_{rs}$; they have separate consumption rates ($EATBF_{fh}$ and $EATBM_{fh}$) and proportions wasted ($WASTFB_{fh}$ and $WASTMB_{fh}$). By default, these larvae consume 25 percent more and waste 5-18 percent more than larvae feeding on current foliage.

Female weight gain—Weight gained by a female during a 20 °D step s is calculated separately for each larval cohort. The model ignores the effects of larval movement among foliage cells on mean budworm weight for a given cell. At the end of the season, these weights ($WEIGHT_{chrs}$) will be used to calculate the number of potential eggs per female. The proportions of female budworms feeding on new and old foliage are calculated in equations 20 and 21 :

$$WTNEW_{chrs} = \frac{BUGSF_{chrs}}{BUGSF_{chrs} + (0.5 \times BACKLV_{rs})} \tag{20}$$

$$WTOLD_{chrs} = 1.0 - WTNEW_{chrs} \tag{21}$$

where: $WTNEW_{chrs}$ = proportion of female budworms of cohort r feeding on new foliage in crown level c of host h during 20 °D step s,

$WTOLD_{chrs}$ = proportion of female budworms of cohort r feeding on old foliage in crown level c of host h during 20 °D step s,

$BUGSF_{chrs}$ = number of female larvae of cohort r in crown level c of host h during 20 °D step s, and

$BACKLV_{rs}$ = number of backfeeding larvae from cohort r during 20 °D step s.

Note the assumption in equation 20 that half of these larvae that are forced to feed on older foliage are female.

For each cohort, r, the weight of a single female larva is accumulated once each 20 °D step, s, as in equation 22:

$$WEIGHT_{chrs} = WEIGHT_{chr(s-1)} + (WTNEW_{chrs} \times EATF_{fh} \times ECIF_{fh} \times FQUALW_{hb}) + (WTOLD_{chrs} \times EATBFF_{fh} \times ECIBFF_{fh} \times FQUALW_{hb}) \tag{22}$$

where: $WEIGHT_{chrs}$ = average weight (milligrams) of a single female budworm larva of cohort r in crown third c of host h during 20 °D step 2,

$WTNEW_{chrs}$ = proportion of female budworm of cohort r feeding on new foliage in crown level c of host h during 20 °D step s, as calculated in equation 20,

$EATF_{fh}$ = grams of new foliage eaten by a single female larva of the life stage f represented by cohort r on host h,

$ECIF_{fh}$ = efficiency of conversion index (which converts new foliage biomass consumed into biomass gained) for female budworm of the life stage f represented by cohort r on host h,

$FQUALW_{hb}$ = index for the effects of foliage quality on female weight gain, for host h of habitat type b,

$WTOLD_{chrs}$ = proportion of female budworm of cohort r feeding on old foliage in crown level c of host h during 20 °D step s, as calculated in equation 21,

$EATBFF_{fh}$ = grams of old foliage eaten by a single female budworm of the life stage f represented by cohort r on host h, and

$ECIBFF_{fh}$ = efficiency of conversion index (which converts old foliage biomass consumed into female budworm biomass gained) for female budworm of the life stage f represented by cohort r on host h.

Efficiency of conversion indices ($ECIF_{fh}$, $ECIBFF_{fh}$) for females are based on laboratory studies by Blake and Wagner (see footnote 10) using foliage from Douglas-fir, white fir, and subalpine fir. These values are used as defaults (table 20); white fir values are used for grand fir and Douglas-fir values for Engelmann spruce. These authors found significant differences in budworm foliage conversion efficiencies among hosts (Wagner and Blake 1983) but not between sexes or among instars (Blake and Wagner 1984). Though instar-specific values may be provided by the user, by default the model uses the same value for all instars and both sexes on a given host. The conversion efficiencies of larvae feeding on older foliage are arbitrarily set by default to the values shown in table 20, which correspond to 75 percent of the efficiency when budworm feed on current foliage.

Cates and others (1983a, 1983 unpubl.) have shown that foliage quality (particularly nitrogen, terpene, and bornyl acetate content) influences adult female weight. Cates and others (1983b) also related foliage quality to tree stress, particularly water stress. Although foliage quality is not directly simulated by the Prognosis Model, the Budworm Model uses host species (h) and habitat series (b) (Pfister and others 1977) to estimate stress on trees ($FQUALW_{hb}$). The values shown in table 21 were arbitrarily chosen and reflect assumptions that climax species of a habitat series are under greater stress than seral species and that budworms grow larger on trees under greater stress. Users may leave all values of FQUALW at 1.0 (the default condition), use a keyword to set FQUALW to the values shown in table 21, or use a set of keywords to supply other values for FQUALW.

Table 2D—Efficiency of conversion indices for new and older foliage used by default In the Budworm Model to convert foliage consumed (grams of dry weight) into weight gained (grams of dry weight) by female larvae

Host	New foliage ($ECIF_{fh}$)[1]	Older foliage ($ECIBFF_{fh}$)[1]
Douglas-fir	0.0878	0.0659
Grand fir	.0583	.0437
White fir	.0583	.0437
Subalpine fir	.0640	.0480
Engelmann spruce	.0878	.0659

[1] By default, all instars were assumed to have identical ECIF and ECIBFF values for a given combination of host and foliage age.

Source: Unpublished work by Blake and Wagner; personal communication, Michael R. Wagner, School of Forestry, Box 4098, Northern Arizona University, Flagstaff, AZ 86011.

Table 21—Indices for effect of foliage quality on female weight gain ($FQUALW_{hb}$) used by default In the Budworm Model (arbitrarily determined); the same values are used by default for the effect of foliage quality on larval survival ($FQUALS_{hb}$)

	Habitat series (b)				
Host (h)	Douglas-fir	Grand fir	Engelmann spruce	Subalpine fir	Western redcedar
White fir	—	1.2	1.1	1.0	0.9
Douglas-fir	1.2	1.1	1.0	.9	.6
Grand fir	—	1.2	1.1	1.0	.9
Subalpine fir	—	—	1.0	1.2	1.0
Engelmann spruce	—	1.1	1.2	1.0	.9

Defoliation—Two measures of defoliation are provided in the model's output: one accounts only for foliage directly destroyed by larvae (DEFOL, equation 23); the other accounts for foliage destroyed both directly and indirectly through killed or damaged buds (EDEFOL, equation 24). Simulation of killed and damaged buds is described in the following section.

These two measures of defoliation are calculated at the end of each 20 °D step:

$$DEFOL_{chs} = 100.0 \times \left[1.0 - \left(\frac{FNEW_{chs}}{FOLIVE_{chs}}\right)\right] \tag{23}$$

$$EDEFOL_{chs} = 100.0 \times \left[1.0 - \left(\frac{FNEW_{chs}}{POTFOL_{chs}}\right)\right] \tag{24}$$

where: $DEFOL_{chs}$ = percentage of foliage actually produced during 20 °D steps 1, ..., s that has been destroyed by budworm in crown level c of host h,

$EDEFOL_{chs}$ = percentage of the total potential foliage produced during 20 °D steps 1, ..., s that has been destroyed by budworm in crown level c of host h,

$FOLIVE_{chs}$ = amount (grams) of new foliage produced by undamaged buds during 20 °D steps 1, ..., s in crown level c of host h,

$FNEW_{chs}$ = amount (grams) of new foliage produced by undamaged buds during 20 °D steps 1, ..., s in crown level c of host h that remains after budworms feed on foliage, and

$POTFOL_{chs}$ = amount (grams) of new foliage that would have been produced by all buds during 20 °D steps 1, ..., s in crown level c of host h in the absence of budworms.

Killed buds and damaged shoots—Larvae may damage or kill expanding buds, depending on the timing and extent of feeding (Carolin and Coulter 1975, Thomson 1979).

Both percentage of shoot expansion to date ($PEXPAN_{chs}$) and current defoliation to date ($DEFOL_{chs}$) are used to determine the number of buds killed. Because bud killing occurs early in the spring (if at all), the model specifies that buds are killed only if shoot expansion is less than EXPMAX (arbitrarily set to 5 percent by default) and defoliation is greater than DEFMIN (arbitrarily set to 30 percent by default). The proportion of buds killed is calculated using equation 25:

$$BUDKIL_{chs} = \frac{(DEFOL_{chs} - DEFMIN) - (PEXPAN_{chs} - EXPMAX)}{100.0} \qquad (25)$$

where: $BUDKIL_{chs}$ = proportion of buds killed in crown level c of host h during 20 °D step s,
$DEFOL_{chs}$ = percentage of current defoliation calculated in equation 23,
DEFMIN = constant for the minimum amount of defoliation required before buds are directly killed by budworm feeding,
$PEXPAN_{chs}$ = percentage of shoot expansion of all shoots in crown level c of host h during 20 °D step s, calculated in equation 15, and
EXPMAX = maximum percentage of shoot expansion of all shoots, above which buds cannot be killed.

The form of equation 25 was arbitrarily chosen; as long as the shoots are still small-that is, shoot expansion is less than EXPMAX-then percentage of defoliation has much greater influence on bud killing than does shoot expansion.

When a larva consumes a given amount of foliage biomass, the effect is much greater if the shoot has just begun to expand than if the shoot has nearly finished elongation because of the lost "potential" foliage that would have been grown by the expanding shoot. The proportion of potential foliage destroyed is calculated in equation 26:

$$BUDDAM_{chs} = \frac{DESTRY_{chs} \times \left(\frac{100.0 - PEXPAN_{chs}}{100.0} \right)}{BUDS_{chs} \times BUDMAS_{ch}} \qquad (26)$$

where: $BUDDAM_{chs}$ = proportion of total potential foliage that is damaged in crown level c of host h during 20 °D step s,

$DESTRY_{chs}$ = grams of foliage destroyed in crown third c of host h during 20 °D step s, as calculated in equation 19,

$PEXPAN_{chs}$ = percentage of shoot expansion for all shoots in crown level c of host h during 20 °D step s, as calculated in equation 15,

$BUDS_{chs}$ = total number of buds in crown third c of host h during 20 °D step s, and

$BUDMAS_{ch}$ = grams of potential foliage per shoot in crown level c of host h (table 5).

Next, the model assumes that having all shoots defoliated by a given proportion is equivalent to having that same proportion of the shoots killed and the rest not affected. "Damaged" shoots are subtracted from live shoots ($BUDS_{chs}$) and are stored in $BUDSD_{chs}$.

Sources of budworm mortality—Four sources of mortality may be simulated during each 20 °D interval: (1) larval dispersal, (2) natural enemies, (3) foliage quality, and (4) insecticide application. Mortality that occurs as a result of lack of food is handled through larval dispersal mortality.

Larval dispersal—In the model, dispersing larvae come from two sources: larvae that have just emerged from hibernacula in the spring, and larvae that have run out of foliage in their particular foliage cells. During each 20 °D step, larval redistribution and dispersal mortality maybe simulated twice: immediately after emergence from hibernacula, and in between simulation of larval feeding and actions of other mortality factors.

Dispersal is simulated by the following steps:

1. Calculate the number of larvae that disperse onto nonfoliage, such as rocks or ground—all these larvae are assumed to die.
2. Calculate which crown third the remaining larvae will land in based on original crown third and distribution of foliage among crown levels.
3. Within each crown third, distribute "incoming" larvae to host and nonhost foliage according to the proportion of total foliage in the crown level that is represented by each tree species.

Larvae that disperse from a given foliage cell have previously been stored in $DISBW_{chr}$. Those larvae that land in a host foliage cell containing new foliage are stored in $SAVEBW_{chr}$ and later are added directly to $BUGSF_{chrs}$ or $BUGSM_{chrs}$.

The model begins by calculating the number of larvae that do not land on foliage- this number is a function of the amount of foliage (all species) below the original crown level. All these larvae die. All the foliage below each of the nine crown levels is summed ($FBELOW_{cs}$); because larvae are more likely to land in lower crown levels (compared to lateral crown levels), only 50 percent of the lateral foliage is added to $FBELOW_{cs}$. The model assumes that the proportion of larvae that do not land on host or non host foliage ($PROPKL_{cs}$) is a function of the foliage below and lateral to the original crown level as shown in equation 27 and figure 9:

$$PROPKL_{chs} = DASYM + DIFF \times e^{(DISERT \times FBELOW_{chs})} \tag{27}$$

where: $PROPKL_{chs}$ = proportion of budworm larvae that disperse from crown level c of host h and do not land on foliage during 20 °D step s,

DASYM = asymptote (lower limit), value that PROPKL approaches as FBELOW increases,

DISINT = intercept (maximum value) of relation between $PROPKL_{chs}$ and $FBELOW_{chs}$,

DIFF = DISINT – DASYM,

DISERT = an exponential rate coefficient, and

$FBELOW_{chs}$ = grams of foliage of all species below crown level c of host h plus half of the foliage (grams) lateral to crown level c of host h during 20 °D step s.

Default values for DASYM, DISINT, and DISERT have been set arbitrarily to 0.05, 0.75, and -0.000004, respectively (fig. 9). The proportion $PROPKL_{cs}$ is calculated separately for each crown level and is applied uniformly to each larval cohort and to each host species within a crown level. .

Next, $CRWNPR_{c'c}$—the probability that a larva leaving crown level c' will enter crown level c (given equal amounts of foliage in all crown levels) —is calculated:

$$CRWNPR_{c'c} = \frac{CPREF_{fq}}{LEVELS_{c'q}} \tag{28}$$

where: $CRWNPR_{c'c}$ = probability of larvae arriving at crown level c after leaving crown level c',

$CPREF_{fq}$ = proportion *of* larvae of life stage f that will move in direction q (down, lateral, or up), where q is the direction from crown level c' to crown level c, and

$LEVELS_{c'q}$ = the number *of* crown levels in direction q (down, lateral, or up) with respect to crown level c'.

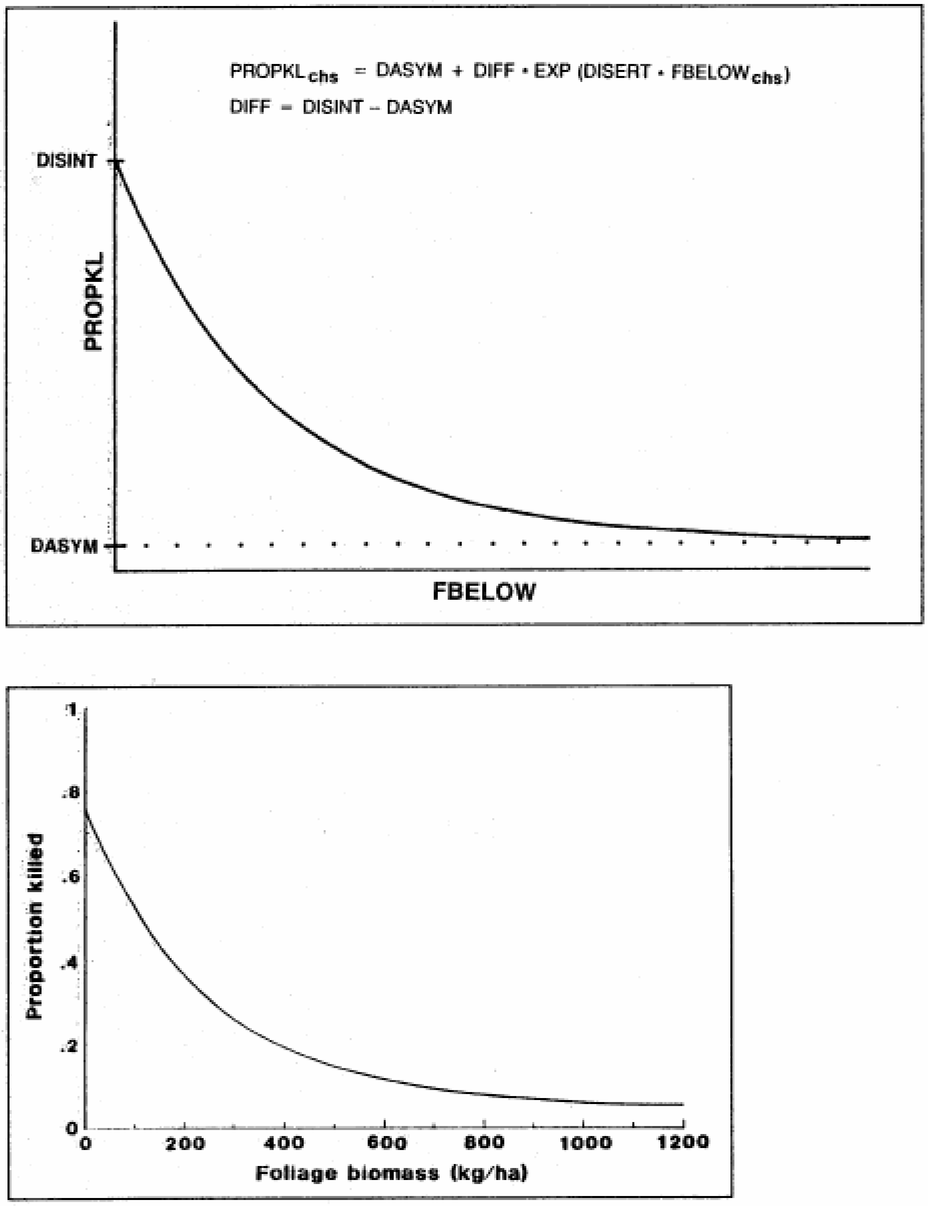

Figure9—The proportion of dispersing larvae that land on nonfoliage is predicted as a function of amount (g) of foliage' below and lateral to original crown level. **A**. The model's general shape and equations. **B**. The model using default parameters.

$CPWNPR_{c'c}$ is a function of the inherent tendency of larvae to move in a given direction (down, lateral, or up; stored in $CPREF_{fq}$) plus the number of crown levels in each direction relative to the original crown level (calculated at the start of the season and stored in $LEVELS_{c'q}$). Larvae are assumed to move with equal probability to different crown levels in the same direction. The default crown preference values ($CPREF_{fq}$) are given in table 22, and an example of model trees used in the following calculations is shown in figure 10.

Table 22—Default values for

	Proportion of larvae that move in a given direction, q		
Instar (f)	Down (q = 1)	Lateral (q = 2)	Up (q = 3)
Second	0.05	0.10	0.85
Third	.10	.20	.70
Fourth	.30	.30	.40
Ffifth	.60	.30	.10
Sixth	.75	.20	.05

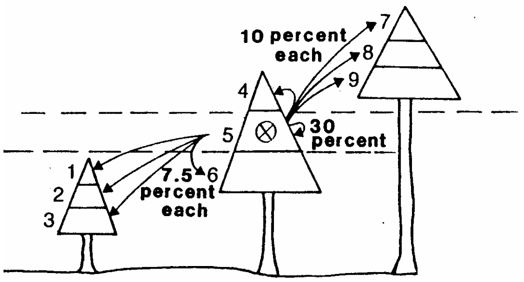

Figure 10—Model trees used in example calculation of CRWNPR for larvae from crown level that land in each of the other crown levels.

These calculations of $CRWNPR_{c'c}$ are for fourth instars dispersing from midcrowns of average trees (c' = 5).

- $CPREF_{fq}$ values for fourth instars (f = IV) are 0.30 (down), 0.30 (lateral), and 0.40 (up).
- 30 percent of larvae from crown level 5 move down to crown levels 1, 2, 3, or 6; $30 \div 4 = 7.5$ percent to each crown level.
- 30 percent of larvae from crown level 5 move laterally; $30 \div 1 = 30$ percent stay in crown level 5.
- 40 percent of larvae from crown level 5 move up to crown levels 4, 7, 8, or 9; $40 \div 4 = 10.0$ percent to each crown level.

For each cohort r, the number of dispersing larvae that land on host foliage in a foliage cell ($SAVEBW_{chr}$) and the number of dispersing larvae that land on nonhost foliage in a foliage cell ($DISPNH_{cr}$) are calculated using equations 29 and 30:

$$\mathrm{SAVEBW}_{chr} = \sum_{c'=1}^{C} \sum_{h'=1}^{H} \mathrm{DISPBW}_{c'h'r} \times [(\mathrm{CRNWT} \times \mathrm{CRWNPR}_{c'c}) + \{(1.0 - \mathrm{CRWNWT}) \times \mathrm{TCLPR}_{c}\}] \times \mathrm{SPECPR}_{ch} \qquad (29)$$

$$\mathrm{DISPBW}_{cr} = \sum_{c'=1}^{C} \sum_{h'=1}^{H} \mathrm{DISPBW}_{c'h'r} + [(\mathrm{CRNWT} \times \mathrm{CRWNPR}_{c'c}) + \{(1.0 - \mathrm{CRWNWT}) \times \mathrm{TCLPR}_{c}\}] \times \mathrm{PROBNH}_{c} \qquad (30)$$

where: SAVEBW_{chr} = total number of budworms in cohort r that land on host foliage in crown level c of host h,

DISPNH_{cr} = total number of budworms in cohort r that land on nonhost foliage in crown level c,

DISPBW_{chr} = total number of budworms in cohort r that will disperse from crown level c of host h,

CRWNWT = proportion that determines weighting of directional preference ($\mathrm{CRWNPR}_{c'c}$) versus proportion of foliage in crown level c (TCLPR_{c}) (default = 0.5),

$\mathrm{CRWNPR}_{c'c}$ = probability of larvae landing on crown level c after leaving crown level c', as calculated in equation 28,

TCLPR_{c} = proportion of total foliage on Budworm Model trees that is found in crown level c, including host and nonhost foliage,

SPECPR_{ch} = proportion of total foliage in crown level c that is host h, and

PROBNH_{c} = proportion of total foliage in crown level c that is nonhost.

For each foliage cell, the destination of larvae that disperse from that cell and land on foliage is a function of the direction those larvae will move (represented by $\mathrm{CRWNPR}_{c'c}$) and the distribution of foliage in the stand canopy (represented by TCLPR_{c}). The weight given CRWNPR is CRWNWT (set to 0.5 by default), and the weight given TCLPR is (1.0 - CRWNWT). Larvae dispersing to crown levels are partitioned to foliage cells according to the proportions of foliage in that crown level that are in specific host species (SPECPR_{ch}) and nonhost species (PROBNH_{c}). The probabilities in SPECPR_{ch} for a given crown level may not sum to 1.0 because of the presence of nonhosts.

If new foliage is (or suitable expanded buds are) present in a crown level of a given host, dispersing larvae are added to the larvae already present. If foliage is not present (that is, buds have not expanded, or new foliage has been destroyed), or if larvae land on nonhost foliage, older larvae may redisperse. The number of times larvae of different instars are allowed to disperse during one 20 °D interval is stored in NDISP_{f}; the model assumes that the greater food reserves of older larvae enable them to redisperse several times. By default, second instars are allowed to disperse once only, third and fourth instars can disperse twice, and fifth and sixth instars can disperse three times. Redispersing larvae repeat the entire dispersal process.

Natural enemies—Four groups of natural enemies are simulated: birds, ants, parasites that attack in the fall, and parasites that attack in the spring. Hypotheses about the effects of augmenting natural enemies—such as releasing parasites or modifying habitats to favor certain predators—may be simulated by changing the values of parameters that determine natural enemy density (for birds) or parameters that determine effects of budworm survival (for ants and parasites). Within a 20 °D interval, the effects of birds and ants are simulated concurrently, followed by the effects of parasites.

Five guilds of birds are modeled: flockers, ground foragers, foliage gleaners, shrub gleaners, and flycatchers. Bird densities and consumption rates are calculated separately for each guild.

The number of budworms eaten per hour per bird (by guild) is estimated first by using equation 31:

$$BIRDHR_g = \frac{SEARCH_g \times SBWPM2_s}{CTERM + e^{-CTERM}} \qquad (31)$$

where:
$CTERM = SEARCH_g * HANDLE_g * SBWPM2_s$,
$BIRDHR_g$ = number of budworms eaten per hour per bird of guild g,
$SEARCH_g$ = searching rate of a bird of guild g in square meters of foliage per hour,
$HANDLE_g$ = handling time of a bird of guild g in hours per budworm eaten, and
$SBWPM2_s$ = standwide average number of budworms per square meter of foliage during 20 °D step s.

Values for $SEARCH_g$ and $HANDLE_g$ are estimated separately for the five bird guilds; default values from Garton[13] are shown in table 23.

The total number of birds per hectare ($BIRDNB_g$) is then calculated in the following equation:

$$BIRDNB_g = \frac{BIRDN_g}{BIRDMS_g} \times OFFSPG \qquad (32)$$

where:
$BIRDNB_g$ = number of birds of guild g per hectare,
$BIRDN_g$ = total adult bird biomass in grams per hectare of guild g,
$BIRDMS_g$ = average biomass in grams of one bird of guild g, and
$OFFSPG$ = offspring multiplier to adjust for offspring of birds.

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[13] Personal communication, Edward O. Garton, Department of Wildlife Resources, University of Idaho, Moscow, ID 83843.

Table 23—Default values of variables used to calculate number of budworms eaten per hectare per bird, plus sample calculations for several budworm densities.

Bird guild	Search rate $(SEARCH_g)$[1]	Handling time $(HANDLE_g)$[2]	Sample calculations: number eaten hour per bird by density			
			0.5/m^2	1.0/m^2	10.0/m^2	30.0/m^2
Ground foragers[3]	6.96	0.325	2.4	2.9	3.1	3.1
Shrub gleaners[3]	10.88	.536	1.8	1.9	1.9	1.9
Flockers	42.29	.061	9.4	11.1	11.4	11.4
Flycatchers[4]	10.88	1.609	0.6	0.6	0.6	0.6
Foliage gleaners	10.88	.536	1.8	1.9	1.9	1.9

[1] Square meters searched per hour per bird of guild g.

[2] Foraging hours per budworm per bird of guild g ($1/HANDLE_g$ = maximum number of budworms consumed per hour).

[3] Search rate and handling time values for foliage gleaners used by default.

[4] Same as footnote 3, except handling time is tripled.

Source: Personal communication, Edward O. Garton, Department of Wildlife Resources, University of Idaho, Moscow, ID 83843.

Table 24—Ranges of crown competition factors (CCF) and mean stand diameter (d.b.h.) for the four categories of stand successional stages used in the Budworm Model

Stand successional stage	Stand description	CCF	D.b.h.	Corresponding stages[1]
			(inches)	
I	Recently disturbed	<30	NA[2]	1-4
II	Mixed tall shrubs & conifers	30<CCF<111	NA[2]	5-6
III	Saplings or poletimber	>111	4<d..b.h.<11	7-8
IV	Mature timber or older	>111	11	9-11

[1] For each stage used by the Budworm Model, the corresponding stand successional stages as defined by Peterson (1982) are listed.

[2] For stages I and II, CCF determines the stage regardless of d.b.h.

Sources: See Peterson (1982) for stand successional stages used in the Prognosis Model. Stand successional stages used in the Budworm Model are by personal communication, Edward O. Garton, Dept. Wildlife Resources, University of Idaho, Moscow, ID 83843.

Garton (see footnote 13) plans to provide equations for predicting total adult bird biomass per stand (by guild) as a function of the Prognosis Model site and stand characteristics. The present version of the Budworm Model uses four stand successional stage categories to predict densities of bird guilds that prey on budworms. These categories are distinguished by two variables that are calculated by the Prognosis Model: crown competition factor and mean stand diameter. These 4 categories are condensed from the 10 categories identified by Peterson (1982), as shown in table 24.

Table 25—Default values for variables used to calculate number of foraging birds per hectare

Bird guild	Mean bird biomass $BIRDMS_g$	Stand successional stage							
		I $BIRDN_g$		II $BIRDN_g$		III $BIRDN_g$		IV $BIRDN_g$	
	g/bird	*g/ha*	*no./ha*	*g/ha*	*no./ha*	*g/ha*	*no./ha*	*g/ha*	*no./ha*
Ground foragers	11.6	26.04	2.24	62.34	5.37	23.84	2.06	19.16	1.65
Shrub gleaners	7.4	0.65	0.088	9.56	1.29	0.836	0.113	0.040	0.00541
Flockers	10.6	1.35	.127	0.262	0.0247	.979	.0924	2.66	.251
Foliage gleaners	7.4	8.24	1.11	19.32	2.61	11.66	1.57	24.03	3.25
Flycatchers	7.4	1.49	.201	3.77	.509	1.59	.215	2.35	.3181

Source: Personal communication, Edward O. Garton, Dept. of Wildlife Resources, University of Idaho, Moscow, ID 83843.

Default values for $BIRDMS_g$ (table 25) and OFFSPG (2.5) are based on work by Garton (see footnote 13). Default values for $BIRDN_g$ by stand successional stage (see footnote 13) are also listed in table 25.

The total number of budworms consumed per hectare by birds of a specific guild during one 20 °D period ($BEAT_{gs}$) is calculated using equation 33:

$$BEAT_{gs} = BIRDNB_g \times BIRDHR_g \times DAYSJ_s \times HPDAY \qquad (33)$$

where: $BEAT_{gs}$ = total number of budworms consumed per hectare by birds of guild g during 20 °D step s,

$BIRDNB_g$ = total number of birds of guild g in the stand, calculated in equation 32,

$BIRDHR_g$ = number of budworms eaten per hour per bird of guild g, as calculated in equation 31,

$DAYSJ_s$ = total number of Julian days in 20 °D step s, and

$HPDAY$ = number of days per day that birds of all guilds may forage (16 hours by default) (see footnote 13).

Total budworm mortality per hectare caused by birds during a 20 °D step is summed for all guilds in $BKILL_s$ and then partitioned to specific foliage cells. Campbell and others (1982 unpubl.) reported that on medium-size, open-grown trees, survival from birds differs between two crown layers (upper crown third versus middle and lower crown thirds), and survival from ants differs between each crown third. The model extrapolates these results from crowns of average-size trees to the entire stand canopy. For bird-caused mortality, one threshold height (BIRDTH, set by default to 10 m to match the boundary between upper and middle crowns of average-size trees) divides the stand's canopy into two layers. A proportion of total budworm mortality per hectare due to birds ($BKILL_s$) occurs in foliage cells above this threshold $BAMORT_1$), and the remainder occurs in cells below the threshold ($BAMORT_2$); the default values for the proportions are set to 0.40 and 0.60, respectively (based on information reported by Campbell and others [1982 unpubl.] and arbitrarily assuming total survival from birds = 0.6). Budworm mortality per hectare within a canopy layer is further partitioned to a specific foliage cell according to the proportion of total budworms in the canopy layer that occurs in that foliage cell. Finally, mortality within a foliage cell per hectare is converted to mortality within a cell of an individual model tree through division by the number of trees per hectare ($BWTPHA_{hz}$). The partitioning of $BKILL_s$ by canopy layer and foliage cell is expressed in equation 34:

$$TBIRDK_{chs} = \frac{BKILL_s \times BAMORT_p \times \left(\frac{BWCELL_{chs}}{BWCAN_{ps}}\right)}{BWTPHA_{hz}} \tag{34}$$

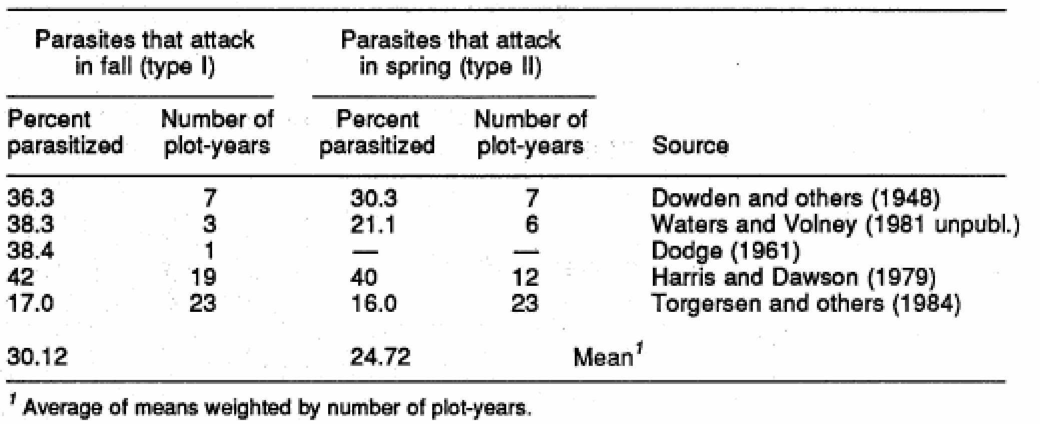
where:

$TBIRDK_{chs}$ = total number of budworms killed by birds in crown level c of host h during 20 °D step s,
$BKILL_s$ = total number of budworms per hectare killed by birds in all guilds in 20 °D step s (that is, the sum of $BEAT_{gs}$ across all guilds),
$BAMORT_p$ = proportion of total bird-induced mortality in the canopy layer p that contains crown level c,
$BWCELL_{chs}$ = total number of budworms in crown level c of host h during 20 °D step s,
$BWCAN_{ps}$ = total number of budworms in canopy layer p that contains crown level c during 20 °D step s, and number
$BWTPHA_{hz}$ = of trees per hectare of host h that are in the size class z that contains crown level c.

The total number of budworms per hectare consumed by ants during one 20 °D interval (TANTKs) is calculated next. Campbell and others (1983) reported standwide survival rates from ants for fourth instar to adult in the Pacific Northwest that range from 0.10 to 0.80 on trees protected from birds (ants were thought to be the main predators acting on the budworms) and from 0.5 to 0.80 on control trees where predation by both birds and ants was allowed. Mortality due to birds and ants during this period was found to be compensatory (Campbell and Torgersen 1983). $SANTS_p$, the survival rate from ants during one 20 °0 period, is estimated for three canopy layers; the default values are 1.0 (top), 0.9968 (middle), and 0.9932 (bottom), corresponding to survival rates of 1.0, 0.90, and 0.80 during the period from second instar through pupae given the default budworm development rates. The two height thresholds for ants are ANTHR1 (separating upper and middle canopies, set to 10 m by default) and ANTHR2 (separating middle and lower canopies, set to 7 m by default). Campbell and others (1984a) found ant predation to be a particularly important source of budworm mortality on Douglas-fir seedlings less than 1 m tall..

Within a foliage cell, birds and ants are assumed to feed on budworms of a particular cohort and sex according to those budworm's relative abundance in the cell. During a given 20 °D period, a proportion (HIOBUG, default arbitrarily set to 0.1) of the budworms present in each cell are assumed to be effectively hidden from predators and parasites. If there are not enough budworms in a cell to "feed" the predators, the number killed by each predator guild is reduced proportionately so that the effectively hidden budworms are not eaten. The number of budworms killed per foliage cell by ants is summed in $ANTKL_{chs}$.

Table 26—Parasitization rates recorded In the literature for western spruce budworm



Parasites that attack in fall (type I)		Parasites that attack in spring (type II)		
Percent parasitized	Number of plot-years	Percent parasitized	Number of plot-years	Source
36.3	7	30.3	7	Dowden and others (1948)
38.3	3	21.1	6	Waters and Volney (1981 unpubl.)
38.4	1	—	—	Dodge (1961)
42	19	40	12	Harris and Dawson (1979)
17.0	23	16.0	23	Torgersen and others (1984)
30.12		24.72		Mean[1]

[1] Average of means weighted by number of plot-years.

The effects of two parasite guilds are simulated next: those that attack in the fall (type I, primarily *Glypta* spp. and *Apanteles* spp.) and those that attack in the spring (type II). Type I parasitism rates have been shown to vary significantly among crown levels for both western (Dodge 1961) and eastern spruce budworms (Jaynes 1954, Miller 1959). Torgersen and others (1984), Waters and Volney (1982 unpubL), and Schmid (1981) generally found no significant differences in parasitism rates among crown levels for either parasite guild. Table 26 summarizes parasitism rates as recorded in the literature for western spruce budworm. The proportions of budworms of a given life stage f that are immobilized by type I and type II parasites during a 20 °D step are stored in PARA1 F_f and PARA2F_f for females and in PARA1 M_f and PARA2Mf for males. The model assumes that immobilization due to type I parasites occurs uniformly during fourth through fifth instars and that immobilization due to type II parasites occurs uniformly during the pupal stage. By default, PARA1F and PARA1 M are set to 0.039 and 0.044, respectively, for fourth through fifth instars, and PARA2F and PARA2M are both set to 0.031 for pupae; these mortality rates per 20 °D step correspond to mortality rates of 30 percent for fourth through fifth instars for type I parasites and 25 percent for pupae for type II parasites (see table 26), given the default budworm-development rates. A small proportion (HIDBUG) of the budworms present during a given 20 °D period are considered effectively hidden from parasites.

Insecticides—An insecticide may be applied when either a given percentage of shoot elongation or a given mean budworm instar has been reached (default values are 30-percent elongation and fourth instar)_ When several stands are simulated in parallel, the first stand serves as the indicator, that is, host or budworm development in that stand is used to trigger insecticide application. Users may specify that certain stands be exempt from spraying or that a minimum waiting period must elapse before a stand may be resprayed. A minimum budworm density and a minimum defoliation in the previous year that must be reached before an insecticide is applied may also be specified (both minimums set to 0 by default). The proportion of budworms killed by the insecticide (SPRAYE$_{fx}$) can be specified for each sex and life stage. The default values for SPRAYE$_{fx}$ are set to 0.91 for all instars and both sexes; this value was calculated using information provided by Force and others (1982) and assuming that budworm populations tolerant to carbaryl were exposed to 70.0 g/ha of this insecticide. Models developed by Dumbauld and others (1980) and Force and others (1982) are available to estimate insecticide efficacy by instar based on insecticide, dosage, budworm population genetics, application techniques, and meteorological contititions.

Foliage quality—Cates and others (1983b) have shown that foliage quality (particularly terpene composition and concentration) may affect budworm survival; however, at present we cannot predict foliage quality from site or stand characteristics normally measured during forest inventory. An index to foliage quality ($FQUALS_{hb}$) that uses host species and habitat series (Pfister and others 1977) has been arbitrarily defined using the same assumptions and default values that were used for $FQUALW_{hb}$ (table 21). Budworm survival is assumed to be higher on trees under greater stress, such as trees on drier habitat series and hosts that are the climax species, for a habitat series. Budworm survival in a given foliage cell is adjusted to account for foliage quality by multiplying the number of surviving budworms by the foliage quality index ($FQUALS_{hb}$).

Adult Emergence

After an surviving budworms have emerged from pupae, several summary variables are_ calculated. The total number of emerged females in each foliage cell is multiplied by. the proportion that will successfully mate (PMATED, set by default to 1.0) and the. number of trees per hectare represented by a given Budworm Model tree ($BWTPHA_{hz}$) to predict the total number of gravid females produced per hectare (FEMTOTI. The effects of mating disruption through pheromone application may be simulated by adjusting PMATED. Total host foliage in each cell is also summed and multiplied by $BWTPHA_{hz}$ to determine the total amount (grams) of host foliage per hectare (HFOLPH).

The total number of potential eggs per hectare in each crown level is calculated in equation 35 and summed for the stand in equation 36:

$$EGGPOT_{chr} = BWTPHA_{hz} \times BUGSF_{chrs} \times [EGGN1_{h} + (EGGN2_{h} \times WEIGHT_{chrs} \times FRESHC_{h})] \qquad (35)$$

$$POTEGG = \sum_{c=1}^{C} \sum_{h=1}^{H} \sum_{r=1}^{R} EGGPOT_{chr} \qquad (36)$$

where: $EGGPOT_{chr}$ = number of potential eggs produced by budworms of cohort r in crown level c of host h,

$BWTPHA_{hz}$ = number of budworm trees per hectare of tree size z by host h,

$BUGSF_{chrs}$ = number of surviving female budworm pupae of cohort r in crown level c of host h,

$EGGN1_{h}$ = regression intercept parameter for relation of female pupal fresh weight to number of eggs per female, by host h,

$EGG2_{h}$ = regression slope parameter for relation of female pupal fresh weight to number of eggs per female, by host h,

$WEIGHT_{chrs}$ = average dry weight of a single female budworm pupa of cohort r in crown level c of host h, calculated in equation 22,
$FRESHC_h$ = factor used to convert female dry pupal weight to fresh pupal weight by host h, and
POTEGG = total number of potential eggs in the stand at the end of the year.

Data from Wagner (see footnote 10) were used to develop the conversion factor ($FRESHC_h$, table 27) for budworm dry pupal weight (accumulated during the feeding season in $WEIGHT_{chrs}$) to budworm fresh pupal weight. Default values for $EGGN1_h$ and EGGN2h (table 27), assuming an 8-day pupal period, were taken from Kirkbride and Wagner (1983 unpubl.); white fir values are used for grand fir.

Table 27—Default values for variables used to calculate potential number of eggs per female. ($FRESHC_h$ converts from dry to fresh [wet] pupal weight; EGGN1 hand $EGGN2_h$ are the regression Intercept and slope, respectively, for

Host (h)	$FRESHC_h$	$EGGN1_h$	$EGGN2_h$
Douglas-fir	3.54	.88	1,911
White fir	4.02	2.92	2,129
Subalpine fir	3.59	22.0	1,746
Engelmann spruce	3.84	–8.56	2,293

Source: FRESHCh by personal communication from Michael R. Wagner, School of Forestry, Box 4098, Northern Arizona University, Flagstaff, AZ 86011;
EGGN1 and EGGN2 from Kirkbride and Wagner (1983 unpubL).

Adult Dispersal and Oviposition (BWFLY)

Subroutine BWFLY is the part of the Budworm Model that simulates adult mortality, dispersal, and oviposition. After budworm feeding and survival have been simulated in each stand for a given year, the Prognosis Model (or the stand-alone driver) calls BWFLY and passes the number of gravid females (ADULTF), number of potential eggs (PEGGS), and grams of host foliage (HFOLPH) per hectare for each stand.

Two options are available for adult dispersal in BWFLY:
1. Net dispersal.
2. Among-stand dispersal.

If only one stand is being simulated (or if specified by the user), a constant net dispersal rate is applied; this rate represents the net effects of immigration, emigration, and mortality during flight. The number of potential eggs in the stand of origin is multiplied by a constant rate (DISNET, arbitrarily set to 0.8 by default) to calculate the number of eggs laid in the stand. The total number of eggs laid per hectare in the stand (EGGNEW) is then stored for use by the Budworm Model during the next budworm generation.

Under the second option, the total potential eggs per stand is decreased to reflect adult mortality occurring before oviposition from causes such as incomplete wing expansion or predation by birds. The mortality rate for this period, PREFLY, arbitrarily set to 0.2 by default, is used as shown in equation 37:

$$\mathrm{PEGGS} = \mathrm{PEGGS} \times (1.0 - \mathrm{PREFLY}) \qquad (37)$$

where: PEGGS = number of potential eggs produced in a stand, and
PREFLY = rate of adult mortality before oviposition.

The number of eggs that females lay in their stand of origin is calculated next. This may be done in either of two ways (selected by user):
a. Each female lays one egg mass (default).
b. Each female lays a given proportion of her total eggs.

The number of eggs per mass (EPMASS) may be set by the user (the default value is 41.7; see table 1). Sanders and Lucuik (1975) note that well-fed female budworms laid one egg mass prior to long-distance flight. For option 2b, the proportion of eggs laid in the stand of origin (ELAID) is set to 0.5 by default based on the observation of Greenbank and others (1980) that females leaving stands carry approximately 50 percent of their total egg complement.

The Budworm Model next uses the mean distance traveled by female moths (RANGE, default arbitrarily set to 25 km) to determine which stands are within the range of budworms dispersing from the current stand (the "candidate" stands).

The model assumes that adult mortality during dispersal is a function of average total host foliage per hectare over all stands within dispersing range. The proportion of potential eggs that have survived preflight mortality (calculated in equation 37) and that are later killed during dispersal is calculated as shown in equation 38:

$$\mathrm{ADKILL} = \mathrm{FLYASY} + \mathrm{FLYDIF} \times e^{(\mathrm{FLYERT} \times \mathrm{HOSTPH})} \qquad (38)$$

where: ADKILL = proportion of potential eggs killed during dispersal,
FLYASY = asymptote (lower limit), the value that ADKILL approaches as HOSTPH increases,
FLYINT = intercept (maximum value) of the relation between ADKILL and HOSTPH,
FLYDIF = FLYINT – FLYASY,
FLYERT = an exponential rate coefficient, and
HOSTPH = mean host foliage (square meters per hectare) for all stands within dispersing range.

Default values for FLYASV, FLYINT, and FLYERT have been arbitrarily set to 0.20, 0.75, and -0.0002, respectively, for all stands (fig. 11).

Surviving eggs are distributed among the candidate stands according to the proportion of host foliage in each stand (relative to the total host foliage among all the candidate stands). Note that some eggs laid by dispersing females will be laid in their stand of origin (because that stand is automatically considered a candidate stand).

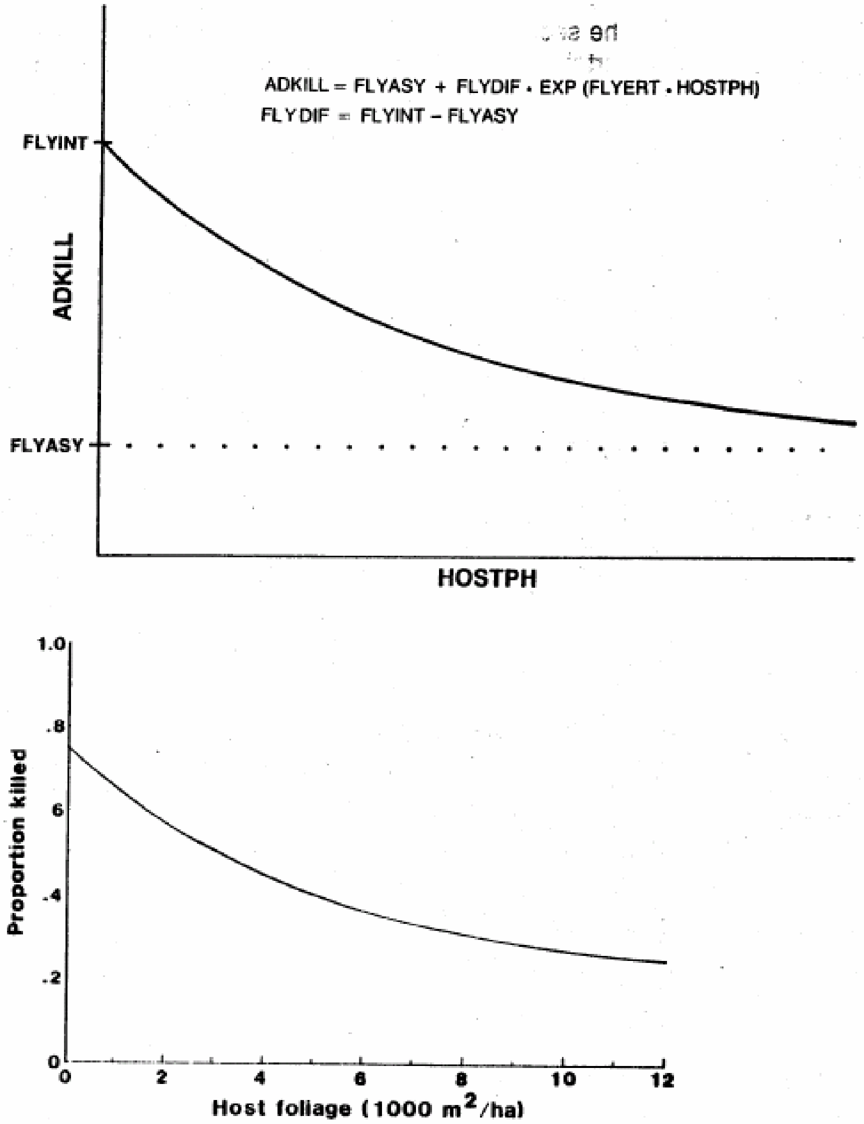


Figure 11—Predicting the proportion of adult female moths that die during dispersal as a function of mean host foliage present (m^2/ha). A. The model's general shape and equations. B. The model using default parameters.

After dispersal is completed, each stand contains a pool of eggs that may include some eggs laid by females in their stand of origin and some laid by dispersing females. Total eggs laid per hectare (EGGNEW) in each stand is used by the Budworm Model at the start of the next budworm generation.

Output From the Budworm Model

All output from the Budworm Model is optional. A keyword system allows users to select one or more of the options described below.

The initial conditions table provides the user with a description of each model tree in the stand (number of actual trees that each model tree represents, crown dimensions, foliage and egg distributions). This table will be produced once for each stand at the beginning of a stand-alone Budworm Model run and once at the beginning of each Prognosis cycle when the Prognosis-Budworm Model is used.

Yearly summaries of budworm activity in each stand are available for two periods: egg through adult emergence (summarizing events simulated by BWMOD) and adult dispersal and oviposition (summarizing events simulated by BYFL V). Output for the first period includes (for each host, tree height class, and crown third) initial egg densities; fourth-instar densities and percentage of shoot elongation at fourth instar; percentage of defoliation of new foliage at the end of the season; number of emerging adults and proportion that are females; and the proportion of total budworm mortality by cause-dispersal, birds, ants, parasites that attack in the fall, parasites that attack in the spring, foliage quality, or insecticide spray. Annual summary adult-dispersal output for each stand includes: number of potential eggs, number of eggs laid before long-distance flight, number of eggs killed when dispersing adults perish, and total number of eggs laid per stand (those laid by females originating in the stand plus those laid by immigrating females).

Foliage summaries can be produced twice for each year; the spring table gives foliage as it would appear if no budworm feeding took place that year and the fall table gives the actual foliage remaining after defoliation has taken place. Each table contains one line for each foliage cell (crown third, model tree, or average tree) and gives the same three statistics for new foliage (current year's growth), 1-year-old foliage, remaining foliage (3 years old or older), and total foliage: (1) summer biomass, (2) percentage of defoliation, and (3) adjusted potential (this gives the effects of previous defoliation on production of new foliage). Two-year-old foliage statistics can be obtained through subtraction.

Additional detailed output that summarizes foliage status or budworm status at the end of every 20 °D interval can be printed for ea._ stand during each year of the simulation. This option should be used with caution, for if many years or many stands are simulated, the amount of output produced could be overwhelming. The foliage status option includes current Julian day; degree-days accumulated to date; budworm density and average development; percentage of shoot elongation; number of live, damaged, and killed buds; amounts of current, 1-year-old, 2-year-old, and older foliage; and percentage of defoliation. The budworm status option provides current Julian day, degree-days accumulated to date, percentage of defoliation and percentage of shoot elongation, mean budworm development, budworm density, and numbers of males and females in each budworm life stage (second through sixth instars, pupae, and adults). For both options, two estimates of budworm density (per square meter and per 100 buds) and defoliation (percentage of total potential foliage, including damaged and killed shoots, and percentage of live foliage, excluding damaged and killed shoots) are provided.

Damage caused by budworm defoliation is summarized for each model tree. The proportion of expected diameter and height growth and the probabilities of tree mortality are given. This information is used to distribute growth and mortality effects to the Prognosis Model trees. At present, users specify top-kill rates based on local history and experience. Research is underway to provide the data necessary to build more broadly based and more accurate mortality models and to build top-kill models.

Research and Development Needs

Although the structure and content of the Budworm Model have been carefully reviewed by both researchers and users, the model's predictions have not been extensively tested against real-life data. We hope that this publication and the user's guide that is being developed will encourage scientists and managers to run this model over a wide range of conditions and compare the model's predictions with their own data or their own experiences. Through this process, sections of the model that perform poorly can be identified and improved.

The Budworm Model has been designed so that western larch may be included as a budworm host; however, the lack of quantitative information about many aspects of larch biology (phenology, biomass production) has forced us to model larch as a nonhost species.

We expect that the Budworm Model will be revised and upated as model testing continues and additional data become available. Examples of processes that may warrant inclusion in the model:

- Propensity of some larvae to pupate (and produce smaller adults) rather than feed on older foliage when there is not enough new foliage (suggested by Thomson 1979).

- Effects of chilling requirements on the phenology of hosts (reviewed by Lavender 1981) and budworm (Schmidt 1977).

- Effects of unusually warm weather in fall, winter, or early spring, which may lead to poor budworm survival (Evenden 1937 unpubl., McMorran 1973, Thomson 1979) .

- Influence of vegetative and reproductive bud phenology on larval survival.

- Larval mortality caused by pathogens—factors that have had minor importance in the Pacific Northwest and the Southwest but variable effects in the northernmost range of the budworm (Dowden and others 1948, Harris and Dawson 1979, Sterner and Davidson 1983).

- Mortality of pupae caused by cannibalism by larvae (McKnight 1971, Thomson 1957, and Volney and Waters 1984 unpubl.).

- Effects of weather on adult dispersal and oviposition (Sanders and others 1978).

Extensive testing will probably reveal certain sections of the model or specific processes that are treated in greater detail than warranted by their effects on long-term model predictions. If so, a revised, more computationally efficient version would probably be of greater use to forest managers. Support for the more detailed, expanded version should continue, however, for use by researchers studying the processes affecting budworm-host dynamics.

Acknowledgments

We thank Alan J. Thomson, Pacific Forest Research Centre, Victoria, BC, for his contributions to the Budworm Model. Our appreciation also goes to P.W. Thomas and Jim Bertling of the University of Idaho for programming assistance. We thank. Robert W. Campbell, Clinton E. Carlson, Melvin E. McKnight, Alan J. Thomson, and Torolf R. Torgersen for their critical reviews of an earlier draft of this manuscript.

Work leading to this publication was funded by the Canada/United States Spruce Budworms Program-West, Pacific Northwest Forest and Range Experiment Station, Portland, OR, through cooperative Agreement PNW-83-252 to the College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID.

Literature Cited

Allen, George S.; Owens, John N. 1972. The life history of Douglas-fir. Ottawa, ON; Environment Canada, Canadian Forestry Service. 139 p.

Barry, Roger G. 1981. Mountain weather and climate. London: Metheun. 313 p.

Beckwith, R.C. 1978. Foliage damage. In: Brookes, Martha H.; Stark, R.W.; Campbell, Robert W., eds. The Douglas-fir tussock moth: a synthesis. Tech. Bull. 1585. Washington, DC: U.S. Department of Agriculture: 64-66.

Beckwith, R.C.; Kemp, W.P. 1984. Shoot growth models for Douglas-fir and grand fir. Forest Science. 30(30): 743-746.

Blais, J.R. 1957. Spruce budworm development in the Gaspe Peninsula in 1956, Quebec. Bi-monthly progress report. Ottawa, ON: Department of Agriculture Canada, Science Service—Forest Biology Division; 13(1): 1-2.

Blais, J.R. 1981. Effects of late spring frosts in 1980 on spruce budworm and its host. trees in Laurentian Park region of Quebec. Res. Notes. Ste. Foy, PQ: Environment Canada, Canadian Forestry Service; 1 (3); 16-17.

Blake, Elizabeth A.; Wagner, Michael R 1984. Effect of sex and instar on food consumption, nutritional indices, and foliage wasting by the western spruce budworm, *Choristoneura occidentalis.* Environmental Entomology. 13: 1634-1638.

Brlx, H. 1967. An analysis of dry matter production of Douglas-fir seedlings in relaion to temperature and lightintensity. Canadian Journal of Botany. 45: 2063-2072.

Bruhn, J.A. 1980. A stochastic model for the simulation of daily weather. Protection Ecology. 2: 199-208.

Bruhn, J.A.; Fry, W.E.; Flck, G.W. 1979. WEATHER: a stochastic simulation model of daily weather: user's manual. Ithaca, NY: Cornell University, New York State College of Agriculture and Life Sciences, Department of Plant Pathology. Mimeo 79-2.

Buchanan, W.D. 1945. Observations on the spruce budworm in Colorado and the Medicine Bow National Forest in Wyoming 1945. Fort Collins, CO: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine. 5 p.

Buchanan, W.D. 1948. Spruce budworm progress report 1947_ Fort Collins, CO: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine. 20 p.

Campbell, Robert K.; Sugano, Albert I. 1979'. Genecology of bud-burst phenology in Douglas-fir: response to flushing temperature and chilling. Botanical Gazette. 140(2): 223-231.

Campbell, Robert W. 1987. Population dynamics. In: Brookes, Martha H.; Campbell, Robert W.; Colbert, J.J.; Mitchell, Russel G.; Stark, R.W., tech. coords. Western spruce bodworm. Tech. Bull. 1694. Washington, DC: U.S. Department of Agriculture: 71-88.

Campbell, Robert W.; Carlson, Clinton E.; Theroux, Leon J.; Egan.; Thomas H. 1984a. Some effects of predaceous birds and ants on the western spruce budworm on conifer seedlings. Res. Pap. PNW-315. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Campbell, Robert W.; Torgersen, Torolf R.1983. Compensatory mortality in defoliator population dynamics. Environmental Entomology. 12(3): 630-632.

Campbell, Robert W.; Torgersen, Torolf R.; Srivastava, Nilima. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. Forest Science. 29(4): 779-790.

Campbell, Robert W.; Torgersen, Torolf R.; Srivastava, Nilima. 1984b. Number, size of eggs in egg masses of the western spruce budworm (Lepidoptera: Tortricidae). Canadian Entomologist. 116(5): 657-661.

Campbell, Robert W.; Torgersen, Torolf A.; Srivastava, Nilima; Beckwith, Roy C. 1984c. Patterns of occurrence of the western spruce budworm (Lepidoptera: Tortricidae): larvae, pupae and pupal exuviae, and egg masses. Environmental Entomology. 13: 522-530.

Carolin, V.M.; Coulter, W.K. 1972. Sampling populations of western spruce budworm and predicting defoliation on Douglas-fir in eastern Oregon. Res. Pap. PNW-149. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 38 p.

Carolin, V.M.; Coulter, W.K. 1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. Res. Pap. PNW-195. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 16 p.

Cates, Rex G.; Redak, R.A.; Henderson, C.B. 1983a. Natural product defensive chemistry of Douglas-fir, western spruce budworm success, and forest management practices. Zeitschrift Angewandte Entomologie. 96: 173-182.

Cates, Rex G.; Redak, Richard A.; Henderson, Colin B. 1983b. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. In: Hedin, Paul A., ed. Mechanisms of plant resistance to insects. ACS Sympos. Ser. 208. Washington, DC: American Chemical Society: 3-19.

Cleary, B.D.; Waring, A.H. 1969. Temperature: collection of data and its analysis . for the interpretation of plant growth and .distribution. Canadian Journal of Botany. 47: 167-173.

Colbert, J.J.; Sheehan, Katharine; Crookston, Nicholas L. 1983. Supporting decisions on western spruce budworm in forest management using simulation models. In: Lauenroth, William K.; Skogerboe, Gaylord V.; Flug, Marshall, eds. Analysis of ecological systems: state-of-the-art in ecological modeling. New York: Elsevier Scientific Publishing Company: 99-105.

Crookston, Nicholas L. 1985. Forecasting growth and yield of budworm-infested forests. Part II: Western North America and summary. In: Sanders, C.J.; Stark, R.W.; Mullins, E.J.; Murphy, J., eds. Recent advances in spruce budworm research: proceedings of the CAN USA spruce budworms research symposium; 1984 September 16-20; Bangor, ME. Ottawa, ON: Canadian Forestry Service: 214-230.

Dodge, H.A. 1961. Parasitism of spruce budworm by *Glypta* and *Apanteles* at different crown heights in Montana. Canadian Entomologist. 93(3): 222-228.

Dowden, P.B.; Buchanan, W.D.; Carolin, V.M. 1948. Natural-control factors affecting the spruce budworm. Journal of Economic Entomology. 41 (3): 457-464.

Dumbauld, R.K.; Bjorkland, J.R.; Saterlle, S.F. 1980. Computer models for predicting aircraft spray dispersion and deposition above and within a forest canopy: user's manual for the FSCBG computer program. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Methods Application Group. 270 p.

Embree, D.G. 1965. The population dynamics of the winter moth in Nova Scotia, 1954-1962. Memoirs of the Entomological Society of Canada. 46.

Everson, D.O.; Amos, D.E.;Rice K.E. 1976. Growing degree-day systems for Idaho. Bull. 551. Moscow, ID: Idaho Agricultural Experiment Station, University of Idaho. 16 p.

Fellin, David G.; Schmidt, Wyman C. 1973. Frost reduces western spruce budworm populations and damage in Montana. Agricultural Meteorology. 11 (2): 277-283.

Force, J.E.; Robertson, J.L.; Stock, M.W.; Williams, C.B. 1982. A probability model of insecticide efficacy for western spruce budworm (*Lepidoptera: Tortricidae*) and Douglas-fir tussock moth (*Lepidoptera: Lymantriidae*). Environmental Entomology. 11(6): 1170-1177.

Franklin, Jerry F.; Ritchie, Gary A. 1970. Phenology of cone and shoot development of noble fir and some associated true firs. Forest Science. 16(3): 356-364.

Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. 1980. Spruce budworm (*Lepidoptera: Tortricidae*) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Memoirs of the Entomological Society of Canada. 110.49p.

Harris, J.W.E.; Dawson, A.F. 1979. Parasitoids of the western spruce budworm, *Choristoneura occidentalis* (*Lepidoptera: Tortricidae*), in British Columbia. Journal of the Entomological Society of British Columbia. 76: 30-38.

Harris, J.W.E.; Dawson, A.F. 1982. Estimating number of western spruce budworm eggs from egg mass measurements in British Columbia. Canadian Entomologist. 114: 643-645.

Henson, W.R. 1948. Influence of meteorological factors in behaviour of the spruce budworm. Bi-Monthly Progress Report. Ottawa, ON: Department of Agriculture Canada, Forest Investigations; 4(6): 2.

Ives, W.G.H. 1973. Heat units and outbreaks of the forest tent caterpillar *Malacosoma disstria* (*Lepidoptera: Lasiocampidae*). Canadian Entomologist. 105: 529-543.

Jaynes, H.A. 1954. Parasitization of spruce budworm larvae at different crown heights by *Apanteles* and *Glypta.* Journal of Economic Entomology. 47(2): 355-356.

Kemp, William Paul. 1983. The influence of climate, phenology, and soils on western spruce budworm defoliation. Moscow, ID: University of Idaho, College of Forestry, Wildlife, and Range Sciences. 143 p. Ph.D. dissertation.

Kemp, William P.; Everson, Dale O.; Wellington, W.G. 1985. Regional climatic patterns and western spruce budworm outbreaks. Tech. Bull. 1693. Washington, DC: U.S. Department of Agriculture. 31 p.

Lavender, D.P. 1981. Environment and shoot growth of woody plants. Res. Pap. 45. Corvallis, OR: Oregon State University, School of Forestry, Forest Research Laboratory. 45 p.

Libby, W.J.; Islk, Kanl; King, James P. 1980. Variation in flushing time among white fir population samples. Annales forestales anali za sumarstvo. 8/6: 123-138.

Logan, Jesse A.; Hilbert, David W. 1983. Modeling the effects of temperature on arthropod population systems. In: Lauenroth, William K.; Skogerboe, Gaylord V.; Flug, Marshall, eds. Analysis of ecological systems: state-of-the-art in ecological modelling. New York: Elsevier Scientific Publishing Company: 113-122.

Lyon, Robert L.; Richmond, C.E.; Robertson, J.L.; Lucas, B.A. 1972. Rearing diapause and diapause-free western spruce budworm *(Choristoneura occidentalis)* (Lepidoptera: Tortricidae) on artificial diet. Canadian Entomologist. 104(3): 417-426.

McGugan, Blair M. 1954. Needle-mining habits and larval instars of the spruce budworm. Canadian Entomologist. 86(10): 439-454.

McKnight, M.E. 1969a. Distribution of hibernating larvae of the western spruce budworm, *Choristoneura occidentalis,* on Douglas-fir in Colorado. Journal of Economic Entomology. 62(1): 139-142.

McKnight, M.E. 1969b. Estimating numbers of eggs in western spruce budworm egg masses. Res. Note RM-146. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.

McKnight, M.E. 1971. Natural mortality of the western spruce budworm, *Choristoneura occidentalis,* in Colorado. Res. Pap. RM-81. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 12 p.

McMorran, Arlene. 1973. Effects of pre-storage treatment on survival of diapausing larvae of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist. 105(7): 1005-1009.

Miller, C.A. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. Canadian Journal of Zoology. 36: 409-422.

Miller, C.A. 1959. The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.) and the parasite *Apanteles fumiferanae* Vier. Canadian Entomologist. 91 (8): 457-477.

Miller, C.A. 1977. The feeding impact of spruce budworm on balsam fir. Canadian Journal of Forest Research. 7(1): 76-84.

Miller, C.A.; Eldt, D.C.; McDougall, G.A. 1971. Predicting spruce budworm development. Bi-Monthly Research Note.. Ottawa, ON: Canadian Department of Forestry; 27(5): 33-34.

Morris, R.F. 1951. The effects of flowering on the foliage production and growth of balsam fir. Forestry Chronicle. 27: 40-57.

Owens, John N.; Smith, Frank H. 1964. The initiation and early development of the seed cone of Douglas-fir. Canadian Journal of Botany. 42: 1031-1047.

Owens, John N.; Smith, Frank H. 1965. Development of the seed cone of Douglas-fir following dormancy. Canadian Journal of Botany. 43: 317-332.

Peterson, S.R. 1982. A preliminary survey of forest bird communities in northern Idaho. Northwest Science. 56(4): 287-298.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-134. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Prebble, M.L. 1945. Spruce budworm. Ontario. Bi-Monthly Progress Report. Ottawa, ON: Department of Agriculture Canada, Science Service—Forest Biology Division; 1(4):2.

Regniere, Jacques. 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). Canadian Entomologist. 114: 811-825.

Regniere, Jacques. 1983. An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist. 115: 1371-1382.

Running, Steven W. 1981. The influence of microclimate on forest productivity: a system to predict the biophysical site quality of forest land. In: Computer techniques and meteorological data applied to problems of agriculture and forestry: a workshop; 1981 March 30-31; [place of meeting unknown]. Boston, MA: American Meteorological Society: 297-316.

Running, Steven W.; Hungerford, Roger D. 1983. Spatial extrapolation of meteorological data for ecosystem modeling applications. In: Proceedings, 16th conference on agriculture and forest meteorology; 1983 April 26-28; Fort Collins, CO. Boston, MA: American Meteorology Society: 192-195.

Sanders, C.J. 1975. Factors affecting adult emergence and mating behavior of the e.astero spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Canadian Entomologist. 107(4): 967-978.

Sanders, C.J.; Lucuik, G.S. 1975. Effects of photoperiod and size on flight activity and oviposition in the eastern spruce budworm (Lepidoptera: Tortricidae). Canadian Entomologist. 107(12): 1289-1299.

Sanders, C.J.; Wallace, D.R.; Lucuik, G.S. 1978. Flight activity of female eastern spruce budworm (Lepidoptera: Tortricidae) at constant temperatures in the laboratory. Canadian Entomologist. 110(6): 627-632.

Schmid, J.M. 1981. Distribution of western spruce budworm (Lepidoptera: Tortricidae) insect parasites in the crowns of host trees. Canadian Entomologist. 113: 1101-1106.

Schmid, J.M.; Farrar P.A. 1982. Distribution of western spruce budworm egg masses on white fir and Douglas-fir. Res. Pap. RM-241. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Schmid, J.M; Morton, M.B. 1981. Distribution of foliage on open-grown white fir and Douglas-fir in northern New Mexico, U.S.A. Canadian Journal of Forest Research. 11(3): 615-619.

Schmidt, Fred H. 1977. Differences in thermal requirements for diapause termination in two western *Choristoneura* spp. (Lepidoptera: Tortricidae). Canadian Entomologist. 109: 1469-1474.

Sheehan, Katharine; Crookston, Nicholas L.; Kemp, William P.; Colbert, J.J. 1987. Modeling budworm and its hosts. In: Brookes, Martha H.; Campbell, Robert W.; Colbert, J.J.; Mitchell, Russel G.; Stark, R.W., tech. coords. Western spruce budworm. Tech. Bull. 1694. Washington, DC: U.S. Department of Agriculture: 117-136.

Shepherd, R.F. 1958. Factors controlling the internal temperatures of spruce budworm larvae, *Choristoneura fumiferana* (Clem.). Canadian Journal of Zoology. 36: 779-786.

Shepherd, R.F. 1961. A comparison of the developmental rates of one- and two-year cycle spruce budworm. Canadian Entomologist. 93(9): 764-771.

Silver, G.T. 1962. The distribution of Douglas-fir foliage by age. Forestry Chronicle. 38: 433-438.

Sorensen, Frank C.; Campbell, Robert K. 1978. Comparative roles of soil and air temperatures in the timing of spring bud flush in seedling Douglas-fir. Canadian Journal of Botany. 56(18): 2307-2308.

Stage, Albert R. 1973. Prognosis model for stand development. Res. Pap. INT-137. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 32 p.

Sterner, T.E.; Davidson, A.G. 1983. forest insect and disease conditions in Canada 1982. Ottawa, ON: Environment Canada, Canadian Forestry Service. 58 p.

Stinner, R.E.; Gutierrez, A.P.; Butler, G.D. 1974. An algorithm for temperature-dependent growth rate simulation. Canadian Entomologist. 106: 519-524.

Terrell, T.T. 1959. Sampling populations of overwintering spruce budworm in the northern Rocky Mountain region. Res. Note INT-61. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.

Thomson, A.J. 1979. Evaluation of key biological relationships of western budworm and its host trees. BC-X-186. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre. 19 p.

Thomson, A.J.; Moncrleff, S.M. 1982. Prediction of bud burst in Douglas-fir by degree-day accumulation. Canadian Journal of Forest Research. 12(2): 448-452.

Thomson, H.M. 1957. A note on the predation of spruce budworm pupae, Ontario. Bi-Monthly Progress Report. Ottawa, ON: Department of Agriculture Canada, Science Service-Forest Biology Division. 13(4): 2.

Torgersen, Torolf R.; Campbell, Robert W.; Srivastava, Nllima; Beckwith, Roy C. 1984. The role of parasites in the population dynamics of the western spruce budworm (Lepidoptera: Tortricidae) in the Northwest. Environmental Entomology. 13: 568-573.

Volney, W. Jan A.; Waters, William E.; Akers, R. Patrick; Llebhold, Andrew M. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Canadian Entomologist. 115: 199-209.

Wagg, J.W. Bruce. 1958. Environmental factors affecting spruce budworm growth. Res. Bull. 11. Oregon State Board of Forestry. 27 p.

Wagner, Michael R.; Blake, Elizabeth A. 1983. Western spruce budworm consumption—effects of host species and foliage chemistry. In: Proceedings, forest defoliator-host interactions: a comparison between gypsy moth and spruce budworms; 1983 April 5-7; New Haven CT. Gen. Tech. Rep. NE-85. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 49-54.

Wang, Jen Yu. 1960. A critique of the heat unit approach to plant response studies. Ecology. 41: 785-790.

Wareing, P.F.; Saunders, P.F. 1971. Hormones and dormancy. Annual Review of Plant Physiology. 22: 261-288.

Washburn, R.I.; Brickell, J.E. 1973. Western spruce budworm egg mass dimensions-an influence on population estimates. Res. Pap. INT-138. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 20 p.

Wellington, W.G. 1949. The effects of temperature and moisture upon the behavior of the spruce budworm, *Choristoneura fumiferana* (Clemens) Lepidoptera: Tortricidae). I: The relative importance of graded temperatures and rates of evaporation in producing aggregations of larvae. Science in Agriculture. 29: 201-229.

Wellington, W.G. 1950. Effects of radiation on the temperatures of insectan habitats. Science in Agriculture. 30(5): 209-234.

Wellington, W.G.; Henson, W.R. 1947. Notes on the effects of physical factors on the spruce budworm,. *Choristoneura fumiferana* (Clem.). Canadian Entomologist. 79(9/10): 168-170.

Wickman, Boyd E. 1976a. Douglas-fir tussock moth egg hatch and larval development in relation to phenology of grand fir and Douglas-fir in northeastern Oregon. Res. Pap. PNW-206. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 13 p.

Wickman, Boyd E. 1976b. Phenology of white fir and Douglas-fir tussock moth egg hatch and larval development in California. Environmental Entomology. 5(2): 316-320.

Wickman, Boyd E. 1977. Douglas-fir tussock moth egg hatch and larval development in relation to phenology of white fir in southern Oregon. Res. Note PNW-295. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 9 p.

Wickman, Boyd E. 1981. Degree-day accumulation related to the phenology of Douglas-fir tussock moth and white fir during five seasons of monitoring in southern Oregon. Res. Note PNW-392. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 10 p.

Wilkes, A.; Coppel, H.C.; Mathers, W.G. 1948. Notes on the insect parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) in British Columbia. Canadian Entomologist. 80(1/2): 138-155.

Wilson, Louis F.; Bean, James L. 1963. Site of spruce budworm egg masses on their preferred hosts in the Lake States. Journal of Economic Entomology. 56(5): 574-578.

Wykoff, William R.; Crookston, Nicholas L.; Stage, Albert R. 1982. User's guide to the stand prognosis model. Gen. Tech. Rep. INT-133. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 112 p.

Literature Cited—Unpublished

Beckwith, Roy C. 1983a. Effects of laboratory temperatures on the western spruce budworm. CANUSA-West progress report. 14 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Beckwith, Roy C. 1983b. Effects of larch and old-growth foliage on the western spruce budworm. CAN USA-West progress report. 10 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Campbell, Robert W.; Srivastava, Nilima; Torgersen, Tarolf R. 1982. Differential intratree responses to western spruce budworm by predaceous birds and ants. 24 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Campbell, Robert W.; Torgersen, Torolf R. 1983. Studies on western spruce budworm population dynamics, CAN USA-West final report. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Campbell, Robert W.; Torgersen, Torolf R.; Srivastava, Nilima. 1983. Number, size, and survival rate of eggs in egg masses of western spruce budworm (Lepidoptera: Tortricidae).20 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Cates, Rex G.; Henderson, Colin B.; Redak, Richard A. 1983. A determination of the effects of nitrogen and terpenes on spruce budworm growth and survival. CANUSA-West final report. 25 p. On file at: U.S. Department of Agriculture, Forest Service; Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Colbert, J.J.; Crookston, Nicholas L.; Kemp, William P.; Srivastava, Nilima. 1981. Description of the combined PROGNOSIS/western spruce budworm model—Version 3.0 CAN USA-West report. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Eldridge, Bruce F.; Egan, Thomas H. 1983a. Distribution, sampling, and mortality factors of the western spruce budworm. CANUSA-West final report for 1980-81. 48 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Eldridge, Bruce F.; Egan, Thomas H. 1983b. Mortality factors of early larvae of the western spruce budworm. CAN USA-West final report. 19 p. On file at: U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, Corvallis, OR 97331.

Evenden, James C. 1937. Spraying program for the protection of scenic value within the Utility Areas of the Cody Canyon. Project S-10 memorandum for Forest Supervisor, Shoshone National Forest. On file at: U.S. Department of Agriculture, Forest Service, Forestry and Range Sciences Laboratory, LaGrande, OR 97850.

Hatch, C.R.; Mika, P.G. 1978. Final report: foliage biomass estimates for Douglas-fir, grand fir, and white fir from selected DFTM outbreak areas in the Western U.S. DFTM Program final report 48 p. On file at: Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Hincley, Thomas M.; van der Val, Dirk W.; Klein, Elizabeth L.; Chapman, Roberta J.; Schulte, Paul J. 1983. Relationship between sapwood basal area/ d.b.h., defoliation and foliage biomass/growth of *Pseudotsuga menziesii.* CANUSA-West final report. 68 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Kirkbride, Dale M.; Wagner, Michael R. 1983. Estimating fecundity of *Choristoneura occidentalis* based on pupal weights. CANUSA-West final report. 31 p. On file at: U.S. Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

McKnight, M.E. [n.d.] Outbreaks of the western spruce budworm recorded in the Central and Southern Rocky Mountains. On file at: U.S. Department of Agriculture, Forest Service, Forestry and Range Sciences Laboratory, LaGrande, OR 97850.

McNamee, Peter; Everitt, R.; Sonntag, N.; Stanley M. 1980. Report—Insect model workshop, 1980 January 28-February 10. CAN USA-West final report. 113 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portand, OR 97208.

Volney, W. Jan A.; Waters, William E. 1984. Study of factors determing the density and quality of western budworm populations in south-central Oregon and northern New Mexico. CANUSA-West final report. 65 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, P.O. Box 3890, Portland, OR 97208.

Waters, William E.; Volney, W.J.A. 1981. Study of factors determining the density and quality of western budworm populations in northern California and southern Oregon and in New Mexico. CANUSA-West progress report. 66 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, P.O. Box 3890, Portland, OR 97208.

Waters, William E.; Volney, W.J.A. 1982. A study of factors determining the density and quality of western budworm populations in New Mexico. CANUSA-West progress report. 49 p. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, P.O. Box 3890, Portland, OR 97208.

Key to Subscripts

Subscript	Upper limit for summation	Description
c	C	Crown level (1,...,9). Relation between crown levels shown as c' to c.
h	H	Host species (1,...,6). Relation between hosts shown as h' to h.
z	Z	Tree size class (1,2,3). Crown levels 1, 2, and 3 are in tree size class 1; crown levels 4, 5, and 6 are in tree size class 2; crown levels 7, 8, and 9 are in tree size class 3. (See fig. 1.)
t	T	Time.
d	D	Julian day.
s	S	20 °D step.
a	A	Age as expressed by number of 20 °D intervals since emergence from hibernacula.
f	F	Life stage.
q		Direction traveled.
b		Habitat series.
g	G	Bird guild.
p	P	Canopy layer (1,2,3).
x		Sex
r	R	Budworm cohort.

Component Models of the Western Spruce Budworm Modeling System

To distinguish the specific models discussed in this publication from general insect or forest growth and yield models, the former will be referred to by the following names:

Name	Description and references
Prognosis Model	Prognosis model for stand development: Stage 1973, Wykoff and others 1982.
Budworm Model	Western spruce budworm model: Colbert and others 1983; Sheehan and others 1987; also this publication (see text footnote 3).
Weather Model	Weather model was developed by Bruhn and others (1979) and modified for use as an extension to the Prognosis Model by Kemp and others (see text footnote 7).
Parallel Processing Extension	Crookston and others are preparing documentation of this Prognosis Model extension. It will allow a user to simulate growth of a number of stands simultaneously and include interactions among stands during each growth cycle or more often if an extension, such as the Budworm Model, requires it (for dispersal).

English-Metric Equivalents

Metric units will be given throughout this publication unless citing work done by others; then, units will be given as published and specific conversions will be provided as appropriate.

Length
1 meter = 100 centimeters = 1 ,000 millimeters = 39.37 inches

Area
1 square meter = 1.20 square yards = 10.76 square feet = 1,549.2 square inches
1 hectare (ha) = 10,000 square meters = 2.47 acres

Mass and Weight
1 gram (g) = 0.0353 ounce
28.35 grams = 1 ounce
1 kilogram = 1,000 grams = 2.2046 pounds = 35.27 ounces
1 gram = 1 ,000 milligrams (mg)

Temperature
For T, temperature in degrees Fahrenheit; and T', temperature in degrees centigrade: $T = 9/5\,T' + 32$ or $T' = 5/9\,(T - 32)$.

GPO 691-133/82080

Sheehan, Katharine A.; Kemp, William P.; Colbert, J.J.; Crookston, Nicholas L. 1989. The western spruce budworm model: structure and Content. Gen. Tech. Rep. PNW-GTR-241. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 82 p.

The Budworm Model predicts the amounts of foliage destroyed annually by the western spruce budworm, *Choristoneura occidentalis* Freeman, in a forest stand. The model may be used independently, or it may be linked to the Stand Prognosis Model to simulate the dynamics of forest stands. Many processes that affect budworm population dynamics are simulated in detail, including budworm and host phenology, larval growth and feeding, larval and adult dispersal, and the effects of natural enemies. This publication describes the structure, assumptions, and default parameter values of the Budworm Model.

Keywords: Model, population dynamics, insect populations, defoliation, stand growth and yield, western spruce budworm, *Choristoneura occidentalis, Tortricidae.*

Pacific Northwest Research Station
319 S.W. Pine St.
P.O. Box 3890
Portland, Oregon 97208

U.S. Department of Agriculture
Pacific Northwest Research Station
319 S.W. Pine Street
P.O. Box 3890
Portland, Oregon 97208

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