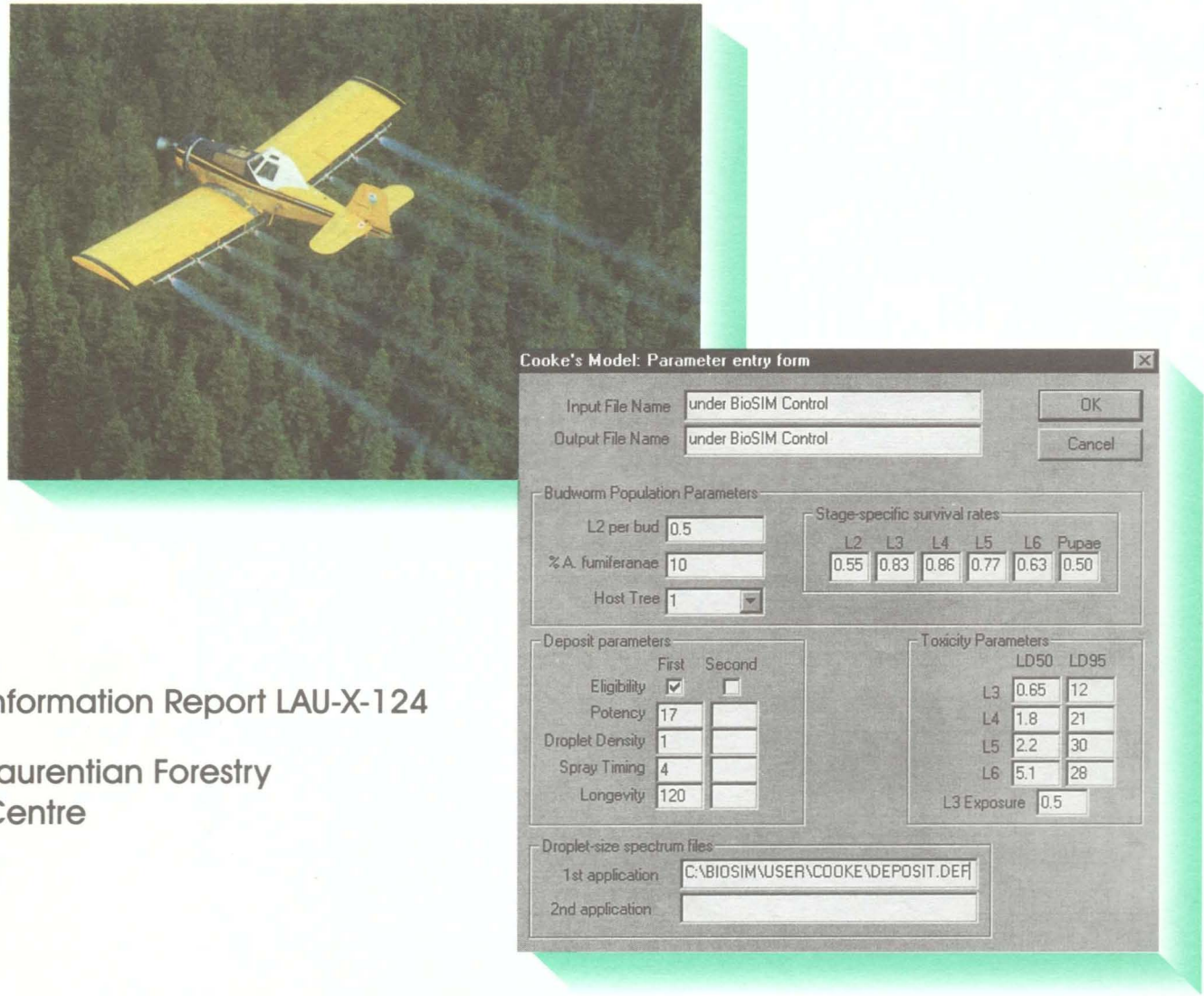
Cooke's *Bt* efficacy model: User's guide to the decision-support tool for control of spruce budworm populations with *Bacillus thuringiensis*

Jacques Régnière and Barry J. Cooke



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Laurentian Forestry Centre

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ABSTRACT

Cooke's model is a computer program, written in object-oriented C^{++} language, that simulates the effects of *Bt* sprays on spruce budworm populations. It is based on well-documented and validated sub-models of budworm development and feeding. It simulates several biological processes that are seen as critical determinants of efficacy: budworm development, survival and feeding, foliage depletion, parasitism by *Apanteles fumiferanae* Vier., *Bt* droplet ingestion, feeding inhibition, mortality, and degradation of *Bt* deposits by ultraviolet radiation and rain. The model has been extensively validated under a variety of application conditions. Cooke's model can be used as a research tool to investigate the intricacies of *Bt*-budworm interactions or as a decision-support tool in the design of optimal application strategies of *Bt* to protect forests against excessive budworm defoliation. The present document describes the model's inputs and outputs, explores its behaviour, and provides a tutorial for its use under the BioSIM simulation control environment. The model's most critical inputs and its most urgent data needs are also discussed.

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RÉSUMÉ

Le modèle de Cooke est un logiciel écrit en langage objet C^{++} qui simule les effets d'applications de *B.t.* sur les populations de la tordeuse des bourgeons de l'épinette (TBE). Il est fondé sur des modules bien documentés et bien validés du développement et de l'alimentation de l'insecte. Le modèle simule plusieurs processus biologiques qui sont considérés comme déterminants critiques de l'efficacité du *B.t.* : le développement, la survie et l'alimentation de la TBE, la consommation du feuillage, le parasitisme par *Apanteles fumiferanae* Vier., l'ingestion de gouttelettes de *B.t.*, l'inhibition alimentaire, la mortalité induite par le *B.t.* et la dégradation de celui-ci par les rayons ultraviolets et la pluie. Le modèle a été validé sous une variété de conditions d'application. Le modèle de Cooke peut être utilisé comme outil de recherche pour examiner la complexité des interactions entre la TBE et le *B.t.*, ou encore comme outil d'aide à la prise de décisions dans l'élaboration de stratégies optimales d'application du *B.t.* dans la protection des forêts contre une défoliation excessive par la TBE. Le présent document contient une description des intrants et sorties du modèle, explore son comportement, et offre un exercice pratique visant à familiariser l'utilisateur avec l'utilisation du modèle dans le cadre du système de gestion des simulations BioSIM. Enfin, ce document discute des intrants les plus critiques du modèle et des besoins les plus urgents de recherche additionnelle.

INTRODUCTION

Cooke (1995) developed a simulation model describing in detail the interactions between the bacterium *Bacillus thuringiensis* var. *kurstaki*, the spruce budworm *Choristoneura fumiferana* (Clem.) and one of its major parasitoids, the braconid *Apanteles fumiferanae* (Vier.). This model, hereafter referred to as Cooke's model, was described in the scientific literature (Cooke and Régnière 1996) and was extensively validated (Régnière and Cooke 1998).

Cooke's model was designed to simulate the effects of a *Bt* spray on a population of spruce budworm. It can be used to predict the efficacy of a *Bt* spray with particular deposit characteristics against a budworm population that also has specific characteristics. A proportion of the simulated budworm population is parasitized by *A. fumiferanae*, an endoparasitic braconid wasp that oviposits in budworm larvae in the hibernaculum in late summer and is usually present as a larva inside the host when a *Bt* spray is applied. Efficacy can be expressed in terms of population reduction, foliage protection or parasitoid conservation.

Cooke's model is an individual-based, stochastic model. It simulates the fate of several hundred spruce budworm individuals that develop and feed independently of each other. These spruce budworm feed on the growing shoots of host trees. Feeding rates and growth of both foliage and insects are temperature-driven. Ingestion of *Bt* droplets is a random event scheduled according to the density of droplets on host foliage and an individual's feeding rate. Budworm larvae feeding on *Bt*-contaminated foliage go through cycles of feeding inhibition and recovery until they either die from *Bt* intoxication or escape the window of vulnerability (pupation or *Bt* weathering). The probability of death from ingestion of a droplet is a function of the amount of *Bt* in the droplet (determined by droplet size, initial product potency and weathering) as well as an individual's *Bt* ingestion history. The model keeps track of key population-level statistics such as defoliation (% of potential foliage remaining on shoots) and population density. These statistics are output each simulated day.

The validation of Cooke's model confirmed its usefulness as a decision support tool for the design of optimal strategies in the use of *Bt* to manage outbreak spruce budworm populations. The present document is a guide for the operational use of Cooke's model. It describes in detail what the model's inputs and outputs are, and what influence various input parameters have, so that users can better control the model and adequately interpret its outputs. Instructions for installation and use of the model, as well as a step-by-step tutorial, can be found in the appendix.

RECENT MODIFICATIONS TO COOKE'S MODEL

Cooke's model is continually evolving as new information regarding the interactions between *Bt* and spruce budworm becomes available. The changes made to the model since its publication (Cooke 1995; Cooke and Régnière 1996) are documented in some detail here for the sake of completeness, although many are of minor importance to most of its applications.

Apanteles fumiferanae parasitism

One of the reasons *Bt* is such a useful population management tool is that it does not directly kill natural enemies of the spruce budworm. Nevertheless, *Bt* can affect parasitoids indirectly by killing parasitized hosts, by reducing host density at the time of parasitoid attack or by changing the phenological synchrony between parasitoids and the susceptible host stages.

A sub-model is available in Cooke's model to simulate the indirect effects of *Bt* on budworm populations parasitized by the braconid wasp *Apanteles fumiferanae* (Cooke 1995). To use this sub-model, the user must provide an estimate of the percentage parasitism by *A. fumiferanae* in the overwintering budworm population (Fig. 1).

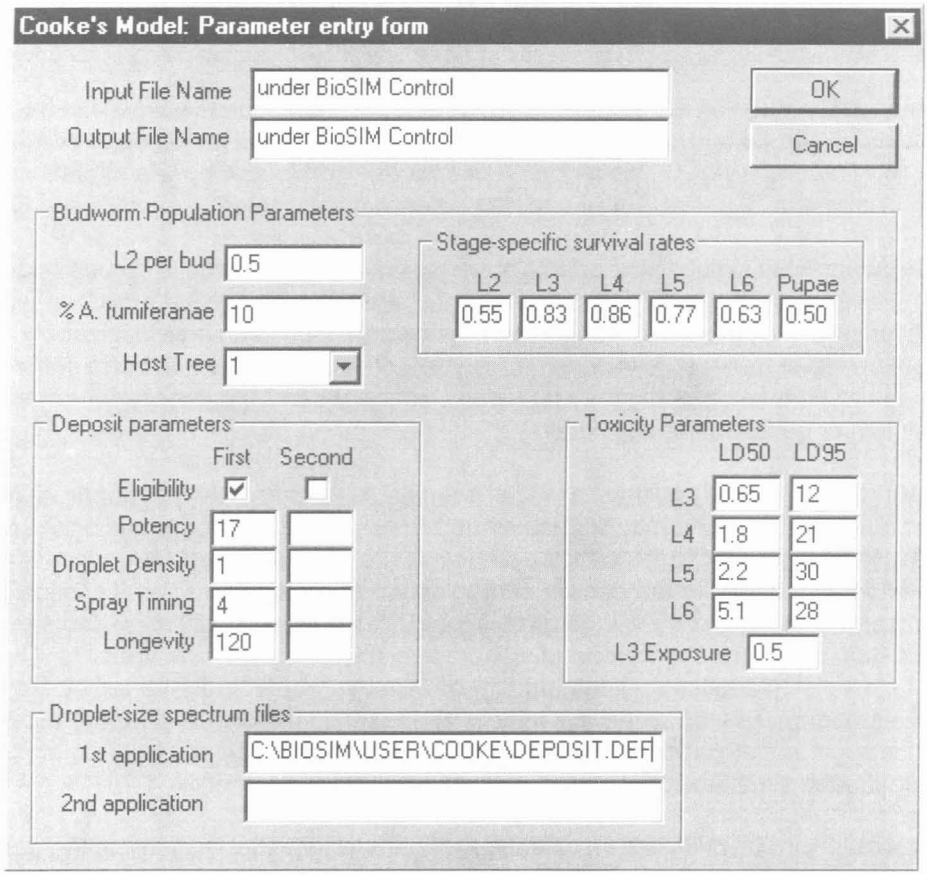

Figure 1. Windows '95 version of the parameter-specification screen for Cooke's model under BioSIM. Parameters are described in Table 1.

Nealis and van Frankenhuyzen (1990) and Nealis (1991) discussed the integration of parasitism, especially by *A. fumiferanae*, in management of spruce budworm populations. In the 2nd instar, parasitized and non-parasitized larvae have similar feeding rates. Therefore, in the presence of sprayed foliage, they would be equally vulnerable to the ingestion of *Bt*. As the parasitoid larva develops, its host's feeding rate decreases sharply (Nealis and van Frankenhuyzen 1990), and the probability of the host ingesting a lethal dose of *Bt* also declines. Just before parasitized host larvae reach the 5th instar, feeding ceases and they are no longer vulnerable to *Bt*-caused mortality so that the parasitoid and its host become immune to a *Bt* spray. The host larva dies from parasitism.

Sprays aimed at 3rd and 4th instar larvae are more likely to kill parasitoids than sprays aimed at later stages. However, delayed sprays imply that more feeding has taken place prior to treatment and that potential foliage protection is reduced. For an IPM practitioner who wants to balance the costs and benefits of parasitoid conservation against the costs and benefits of foliage protection, this addition to Cooke's model can be helpful in forecasting efficacy under various treatment scenarios. The mathematical details of this model component were described by Cooke (1995).

Effects of *Bt*

Minimum effective dose

Very small amounts of *Bt* have no measurable effect on budworm feeding, growth and survival. A so-called "minimum effective dose" was initially estimated to be 0.5 IU/larva. More sensitive bioassays (personal communication, K. van Frankenhuyzen, Canadian Forest Service, Sault Ste. Marie, Ontario) indicate that the minimum effective dose is in fact much smaller, in the order of 0.1 IU/larva. This value is now implemented in the model.

Chronic vs. acute toxic effects

Originally, Cooke's model allowed the probability of death after ingesting a *Bt* dose to be a function of either the amount of toxin most recently ingested (acute dosage) or the cumulative amount ingested by the individual (cumulative dosage). Recent research (personal communication, K. van Frankenhuyzen, Canadian Forest Service, Sault Ste. Marie, Ontario) has shown that the probability of death is more a function of acute dose than of cumulative dose, although recovery time after ingesting a sub-lethal dose is more a function of cumulative dose acquired. These are now features of the model.

Retardation of budworm development

Originally, the model retarded the development of a budworm that had ingested *Bt* by a factor of 70% for the remainder of its life. Pedersen *et al.* (1997) have shown this value to be approximately correct, although the retardation factor varies as a function of the amount of *Bt* ingested and the instar involved. These new data were incorporated in the model.

Susceptibility of the various larval instars

Originally, toxicity was assumed to be independent of larval instar. Recently, van Frankenhuyzen *et al.* (1997) determined that the various instars differ in their responses to formulations and strains of *Bt*. The model requires a product-specific toxicity matrix describing the amounts of *Bt* that must be ingested to kill 50% and 95% (LD_{50} and LD_{95}) of larvae in the 3rd, 4th, 5th and 6th instars (Fig. 1). The model uses this input table to calculate stage-specific dose-response curves. It also assumes that the LD_{50} and LD_{95} of 2nd instars are the same as those of 3rd instars.

Spray deposit

Number of applications

The new version of Cooke's model can simulate single and double applications of *Bt*, each timed separately. The model uses the same LD_{50} and LD_{95} matrix for both applications (and thus cannot simulate successive applications with different formulations unless the formulations share the same toxicity matrix).

Spray timing

The timing of a spray can now be specified in terms of budworm development (average instar), which is a weighted mean of a population's age frequency distribution, as well as by Julian date.

Droplet size spectrum

Originally, the droplet size spectrum was approximated by an upper-limit log-normal (ULLN) distribution of droplet diameters, specified by its mean, variance, and upper limit. Now, the user can provide a droplet-size spectrum distribution stored in an ASCII (text) file. The user also has the choice of using a default ULLN distribution (mean 50 µm, maximum 180 µm). A default droplet size spectrum file named DEPOSIT.DEF is also distributed with the model (Fig. 2, Table A1 (appendix)). The structure of the droplet size spectrum file is described in the "MODEL INPUT PARAMETERS" section.

Bt *droplet encounter scheduling*

Originally, the distribution of *Bt* droplets on foliage could be simulated as a random or uniform process. Currently, droplet encounters are simulated strictly as a random process, assuming a Poisson distribution of droplets (and thus an exponential distribution of encounter intervals).

Time of day for spray application

Preliminary simulations indicated that this parameter had little effect on efficacy, so currently this parameter cannot be set. Sprays occur either as soon as the budworm population has reached the target average instar, or as soon as the target date is reached (depending on the user's specifications).

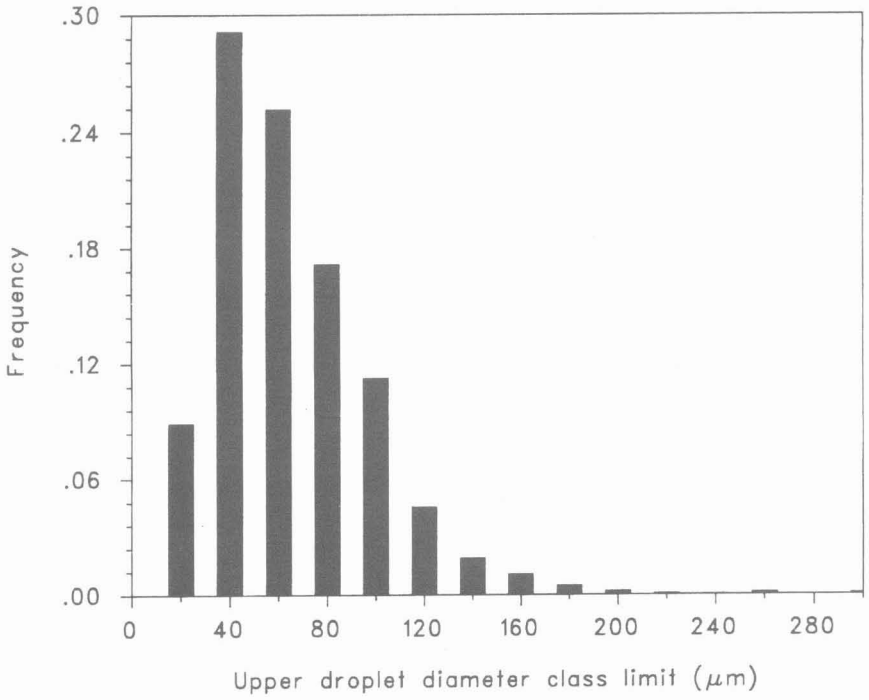

Figure 2. Typical droplet size spectrum used as input for Cooke's model. The data are found in file DEPOSIT.DEF distributed with the model (appendix).

Ultraviolet protection

The ability to add ultraviolet radiation protection of the *Bt* formulation (over and above the standard) has been removed.

Host-plant types

Originally, Cooke's model was calibrated to simulate budworm feeding on healthy balsam fir trees. Now, feeding on four types of host plants can be simulated (Table 1). See the "MODEL INPUT PARAMETERS" section for details.

Table 1. Host plant conditions available for simulation in Cooke's model.

	Tree			Budworm	
ID	Species	Tree condition	U_{max} [a]	Feeding	Development
1	Balsam fir	Healthy	231.3	Normal	Normal
2	Balsam fir	Defoliated	115.7	Normal	Normal
3	Balsam fir	Heavy flowering	115.7	Normal	Fast
4	White spruce	Healthy	299.5	Fast	Fast

[a] Maximum dry weight of non-defoliated shoots, in mg.

Programming details

Time step

Cooke's model simulates budworm biology in discrete time steps. Originally, the time step was 4 h through most of the simulation, and 1 h for the period where active *Bt* is present on foliage. Currently, a 4-h time step is used throughout the simulation.

Number of individuals

Cooke's model is an individual-based model. The number of budworm individuals simulated has been fixed at 400, a number that provides optimum precision and simulation speed.

MODEL INPUT PARAMETERS

The input parameters needed by Cooke's model are divided into three categories (Table 2): (1) those describing the budworm population, (2) those describing the attributes of the spray deposit and (3) those describing the toxicity of the *Bt* product to spruce budworm. The input-parameter dialog box for Cooke's model in BioSIM reflects this parameter arrangement (Fig. 1).

Table 2. An ordered list of Cooke's model input parameters. Parameters appear in the same order in the input-parameter file read by the model at run time.

Parameter group	Symbol (in Fig. 1)	Description
Budworm population	L_2 per bud	Overwintered larval density, in larvae per bud
	% *A. fumiferanae*	Parasitism by *A. fumiferanae*, in % of SBW hosts
	Host tree	Type of host tree (1, 2, 3 or 4; see Table 2)
Stage-specific survival rates	L_2	Feeding L_2 survival (proportion)
	L_3	L_3 survival (proportion)
	L_4	L_4 survival (proportion)
	L_5	L_5 survival (proportion)
	L_6	L_6 survival (proportion)
	Pupae	Pupal survival (proportion)
Deposit parameters (first application, then second)	Eligibility	Spray eligibility YES/NO toggle
	Potency	*Bt* nominal potency [BIU/L]
	Droplet density	*Bt* droplet density [drops/4.1 mg]
	Spray timing	Time of spray application, either in AI or Julian date
	Longevity	Time deposit remains on foliage before wash off
	Droplet size	Name (complete path) of the droplet-diameter file
Toxicity parameters (LD_{50} first, then LD_{95})	L_3	Lethal dose (for 50 or 95%), in IU per larva
	L_4	Lethal dose (for 50 or 95%), in IU per larva
	L_5	Lethal dose (for 50 or 95%), in IU per larva
	L_6	Lethal dose (for 50 or 95%), in IU per larva
	L_3 Exposure	Exposure of L_3 to *Bt* (proportion of droplet density)

Budworm population parameters

Budworm density

Budworm density is expressed as the number of overwintered larvae per bud (such as would be measured in a pre-emergence foliage sample taken in late spring). If overwintering larval density is measured in the fall of the previous year, then one must discount overwintering mortality. This mortality was studied in some detail by Miller

(1958) and Régnière and Duval (1998). In addition, overwintering larval density is often measured from whole branches, while density of the feeding larval stages is often calculated from 45-cm branch tips. In this case, corrections should be applied to overwintering larval density because of convergence of larvae towards branch tips after emergence (see Régnière *et al.* 1989). In all cases, it is important to measure the number of buds on the sample branches so that density can be expressed relative to the number of buds.

Parasitism by Apanteles fumiferanae

This is the percentage of overwintered budworm larvae that are parasitized by *A. fumiferanae*. Estimates of this can be obtained by dissection or rearing of overwintered larvae or feeding larvae obtained from foliage samples taken before the budworm population reaches peak 4th instar. This is useful only if the user wishes to analyze the effect of the spray on parasitoid populations. Otherwise, this parameter can be set to 0 and parasitism by *A. fumiferanae* can be considered as being part of exogenous mortality (i.e., included in stage-specific survival rates).

Host tree type

This can take one of four values {1,2,3,4} that represent four different host types (Table 1):

Host type 1

Normal balsam fir, with budworm feeding and development as described by Cooke and Régnière (1996).

Host type 2

Normal budworm feeding and development on balsam fir damaged by previous years' defoliation that produce numerous smaller shoots from epicormic buds (Batzer 1973; 50% reduction in maximum dry weight of shoots).

Host type 3

Budworm developing at an accelerated rate in all feeding larval instars in the presence of abundant staminate flowers on balsam fir trees (Carisey and Bauce 1997). These trees produce vegetative shoots that are 50% smaller than normal balsam fir shoots (Blais 1952).

Host type 4

Budworm developing at an accelerated rate in all feeding larval stages, and feeding at higher rates on white spruce, which produces heavier shoots than balsam fir. Feeding rates and foliage growth parameters for white spruce were taken from Régnière and You (1991). Development rate modifiers were estimated from several years of observation of budworm development on balsam fir and white spruce near Black Sturgeon Lake and Gargantua Harbor (Ontario) and near Armagh (Quebec).

Stage-specific survival rates

There are six values of expected survival from factors other than *Bt* during the six active life stages (2nd to 6th instars and pupal stage). As budworm larvae proceed through their development, they are exposed to many causes of mortality, such as dispersal losses, disease, parasitism and predation. These mortality factors cause a gradual decrease in budworm density over the growth season, and as a result can have a considerable impact on the defoliation caused by a budworm population of a given initial density. Further, the set of mortality factors can vary between stands and between years. While this variation is not well understood, it is clear that survival rates are especially high during the rising phase of a spruce budworm outbreak, and are lower during the declining phase (Royama 1984). Model predictions are most accurate if the stage-specific survival rates are estimated from adequate control populations prior to running the model. However, this is not a situation that would occur normally. Under most circumstances, a user would have to use estimates obtained from previous years and locations. Table 3 contains estimates of stage-specific survival rates that are typical of outbreak and declining populations. These values were obtained from Régnière and You (1991) and Royama (1984). In atypical situations, such as when poor synchrony between host plant and insect development causes high mortality rates, larval survival in the early instars can be fairly low. This phenomenon was observed in 1997 in the Ottawa River valley during the model validation campaign. Estimates of 2nd, 3rd and 4th instar survival rates recorded at that time are also listed in Table 3.

Table 3. Typical stage-specific survival rates under three different sets of circumstances.

Life stage	Outbreak	Declining population	Poor synchrony with bud break
Feeding 2nd	1.0	1.0	0.80
3rd	0.99	0.99	0.73
4th	0.93	0.93	0.83
5th	0.84	0.60	0.84
6th	0.55	0.26	0.55
Pupa	0.39	0.35	0.39
Total survival	0.16	0.05	0.09

Attributes of the spray deposit

There are two sets of spray parameters, one for each application. Values are specified sequentially for the first and then for the second application.

Spray eligibility

This is a logical variable (0: no, 1: yes) that determines if a spray is to be delivered. Specifying 0 (no) renders the remaining parameters for that application meaningless.

Nominal Bt *potency*

This is the nominal (label) potency of the *Bt* formulation being applied. Product potency is expressed in BIU/L of tank mix. It is a measure of the amount of *Bt* per unit of volume of the sprayed product, not an application rate. A typical potency is 12.7 BIU/L (FORAY 48B applied at 30 BUI/ha in a 2.47 L volume).

Droplet density

This is the number of droplets of *Bt* per mature balsam fir needle on a healthy, non-flowering tree (4.1 mg dry weight). This method of expressing droplet density normalizes the measure with respect to the size of the growing shoots. Droplet density is the result of the application rate (litres per hectare), and the atomization (droplet size). It is normally determined from microscopic examination of samples of sprayed foliage for the presence of dyed *Bt* droplets. Once droplets have been counted, the shoot is oven-dried (70°C for 24-48 h). Methods are being developed to provide a correlation between protein toxin concentration (such as provided by Abbott's ADAM kit) and droplet density, given a certain droplet size spectrum, so that this measurement can be made more easily.

Spray timing

This is the time when the spray is applied. Timing is expressed either in units of average instar ($2 < \text{Time} < 8$) or in Julian date ($\text{Time} \geq 100$). Average instar refers to the weighted mean of the budworm population's stage frequency distribution, where overwintering larvae are assigned to stage 2, pupae to stage 7 and emerged pupal cases to stage 8. Thus, a spray timing of 4.5 would be applied when the population was half in 4th instar or younger and half in 5th instar or older.

Longevity of deposit

This is the number of hours that a *Bt* deposit is allowed to linger on foliage before it is "washed" away. Note that the model also simulates *Bt* degradation due to ultraviolet radiation. The longevity parameter does not affect the process of ultraviolet degradation. Unless the user wishes to simulate the effect of severe rainfall events on efficacy, this parameter should be ≥ 120 h (5 days). *Bt* deposits should normally have been completely degraded by UV light after the 5th day.

Droplet size spectrum file

This is the name of a file (complete path) that contains the diameter spectrum data. This is an ASCII (text) file containing two values per line (space or tab separated): the first value is the upper boundary of a droplet diameter class (thus increasing values > 0, up to largest diameter found on the foliage samples), expressed in µm (often in 10 or 20 µm increments). The second value on each line is the frequency of droplets in each diameter class. These frequencies can be expressed either in relative terms (i.e., they can sum to 1 or 100%), or they can be absolute frequencies. Cooke's model scales these frequencies so that they sum to 1 prior to simulation. A default droplet-size spectrum file (DEPOSIT.DEF) is distributed with the model (Fig. 2, Table A1 (appendix)). This default deposit spectrum is a pooled deposit spectrum obtained during the 1996-1997 model validation campaign in the Ottawa River valley (Régnière and Cooke 1997). Droplet-size spectra are specific to aircraft and atomizing equipment combinations, and vary also with flow rate, atomizer rotation speed as well as a product's fluid characteristics. Spectra can be generated by simulation models such as PKBW2 (Wallace *et al.* 1987) or AGDISP (Bilanin *et al.* 1987).

Toxicity to spruce budworm

Stage-specific susceptibility matrix

Different *Bt* formulations may have different stage-specific dose-response curves. The stage-specific susceptibility matrix is a 4x2 matrix of the LD_{50} and LD_{95} for 3rd, 4th, 5th and 6th instars for the *Bt* formulation being sprayed obtained by the droplet imbibing assay method of van Frankenhuyzen *et al.* (1997). The method has been refined and can now be applied to 3rd instar larvae. Preliminary results indicate that this instar is even more susceptible to *Bt* than the 4th instar (personal communication, K. van Frankenhuyzen, Canadian Forest Service, Sault Ste. Marie, Ontario). Table 4 lists LD_{50} and LD_{95} values obtained or estimated from these sources for FORAY 48B, FORAY 76B and DIPEL 48AF. Second-instar larvae are assumed to have the same LD_{50} and LD_{95} as 3rd instars. The differences between products and formulations in Table 4 are in fact negligible, given the width of associated confidence intervals (van Frankenhuyzen *et al.* 1997).

Table 4. Stage-specific toxicity matrices for FORAY 48B and DIPEL 48AB. LD values given in IU per larva. Data from van Frankenhuyzen *et al.* (1997) and unpublished data from K. van Frankenhuyzen for L3.

	FORAY 48B		FORAY 76B		DIPEL 48AF	
Instar	**LD_{50}**	**LD_{95}**	**LD_{50}**	**LD_{95}**	**LD_{50}**	**LD_{95}**
3rd	0.65	12.7	0.86[a]	13.1[b]	0.77[a]	11.2[b]
4th	1.8	20.9	1.8	23.4	1.6	23.7
5th	2.2	30.1	2.9	31.1	2.6	26.3
6th	5.1	27.8	5.1	43.5	7.5	68.7

[a] Estimated from the ratio (0.295) of toxicity to 3rd and 5th instars observed with FORAY 48B.

[b] Estimated from the ratio (0.422) of toxicity to 3rd and 5th instars observed with FORAY 48B.

3rd instar exposure

Compared with later instars (4th to 6th), the 2nd and 3rd instars have more cryptic feeding habits. Second instars mine old needles or unflushed buds, while 3rd instars are most often found feeding on the inside needles of unflared shoots rather than on exposed needles. While this feeding behaviour has not been quantified, it is clear that the exposure to *Bt* during these younger stages is somewhat less than in the later stages. Thus the probability of ingesting a *Bt* droplet would be lower in these younger stages. The 3rd instar exposure parameter takes this into account. It effectively adjusts the density of droplets to reduce the probability of encounter by early larval instars. Values of this parameter have yet to be estimated experimentally, but it is likely to be < 0.5.

MODEL OUTPUT

Cooke's model outputs a daily population level summary. The output file, named on the second line of the parameter-value specification file, is an ASCII (text) file (see Table A3 (appendix)). Each line of this file contains a day's output, where the first value is the Julian day. There are 17 output variables (other than the date).

1. Defoliation
   This is the average percentage of foliage removed from the growing shoots. The model determines this from foliage weight consumed and accumulation through shoot growth (see Régnière and You 1991 for details). This is directly comparable to measurements of current defoliation from mid-crown samples using the Fettes method (Allen *et al.* 1984).

2. Relative density
   This is the Log_{10} of the average number of live spruce budworms per bud. It is directly comparable to values obtained from 45-cm branch tips collected at mid-crown, once applicable sampling bias corrections have been applied (Régnière *et al.* 1989).

3-9. Stage-specific relative densities
   There are 6 output variables describing the age (stage) structure of the live budworm population, in % (one value for each life stage from emerged 2nd instar to the pupa).

10. Average instar
   This is the average instar, which is the average life stage of the population, with values starting at 2 (unemerged or active 2nd instars) and ending at 8 (instar 7 is the pupa, instar 8 the emerged adult; see Equation [8] in Cooke and Régnière (1996) for a mathematical definition).

11. Parasitoid:host ratio
   This is the ratio of live *A. fumiferanae* parasitoids (all stages) to live spruce budworms (all stages). This output variable is useful when parasitism by *A. fumiferanae* is set to a value > 0.

12-13. Spray potency
   Two variables give the residual potency of *Bt* deposits remaining on the foliage (in BIU/L) after each application. Potency declines gradually as a function of ultraviolet radiation and drops to 0 when the longevity period has expired (due to a catastrophic event such as rain). When no application is simulated, potency remains at 0.

14. % *Bt*-caused mortality of budworm
   This is the cumulative number of spruce budworm larvae killed by *Bt*, expressed as a percentage of the 400 individuals initially in the simulation.

15. % *Bt*-caused mortality of *A. fumiferanae*
   This is the number of *A. fumiferanae* larvae that were killed after parasitized spruce budworm larvae ingested *Bt*, expressed as a percentage of the number of parasitoids among the 400 larvae initially in the simulation. This output variable is useful when parasitism by *A. fumiferanae* is set to a value > 0.

16. % Ingestion
   This is the number of budworm that ingested at least one droplet of *Bt* expressed as a percentage of the 400 individuals initially in the simulation.

17. % Kill efficiency
   This is the number of budworm that died from *Bt* expressed as a percentage of the number that ingested at least one droplet.

DISCUSSION OF MODEL BEHAVIOUR

Cooke's *Bt* efficacy model is highly complex, and for this reason it can exhibit intricate responses to changes in input parameter values. In this section, the main features of model behaviour are highlighted through sensitivity analysis. In all cases, input air temperature data were those recorded in the Ottawa River valley in 1997 (La Pêche weather station). In all cases except in simulations specifically addressing droplet size, the default droplet size spectrum in DEPOSIT.DEF was used (Fig. 2, Table A1 (appendix)). Unless otherwise specified, product potency used in all simulations was 12.7 BIU/L. All simulations were replicated 3 times, and average outputs are presented.

Examples of the model's daily output are illustrated in Fig. 3. The two major output variables are budworm density per bud (Fig. 3a), and current defoliation in % of potential shoot weight (Fig. 3b). In this example, the three sets of stage-specific survival rates in Table 3 were used, with an initial density of 0.35 overwintered 2nd instars per bud. Parasitism by *A. fumiferanae* was set to zero, and the host plant was healthy balsam fir. No *Bt* application was simulated. The results of these simulations illustrate the importance of stage-specific (non-*Bt*) mortality on the seasonal patterns of population density and defoliation. The simulated budworm population drops sharply in the later stages in all cases. The drop is far more pronounced in the case of declining populations, although this increased mortality of late larval stages does not translate into a large change in defoliation, mainly because of the high initial density. When mortality occurs in the early instars, such as in populations suffering poor synchrony with flushing buds, defoliation is decreased far more markedly although overall survival of the budworm population is better than in a declining population. This is because early mortality reduces population density before much feeding has taken place, rather than at the end of the feeding period as is the case for mortality in declining populations. This series of simulations also illustrates that defoliation predictions made by the model will tend to be inaccurate in years where pronounced and unforeseen changes in stage-specific survival of the early larval stages occur.

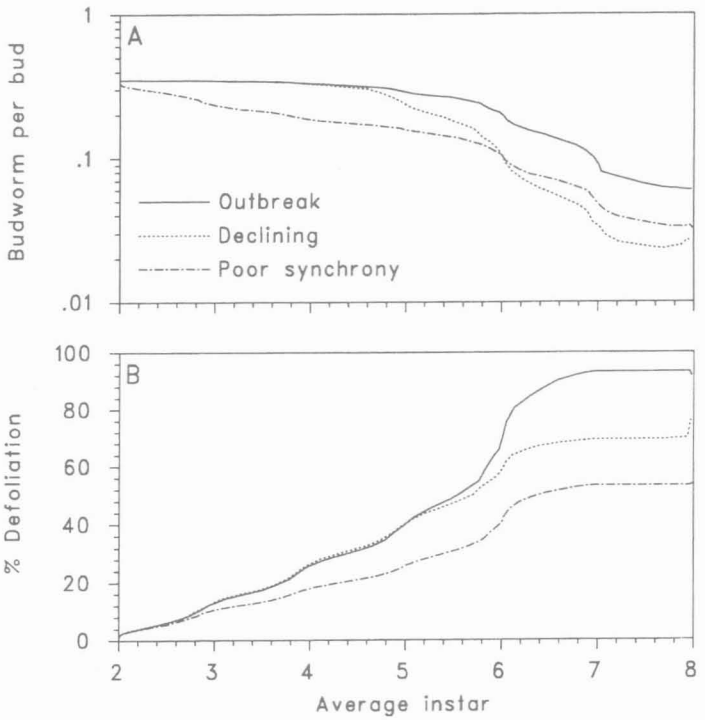

Figure 3. Examples of daily output from Cooke's model: (A) budworm population density; (B) defoliation of growing shoots. Solid line: outbreak population. Dotted line: declining population. Dot-dashed line: poor synchrony between larval emergence and bud break.

Budworm population parameters

Initial population density

Two series of simulations were run, each varying overwintered larval density from 0.05 to 0.5 larvae per bud on healthy balsam fir. The first series was run with stage-specific survival rates typical of outbreak populations and the second series with rates typical of declining populations (Table 3). No spray application was simulated and parasitism by *A. fumiferanae* was set to zero. In both series, there was a linear relationship between initial density and defoliation, up to 100%, and defoliation was lower in declining populations than in outbreak populations (Fig. 4a). Thus, an accurate estimate of initial budworm density (per bud) is a fairly critical model input, as expected.

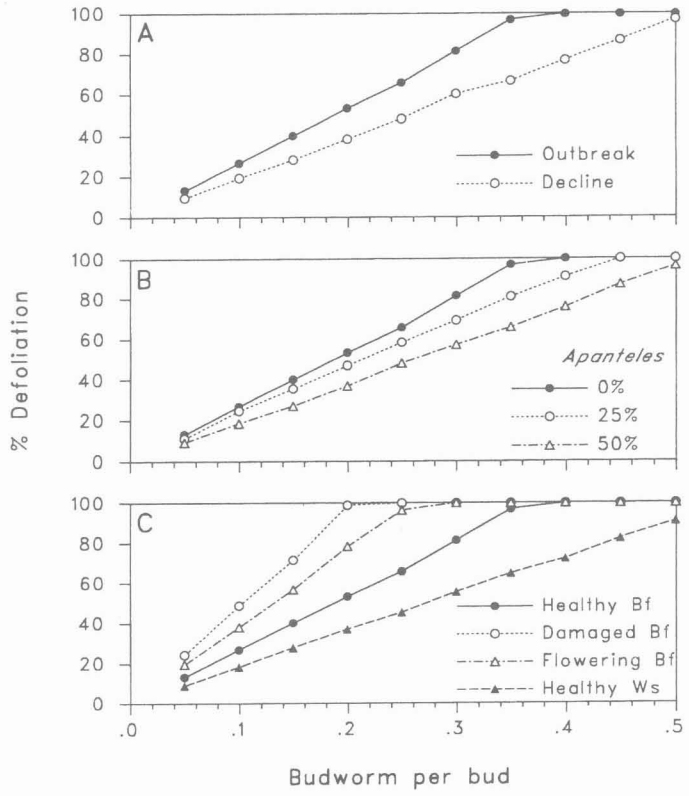

Figure 4. Influence of the initial density of spruce budworm larvae (per bud) and end of season defoliation of growing shoots. (A) Comparison of outbreak and declining populations. (B) Outbreak populations with increasing parasitism rates by *Apanteles fumiferanae*. (C) Outbreak populations feeding on four different host types.

Parasitism by Apanteles fumiferanae

Mortality by this parasitoid is normally included in stage-specific survival rates unless the model is being used to investigate this non-*Bt* source of mortality specifically. In three series of simulations, overwintered larval density was varied from 0.05 to 0.5 larvae per bud on healthy balsam fir, with stage-specific survival rates typical of outbreak populations and no spray application. Parasitism by *A. fumiferanae* was set to 0%, 25% and 50% of the initial budworm population. The rate of parasitism had a pronounced effect on defoliation levels, because the parasitoid reduces its host's feeding and eventually kills before it has done most of its damage (Fig. 4b). From the point of view of population levels or defoliation, increasing parasitism rate is equivalent to decreasing the survival rates of 4th and 5th instar larvae.

Host plant type

The type of host plant influences the potential weight of shoots, and the budworm's feeding and development rates (Table 1). These, in turn, determine the amount of defoliation that is caused by the budworm population. Four series of simulations were run, again varying overwintered larval density from 0.05 to 0.5 larvae per bud, with stage-specific survival rates typical of outbreak populations in the absence of a *Bt* application and with parasitism by *A. fumiferanae* set to 0. Each series simulated feeding on a different host plant type, and the results indicate the vast differences in defoliation levels that can be expected (Fig. 4c). Healthy white spruce shoots are heavier than healthy balsam fir shoots. Thus they suffer less defoliation at equal budworm density (per bud). Flowering or damaged (severely defoliated) balsam fir produce small shoots that consequently suffer more defoliation. Because development is faster on flowering balsam fir trees, the insect has less time to feed and this leads to somewhat lower defoliation than on severely damaged trees. The model should therefore be parameterized to reflect tree conditions

as much as possible. There is a need to validate model predictions on host plant types other than healthy, mature balsam fir, particularly under heavy flowering conditions or severe cumulative defoliation.

Attributes of the spray deposit

Product potency

Two series of simulations were run, each varying product potency from 2 to 20 BIU/L (equivalent to a 50 BIU/ha application at 2.46 L/ha). The first series was run for a high budworm density (0.6 larvae per bud) and the second for a lower population (0.3 larvae per bud), both on healthy balsam fir, with stage-specific survival rates typical of outbreak populations and parasitism by *A. fumiferanae* set to 0. Protection effectiveness (in terms of foliage conservation) was not very strongly influenced by product potency, except at very low potencies (Fig. 5a). There was not much gain in increasing potency from 10 to 20 BIU/L, at the simulated droplet density of 1 droplet per needle. The highest return on investment here would occur at the very high end of the budworm density range.

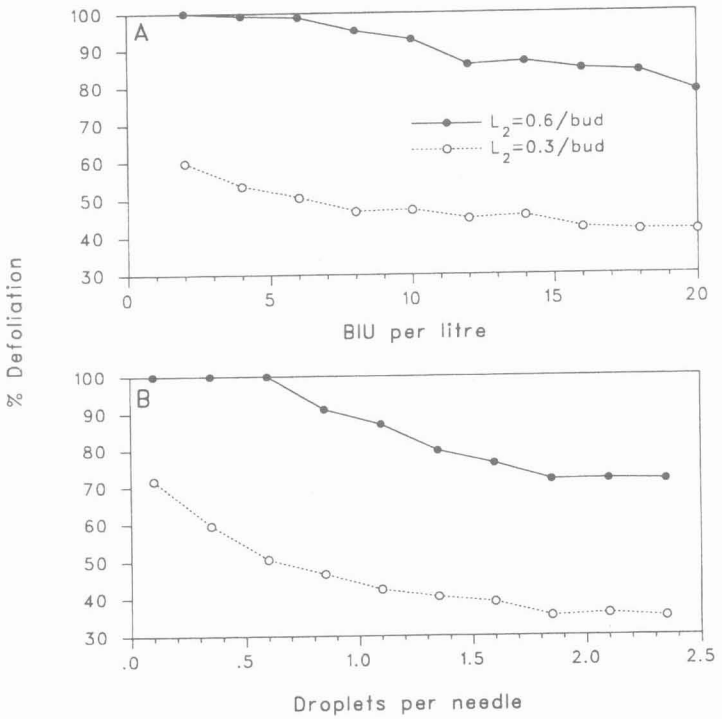

Figure 5. Relationship between end of season defoliation and spray characteristics. (A) Influence of product potency. (B) Influence of droplet density (application rate). Solid lines: high-density budworm population. Dotted lines: medium density populations.

Droplet density

Two series of simulations were run, each varying droplet density from 0.1 to 2.35 droplets per needle (4.1 mg of needles, dry weight). Densities of 1 droplet per needle are often achieved in operational programs. Other parameters were as in the previous series. Droplet density had a far more pronounced effect on defoliation than did product potency (Fig. 5b). There is a considerable advantage in increasing droplet density, especially against very high population densities. If one considers spraying as distributing *Bt* on foliage, it is thus more profitable to obtain a higher number of droplets containing less active ingredient than to distribute fewer droplets with a higher *Bt* content.

Spray timing

The issue of the optimal spray timing rests on two sets of parameter values: the product's stage-specific toxicity matrix, such as found in Table 4, and the 3rd instar exposure parameter. Five series of simulations were run, each varying the average instar of the budworm population at spray time from peak 3rd to peak 6th. In the first two simulations, defoliation on balsam fir was simulated, first with L_3 exposure X_3=0.5 then with X_3=1. In the next two series, defoliation on white spruce was simulated under the same conditions as in the first two series. The fifth simulation series (using healthy balsam fir and X_3=0.5) was conducted with the toxicity matrix of DIPEL 48AF instead of FORAY 48B to determine the influence of the change in product on efficacy and optimal timing. In all cases, product potency was set to 12.7 BIU/L and droplet density to 1 per needle. The initial budworm population was set at 0.5 larvae/bud and stage-specific survival rates typical of outbreak populations were used (no parasitism by *A. fumiferanae*).

Not surprisingly, optimal spray timing depended on host type as well as on the value of X_3 (Fig. 6). With X_3=0.5, optimal timing was about 3.6-4.0 for balsam fir and anywhere from 4.0 to 5.3 for white spruce. However, FORAY 48B and DIPEL 48AF produced very similar efficacy and optimal timing. This is due to the fact that the toxicity matrices of these two products are very similar. The model may generate very different results with drastically different toxicity matrices.

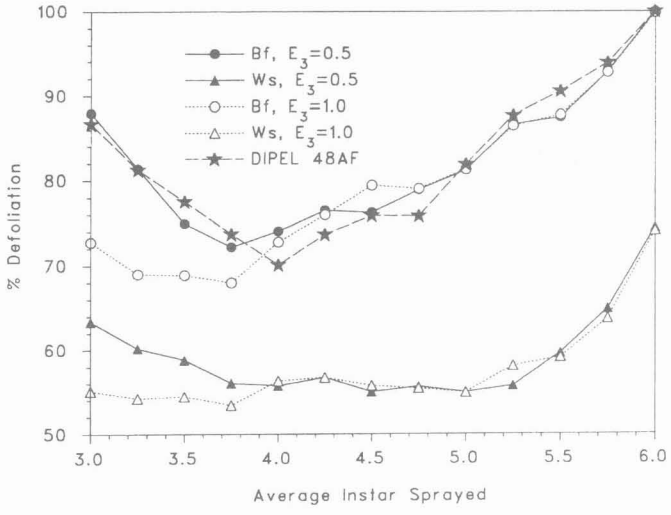

Figure 6. Relationship between spray timing (expressed as the average instar of the population at the time of application), and end of season defoliation under different sets of conditions. Closed symbols: 3rd instar exposure X_3=0.5, on balsam fir (circles) and white spruce (triangles). Open symbols: 3rd instar exposure X_3=1.0, on balsam fir (circles) and white spruce (triangles). Stars: DIPEL 48AF on balsam fir, with X_3=0.5.

Droplet diameter and size spectrum

Fourteen series of simulations were run, each with a different distribution of droplet diameters (mean and dispersion). These distributions were generated from the lognormal probability function, with a maximum diameter of 320 µm. The mean diameter (µ) was varied between 20 and 140 µm, in steps of 10 µm. The spread of the distribution (s) was made proportional to $1/\mu^2$ to generate a realistic series of droplet-size spectrum distributions (Fig. 7a). To maintain a constant application rate (volume per ha), the droplet density (δ) was made inversely proportional to the volume of each frequency distribution of droplet diameters ($\delta \propto 1/V$ where $V = \pi/6 \sum (f_i D_i^3)$, where f_i is the relative frequency of diameter class i and D_i is the diameter class centre; see shaded area in Fig. 7b). The initial density of the budworm population was set at 0.5 larvae per healthy balsam fir bud, with outbreak-level survival rates and no parasitism by *A. fumiferanae*. The toxicity matrix of FORAY 48B was used, with X_3=0.5. Each series was run twice, the first time with a spray aimed at peak 4th instar, and again with a spray aimed at peak 5th instar. The results (Fig. 7b) indicate that the model is relatively insensitive to the droplet diameter distribution over a wide range of distributions (with mean diameters ranging from 10 to 90 µm). Distributions with diameters > 90 µm were less efficient because of decreased droplet density leading to lower probabilities of ingestion.

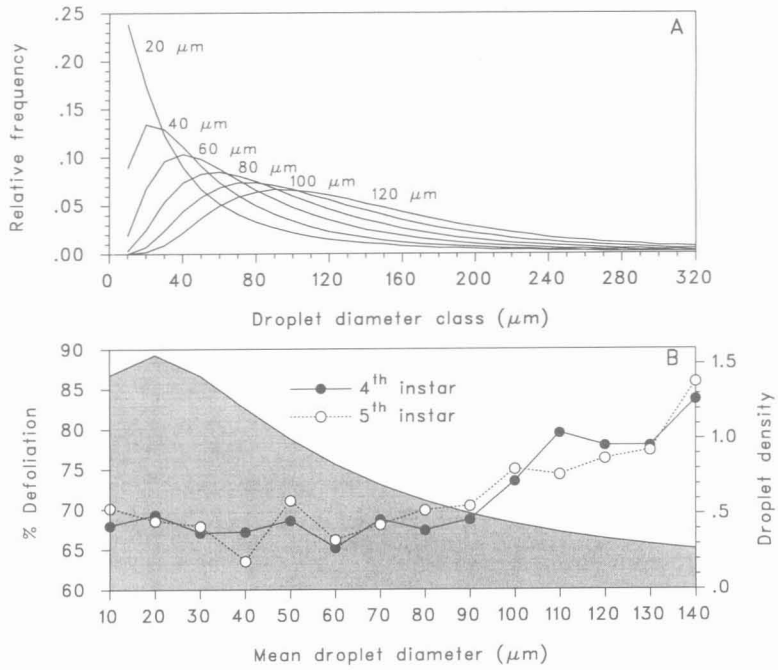

Figure 7. Analysis of the influence of droplet diameter distributions on efficacy. (A) Droplet diameter spectra used as model input. (B) Shaded area: droplet densities associated with each spectrum's mean droplet diameter; and resulting end of season defoliation. Full circles: sprays aimed at average instar AI=4.0. Open circles: sprays aimed at AI=5.0.

CONCLUSIONS

Cooke's model can be used to generate prescription tables recommending products, application rates, timing and number of applications as functions of initial budworm population density and host plant type. Such tables would, of course, be conditional on the protection objectives. For example, a manager may set an objective of 50% maximum tolerable defoliation. With this criterion, the model could be run to determine the least costly application strategy needed (if any) to achieve the objective under the specified circumstances (if achievable at all).

Analysis of model behaviour has shown that input temperatures have only a limited impact on model output (over reasonable ranges of course). But several input parameters are quite critical and must be known in order to evaluate the protection potential of different *Bt* use strategies. These are, in decreasing order of importance:

- Initial population density relative to the number of buds. This can be measured from samples taken in the fall, as long as overwintering mortality and convergence of larvae to the branch tips after emergence are taken into account (see Régnière *et al.* 1989 and Régnière and Duval 1998).

- Host plant condition (species, flowering and potential size of shoots).

- Stage-specific survival rates, especially in years where poor synchrony with bud break or population declines are expected.

- Deposit, especially droplet density per needle (4.1 mg dry weight of current-year foliage). Indeed, model results suggest that sprays, as current technology delivers them, are fairly optimal in terms of potency, and that much of the room left for improvement of efficacy resides in application rates. That is, droplets normally encountered by feeding larvae already contain lethal amounts of *Bt*. The most promising approach to increased kill (and foliage protection) is to heighten the odds of encounter (droplet density). Simulations have shown that the model is not very sensitive to droplet diameter spectra, over a wide range of diameters. Thus,

obtaining such data is not a high priority unless the spectrum is expected to be vastly different from a typical spectrum (Fig. 2).

- Product potency is a label-level input that needs no measurement. However, a product-specific toxicity matrix (LD_{50} and LD_{95} to instars 3 to 6) is required input. Once again the model is not highly sensitive to the toxicity matrix, so experimental error in their measurement should not have an undue influence on model output. However, marked differences between products could exist in their overall toxicity to spruce budworm, and in their relative toxicity to the various instars. Such differences must be taken into account. The prudent approach would be to conduct droplet-feeding bioassays for any new batch of product on a routine basis (see van Frankenhuyzen *et al.* 1997).

- Optimal spray timing is mainly a function of a product's toxicity matrix. But one factor that is currently not quantified can have a large influence on the optimal timing predicted by the model with most *Bt* products: exposure of 3rd instar larvae. This is an issue that should be addressed scientifically, although it seems unlikely that prescriptions for sprays earlier than average instar 3.5 should be made.

There are several key issues remaining in the further refinement of Cooke's model as a decision support tool for management of spruce budworm populations. An obvious one concerns the validation of model predictions regarding application rate (volume per hectare, translating into droplet density). This should be the object of field trials in the near future. But perhaps the most pressing need is to address scientific issues related to the use of the model on host plant types other than healthy, mature balsam fir. Although much is known of budworm development and feeding on healthy mature white spruce, Cooke's model has not been validated for this host plant. Significant knowledge gaps remain concerning budworm development and feeding rates on host plant species such as red and black spruce, or on heavily defoliated balsam fir. There is also an issue with predicting defoliation and protection efficacy on heavily flowering balsam fir. In this case, not only are shoot and budworm development and growth different from those on non-flowering trees (Carisey and Bauce 1997), but feeding behaviour and exposure of larvae feeding on flower clusters is also quite different than on vegetative buds (Blais 1952). These differences must be described quantitatively and taken into consideration in further refinement and validation of Cooke's model.

Finally, attention must be paid to the development of deposit assessment methods that do not require the counting of droplets on foliage. Biochemical assays providing information on the amount of active ingredient per unit of foliage (dry weight) can be translated into droplets per needle as long as a reasonable estimate of the distribution of droplet diameters is available. This ability would greatly simplify the task of making decisions about the likelihood of control success (given protection objectives) and the need for second applications.

ACKNOWLEDGMENTS

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APPENDIX

Model installation

Cooke's model is an independent console application (no user interaction while running) that is activated at the operating system prompt level. The current version runs under DOS (at the DOS prompt or in a DOS window). Because it was written in ANSI-compliant C++, Cooke's model is portable to a wide variety of platforms, including UNIX systems.

Cooke's model is best used under the control of the BioSIM system on IBM-compatible microcomputers. BioSIM allows the user to easily specify model parameters, run series of simulations, and interpret model output. Cooke's model is distributed with the most recent version of BioSIM (obtainable from the senior author), but can be obtained separately and linked to an existing BioSIM installation by following the linkage instructions in Section 2.7.2 of the BioSIM user's manual (Régnière *et al.* 1995).

Model usage

Figure A1 illustrates the relationships between the model, BioSIM, the computer's operating system and disk input and output files. Once launched by an operating system command (either by the user or by BioSIM), Cooke's model reads and writes necessary information from and to four files stored on disk in standard ASCII (text) format. Samples of all four are given in Tables A1-A4 in this appendix. The daily temperature input is read from a file in which each line contains four values (space- or tab-separated): year, Julian date, minimum and maximum daily air temperature (in °C) (see Table A4). This file can be generated automatically with BioSIM, but can also be provided by the user.

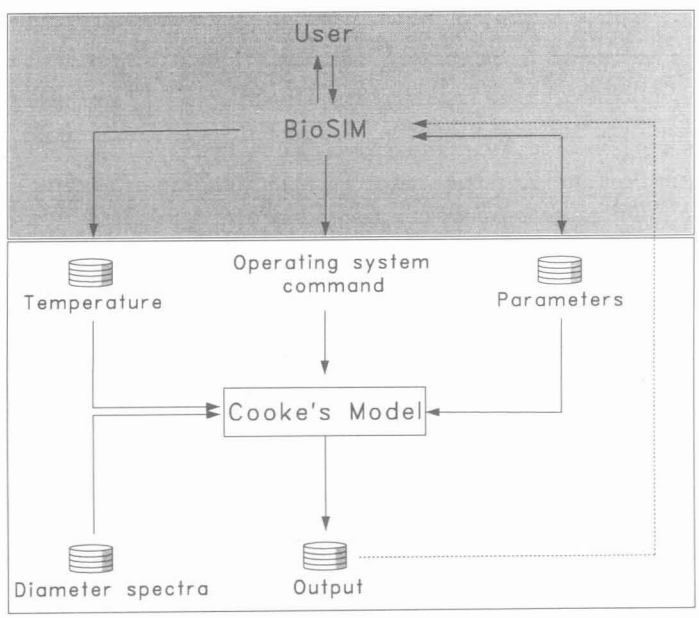

Figure A1. Diagram of Cooke's model interactions with the BioSIM simulation control system, the computer's operating system and disk storage. BioSIM control of the model is optional. The user can use the model at the operating system's command level.

The second model input file contains all user-specified input parameter values. The name of this file is passed on to the model as a command-line argument. These parameters are discussed in detail in the "MODEL INPUT

PARAMETERS" section. The parameter-specification file (ASCII text format) that is passed to Cooke's model as a command-line argument contains, as its first line, the name of the file (complete path) containing the input temperature data. The second line of the parameter-specification file contains the name (complete path) of the file in which the model writes its output. Other lines of this file specify the model parameters, one value per line, in the order in which they appear in Table 2 (see Table A2 for a sample input-parameter file). When Cooke's model is used in conjunction with BioSIM, parameter values are specified by the user via the model's parameter-specification dialog (Fig. 1), and BioSIM handles the writing and passing of the parameter file to the model. When the model is used outside the BioSIM context, the parameter file can be modified with a text editor.

Table A1. Sample droplet diameter distribution (spectrum) file (DEPOSIT.DEF provided with Cooke's model). (Note that headings are not actually part of the file.)

Diameter-class centre	Relative frequency
20	0.0890
40	0.2910
60	0.2520
80	0.1720
100	0.1123
120	0.0454
140	0.0189
160	0.0107
180	0.0047
200	0.0018
220	0.0006
240	0.0003
260	0.0012
280	0.0000
300	0.0006
320	0.0000
340	0.0000

Table A2. Sample model input-parameter file. (Note that the file contains no headings or explanatory text.)

Value in file	Explanation
C:\BIOSIM\USER\COOKE\INTEMP.DAT	Name of the temperature-input file
C:\BIOSIM\USER\COOKE\MODEL_OUT.BTO	Name of the model's output file
0.763	Initial budworm density
10	% *A. fumiferanae*
1	Host plant type
0.55	2nd instar survival rate
0.83	3rd instar survival rate
0.86	4th instar survival rate
0.77	5th instar survival rate
0.61	6th instar survival rate
0.5	Pupal survival rate
1	1st application eligibility flag
17	1st application potency
2	1st application droplet density
5	1st application timing
120	1st application longevity

(Table A2 cont'd)

Value in file	Explanation
C:\BIOSIM\COOKE\DEPOSIT.DEF	1st application diameter-spectrum file
0	2nd application eligibility flag
0	2nd application potency
0	2nd application droplet density
0	2nd application timing
0	2nd application longevity
C:\BIOSIM\COOKE\DEPOSIT.DEF	2nd diameter-spectrum file
0.65	3rd instar LD_{50}
1.8	4th instar LD_{50}
2.2	5th instar LD_{50}
5.1	6th instar LD_{50}
10.0	3rd instar LD_{95}
20.9	4th instar LD_{95}
30.1	5th instar LD_{95}
27.8	6th instar LD_{95}
0.5	3rd instar exposure

Table A3. Sample model output file. (Note that headings are not included in the actual files.)

			Proportion in stage								Potency							
Date	% Defo.	Log_{10} Density	active 2nd	3rd	4th	5th	6th	Pupae	AI	P:H Ratio	1st	2nd	Various efficacy statistics					
121	0.9	-0.13205	0.339	0.000	0.000	0.000	0.000	0.000	2.00	0.06	6.3	0.0	0	0	0	0	0	
122	2.1	-0.16152	0.463	0.000	0.000	0.000	0.000	0.000	2.00	0.06	5.8	0.0	0	0	0	0	0	
123	2.8	-0.17768	0.438	0.000	0.000	0.000	0.000	0.000	2.00	0.06	6.1	0.0	0	0	0	0	0	
124	3.5	-0.18923	0.496	0.000	0.000	0.000	0.000	0.000	2.00	0.06	6.2	0.0	0	0	0	0	0	
125	4.5	-0.21604	0.453	0.004	0.000	0.000	0.000	0.000	2.01	0.05	5.6	0.0	0	0	0	0	0	
126	5.8	-0.23876	0.496	0.014	0.000	0.000	0.000	0.000	2.02	0.06	5.9	0.0	0	0	0	0	0	
127	7.5	-0.27049	0.387	0.081	0.000	0.000	0.000	0.000	2.15	0.06	6.0	0.0	0	0	0	0	0	
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
186	53.0	-1.93482	0.000	0.000	0.000	0.000	0.000	0.006	7.50	1.50	0.0	0.0	0	25	32	78	0	
187	53.0	-2.01400	0.000	0.000	0.000	0.000	0.000	0.002	7.80	1.80	0.0	0.0	0	25	32	78	0	
188	53.0	-2.01400	0.000	0.000	0.000	0.000	0.000	0.002	7.80	1.80	0.0	0.0	0	25	32	78	0	
189	53.0	-2.01400	0.000	0.000	0.000	0.000	0.000	0.002	7.80	1.80	0.0	0.0	0	25	32	78	0	
190	53.0	-2.01400	0.000	0.000	0.000	0.000	0.000	0.002	7.80	1.80	0.0	0.0	0	25	32	78	0	
191	53.0	-2.01400	0.000	0.000	0.000	0.000	0.000	0.002	7.80	1.80	0.0	0.0	0	25	32	78	0	

Table A4. Sample temperature input file. (Note that the actual file contains no headings, and that data need not start on 1 January or end on 31 December.)

Year	Julian date	Minimum	Maximum
1997	60	-12.5801	-3.9760
1997	61	-13.5182	-1.4827
1997	62	-6.7033	9.9202
1997	63	-13.8756	-4.9624
1997	64	-16.4398	-9.6732
1997	65	-14.7718	-4.4567
1997	66	-17.8334	-5.8291
1997	67	-9.3149	0.4111
1997	68	-8.4099	4.2803
1997	69	-7.5874	8.5970
1997	70	-3.6060	9.8164
1997	71	-4.9374	7.5963
1997	72	0.0657	11.3551
1997	73	-7.2928	2.6886
1997	74	-15.6225	-4.0014
1997	75	-14.6955	-2.0945
.	.	.	.
.	.	.	.
.	.	.	.
1997	238	6.7397	17.3748
1997	239	9.2886	21.8483
1997	240	9.1274	24.4854
1997	241	7.9615	26.5016
1997	242	8.1129	23.1880
1997	243	9.7305	20.2102

The third input file is optional, and contains a frequency table of droplet diameters. There can actually be two of these, one for each simulated spray. A sample diameter-spectrum file is shown in Table A1. For more details on this file, see the "MODEL INPUT PARAMETERS" section.

The model's output file contains a daily time series of Julian dates plus values for each of the output variables, one line per day, starting as soon as budworm emergence begins in the spring, and until all individuals have either died or become adults. Output variables are described in the "MODEL OUTPUT" section. A sample output file is shown in Table A3.

Tutorial

This tutorial is a demonstration of the use of Cooke's model under the control of BioSIM version 4.0 for DOS. It aims to answer the question: "How would the nominal potency of a *Bt* product affect its expected efficacy?". The goal of the exercise is to reproduce Fig. A2. This goal will be reached in five steps, described in detail hereafter.

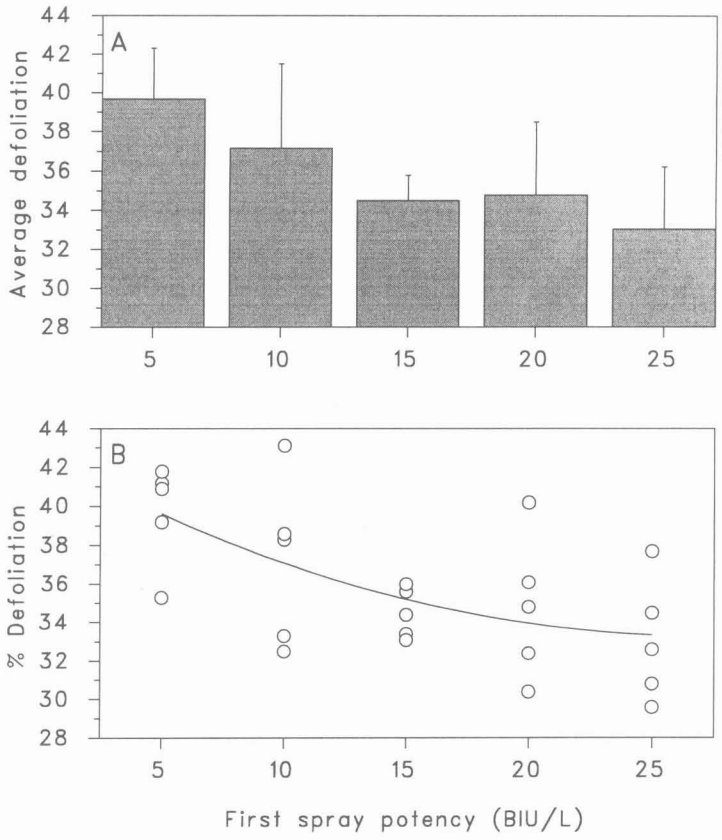

Figure A2. Tutorial examples of model output analysis with BioSIM. (A) Average defoliation as a function of spray 1 potency. (B) Regression analysis of the influence of spray 1 potency on end of season defoliation using outputs from individual runs rather than averages.

To proceed quickly through the tutorial, follow the underlined instructions. For more detailed explanations, read the regular type as well. In this example, we assume that BioSIM was installed in the \BIOSIM\ directory. If this is not the case, replace all occurrences of \BIOSIM\ in sub-directory names by the appropriate BioSIM installation directory. Proceed with this tutorial once BioSIM is installed on your system.

Step 1: Defining a new BioSIM project

- Click on the BioSIM icon to start the program, then click on <System> => <Project>

- Create a \BIOSIM\USER\COOKE\ sub-directory. Navigate through the filebox to find the \BIOSIM\USER\ sub-directory. In the field where the directory name appears, type COOKE to create a new folder in the \BIOSIM\USER\ directory. BioSIM will ask you if you really want to create this folder. Click on <OK>. You have now defined a new project in sub-directory \BIOSIM\USER\COOKE\. This is the folder where information pertaining to subsequent simulations will be stored. Each project you define should conform to a particular theme. You can switch between different projects at any time during a BioSIM session.

Step 2: Defining a simulation task

- Click on <Simulations> => <Tasks>. The task definition screen should pop up. As this is a new project, the task list should be empty. You are now going to define a task which, when executed, will automatically perform the desired simulations. Defining a simulation task consists of three main steps: creating a new entry in the task list, filling out the task-definition form, and validating the task specification.

- Create a new entry in the task list by clicking on <Add Task>. A sliver window should appear in the task list, presenting you with a new task specification form. You will next fill in the necessary fields. If at any time you click outside the task specification form, the form will be canceled and the task will not be added to the task list. Filling in the task specification form is done in 7 steps:

  1. Click on the field labeled "T" (for Type) in the task specification form, and choose "Parametric" from the pop-up menu. The symbol "P" in the Type field indicates you have chosen to define a parametric task. BioSIM accommodates four kinds of simulation tasks differentiated by which type of input parameters are kept constant and which are allowed to vary (see Régnière *et al.* 1995 for details).

  2. Click on the field labeled "ID" and choose "Cooke's *Bt* efficacy model" from the pop-up menu. The symbol "bt" should appear in the Model Identification field.

  3. Type "5" in the field labeled "n". In simulations where either temperature regimes are randomized or a model is stochastic, some replication is desirable in order to achieve more precise predictions. However, there is a limit to the precision gained by replication. Replication also takes time. Consequently we choose n=5 replicates as a compromise.

  4. Click on the field labeled "Name" and choose "Spray 1 Potency" from the pop-up menu. That parameter name should appear in the Parameter Name field of the task specification form. Every model has its own unique roster of input parameters. In this series of simulations we want to vary the input parameter "Potency1".

  5. Type "5" in the field labeled "Min", "25"in the field labeled "Max" and "5" in the field labeled "Step". The result of this is that "Potency1" will be varied from 5 to 25 BIU/L in steps of 5 (5 levels).

  6. Click on the "TG parameter file name" field. Fill in the menu with the information given in the table below. Click on <Save>. Type PECHE96 in the "File" field. Press return. Click <OK> to save the parameters in a file. Click <OK> to store that file name in the task list. Cooke's model requires a file that contains daily temperatures throughout the field season. BioSIM can do the temperature generation automatically if you provide it with specifications for simulation, such as:

     - Year of simulation: 1996
     - Latitude: 45° 35' N; Longitude: 76° 02' W
     - Elevation: 130 m; Exposure: 0
     - Elevation tolerance: 250 m; Use climatic zones: NO
     - Weather trace duration: 1 to 365; Last day of real-time data: 365
     - Hourly output: NO; Simulation method: 1

  7. Click on the "Model parameter file name" field. Fill in the menu with the information given in Fig. 1. Click on <Save>. Type TEST in the "File" field. Press return. Click <OK> to save the parameters in a file. Click <OK> to store that file name in the task list. Cooke's model needs to know what the values are for input parameters other than the one that BioSIM will vary.

- Validate the newly defined task by clicking on <OK> at the far right of the task specification form. If the form has not been filled out correctly (e.g. some fields left empty), the task specification will not be validated. Fill out the form correctly. If you have correctly filled out the task specification form, you are ready to run the task you defined. At this point you can add new tasks to the task list if you wish.

Step 3: Running the simulations

Once the task list has been filled out, make sure that the tasks you want to run have a check mark (√) to the left of the task specification. Only checked tasks are run. The checks toggle off and on with the click of the mouse.

- Click on <Run √ Tasks> to run the simulations. BioSIM will indicate that it is setting up some files. Then, BioSIM opens a DOS window to run the requested simulations. The time needed to run the simulations depends on the number of replications, the number of steps in the parametric series and the speed of your computer. When BioSIM has finished running the task, it will reappear on your screen, with a task report. If the task report indicates that all the tasks ran successfully, then you are ready to proceed to summary and analysis. In the unlikely event that some tasks ran unsuccessfully, then you must figure out why and re-run the tasks.

Step 4: Summarizing the output

- Press the Escape key to erase the task report. From the main screen, click on <Analysis>. You should be presented with the task list. This list is slightly different from the one used for defining tasks, as it is used to analyze simulation outputs. There are three active fields for each task: the task definition field to the left, and the two parameter file name fields to the right. Clicking on either parameter file name field will cause the parameter menu to be displayed, although the fields of that menu will be locked. This allows you to review what the parameters were for that task. Clicking on the task description field will cause that task to be selected for analysis.

- Click on the task description field to select this task. Click on <Summary>. Now you are presented with an event summary menu. This menu allows you to automatically scan through a large amount of output to find the occurrence of particular events or features, and relate these to changes in input parameter values. In this example, you will relate defoliation level to changes in nominal potency.

- Click on the "Event-type" field to produce a list of possible event-types. Choose "Maximum value of Y". Click on the "Output Variable" field to produce a list of possible output variables for analysis. Choose "Defoliation" from the top of the list. Ensure that the "Transformation type" field is set to "NIL" and that the "Summary type" field is set to "Table of means". (These fields are like the last two in that they offer pop-up menu choices when they are clicked on.)

- Click on <Run> to run the analysis. After performing some calculations, a table of means is produced which lists the values of the input parameter that was systematically varied in the simulations, and the corresponding defoliation levels that resulted.

Step 5: Analyzing the summarized output - Graphics

- To graph the summarized output, click on <Graphics> from the table of means that was produced in the last step. BioSIM will shell out and invoke the graphics program PLT to produce a bar graph of defoliation versus product potency. This graph is shown (with cosmetic changes) in Fig. A2a. At this point, PLT offers full graphics capabilities so that you can customize the graph, print it out, or export it to some other graphics package. For more information on PLT, refer to the PLT user's manuals (Régnière 1989, 1990, 1992).

- Press the Enter key or space bar to terminate display of the bar graph. Type "quit" to leave the PLT graphics program. You should automatically return to BioSIM with the most recent event summary menu being displayed.

Step 6: Analyzing the summarized output - Graphics - Regression analysis

- Click on the "Summary type" field. Choose "Regression" from the list. A small menu that asks for the degree of the polynomial regression should pop up to the right.

- Type in 2, and click <OK>. Click on <Run> to run the polynomial regression of defoliation on potency. After performing some calculations, the next screen to pop up is the regression summary report. It reports the intercept (b_0) and the regression parameters b_1 and b_2 along with the r^2 value from fitting the model $Y = b + b_1X + b_2X^2$ where Y is defoliation and X is spray 1 potency.

- Click on <Graphics> to view a plot of the regression model. PLT is invoked to plot the regression, which should look like Fig. A2b (give or take stochastic differences in model output and cosmetic changes). You can modify the graphic or print it out. Refer to PLT documentation for help.

- Press the Enter key or the space bar to remove the graphic from the screen. Type "quit" and press the Enter key, once you are finished working with the graphic. PLT should terminate and BioSIM should return on-screen.

You have completed the tutorial and you can press the escape key until you are out of BioSIM.