

A LIFE SYSTEM SIMULATION MODEL FOR IMPROVING INUNDATIVE RELEASES OF THE EGG PARASITE, *Trichogramma minutum* AGAINST THE SPRUCE BUDWORM

S.M. SMITH and M. YOU¹

Faculty of Forestry, University of Toronto, Toronto, Ont. M5S 1A1 (Canada)

(Accepted 15 September 1989)

ABSTRACT

Smith, S.M. and You, M., 1990. A life system simulation model for improving inundative releases of the egg parasite, *Trichogramma minutum* against the spruce budworm. *Ecol. Modelling*, 51: 123–142.

A model, based on the concept and analysis of the population life system, is described for the spruce budworm, *Choristoneura fumiferana* (Clemens). Four years of field data collected from northern Ontario were used in the model to simulate inundative releases of the egg parasite, *Trichogramma minutum* Riley, for suppression of spruce budworm populations and determine the best strategy for parasite release in terms of frequency, timing and rate of release. Hypothetical releases, either 'single 24-h releases', 'single staggered releases' or 'double releases', were assumed to occur from 2 to 19 days after the first spruce budworm egg masses appeared. The model predicts that, if properly timed during the oviposition of spruce budworm, 'double releases' and 'single staggered releases' of parasites can be more effective than 'single 24-h releases' with the same rate of release. The best timing for either type of 'single release' was 14 days after the first egg masses appeared. For 'double releases', the best timing of the first release was 12 days after the first egg masses appeared with a second release 4 days later. 'Single staggered releases', at 12×10^6 ♀♀ per ha, provided the best suppression of spruce budworm populations (49%) when the emergence of the parasites increased over a 5-day period from 10, 15, 20, 25 and 30% per day. The simulated results varied slightly from year to year based on mean daily temperatures in the field.

INTRODUCTION

The spruce budworm (SBW), *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is the most important insect in the fir-spruce forest of

¹ Visiting Scientist from the Department of Plant Protection, Fujian Agricultural College, People's Republic of China.

eastern North America (Powell, 1980). Extensive areas of this forest have been destroyed by SBW from the Maritime Provinces in Canada to the Great Lake States in the United States (Blais 1983; Coulson and Witter, 1984). The life history of this species has been well documented (Morris, 1963; Sanders, 1985) with a number of studies focusing on its population dynamics (Morris, 1963; Royama, 1984; Blais, 1985). To date, however, these biological components have not been examined from a life system approach.

Trichogramma minutum Riley (Hymenoptera: Trichogrammatidae) is currently the only identified egg parasite of SBW in eastern North America. Parasitism of SBW eggs by *Trichogramma* is usually less than 15%, although levels greater than 70% have been observed (Anderson, 1976). Under natural conditions, parasitism levels by *T. minutum* are considered to be too low to have a significant impact on SBW populations (Houseweart et al., 1982), however, in recent years, studies have shown that through mass rearing and inundative release, parasitism of SBW eggs can be increased significantly (Houseweart et al., 1984). Smith et al. (1987) demonstrated the potential for ground releases of *T. minutum* to control SBW on 12-to-20-year-old white spruce stands in northern Ontario while Smith et al. (in press) has shown the effectiveness of aerial releases in reducing SBW populations, even in areas of high density.

In further developing this biological approach for controlling SBW, it is important to recognize and understand the effects of different strategies for the timing, frequency, and rate of *T. minutum* release on egg parasitism as well as their subsequent impact on larval populations (Houseweart et al., 1984; Smith et al., 1987). Previous studies have shown that by correctly synchronizing ground releases with the host's oviposition, two releases, at ca. 12×10^6 ♀♀ *T. minutum* per ha, can have a significant impact on overwintering larval populations (Smith et al., 1987). The best strategy for release, in terms of effectiveness and economy, however, has yet to be determined.

The evaluation of different strategies for release is prohibitively expensive when each strategy or combination of strategies must be tested in the field (Watt, 1964). The development of realistic population dynamics models which can provide accurate simulations allows such strategies to be examined relatively cheaply and easily in the laboratory. Techniques for analyzing population dynamics are used in various ways, but the life system approach can provide an intuitively satisfying framework for such studies (Hughes et al., 1984). Based on life table data of the SBW, the present paper outlines a life system simulation model which analyzes the population dynamics of SBW when *T. minutum* is released inundatively. The model uses 4 years of field data in computer experimentation to compare the outcome

of various strategies of release and identify the best approach for SBW suppression.

METHODS

Spruce budworm simulation model

The population dynamics of SBW was simulated using life system analysis. The model considered the life system of the SBW as a set of interacting components which included the 'internal' components of the population, known as state variables of the system, and the 'external' agencies which represented the sum of all various environmental factors influencing the population (Fig. 1).

Based on the known biology of SBW, each generation was considered to be approximately 1300 degree-days long with an average threshold temperature of 3.5°C (4.4°C for 3rd instar larvae through 6th instar; 2.8°C for pupae; and 2.5°C for overwintering 2nd instar larvae). For simulation, the annual life cycle of SBW was divided into ten stages (eg. egg, 1st, 3rd, 4th, 5th, 6th, 2nd overwintering instar and 2nd feeding instar larva, pupa, and adult). Each stage was subdivided into a variable number of 10 degree-day age-classes according to the thermal constant for that stage. The thermal

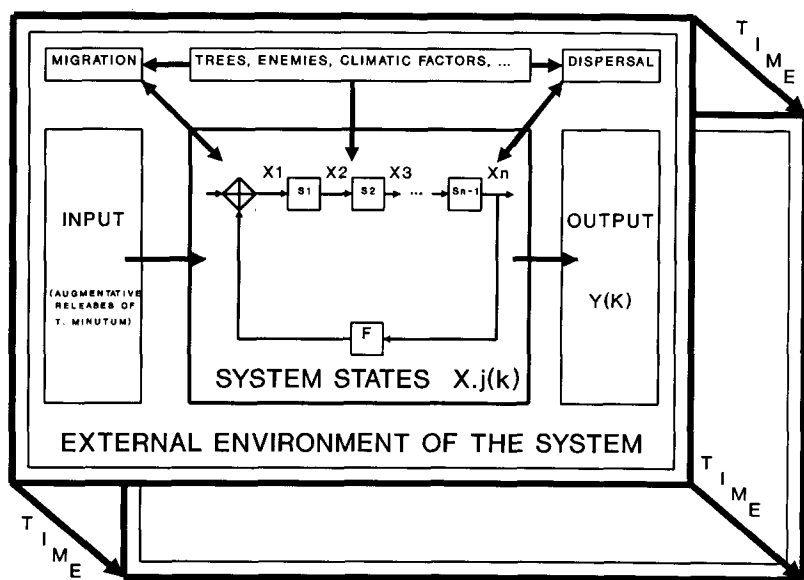


Fig. 1. Structure of the spruce budworm life system with inundative releases of the egg parasite.

TABLE 1

Structure of the matrix, X , from the output of the SBW simulation model

Age-classes of spruce budworm	Life stage of spruce budworm									
	$L_{2(FD)}^a$ ($x_{i,1}$)	L_3 ($x_{i,2}$)	L_4 ($x_{i,3}$)	L_5 ($x_{i,4}$)	L_6 ($x_{i,5}$)	P ($x_{i,6}$)	A ($x_{i,7}$)	E ($x_{i,8}$)	L_1 ($x_{i,9}$)	$L_{2(OW)}$ ($x_{i,10}$)
$x_{1,j}$	$x_{1,1}$	$x_{1,2}$	$x_{1,3}$	$x_{1,4}$	$x_{1,5}$	$x_{1,6}$	$x_{1,7}$	$x_{1,8}$	$x_{1,9}$	$x_{1,10}$
$x_{2,j}$	$x_{2,1}$	$x_{2,2}$	$x_{2,3}$	$x_{2,4}$	$x_{2,5}$	$x_{2,6}$	$x_{2,7}$	$x_{2,8}$	$x_{2,9}$	$x_{2,10}$
$x_{3,j}$	$x_{3,1}$	$x_{3,2}$	$x_{3,3}$	$x_{3,4}$	$x_{3,5}$	$x_{3,6}$	$x_{3,7}$	$x_{3,8}$	$x_{3,9}$	$x_{3,10}$
$x_{4,j}$	$x_{4,1}$	$x_{4,2}$	$x_{4,3}$	$x_{4,4}$	$x_{4,5}$	$x_{4,6}$	$x_{4,7}$	$x_{4,8}$	$x_{4,9}$	$x_{4,10}$
$x_{5,j}$	$x_{5,1}$	$x_{5,2}$	$x_{5,3}$	$x_{5,4}$	$x_{5,5}$	$x_{5,6}$	$x_{5,7}$	$x_{5,8}$	$x_{5,9}$	$x_{5,10}$
$x_{6,j}$	$x_{6,1}$	$x_{6,2}$	$x_{6,3}$	$x_{6,4}$	$x_{6,5}$	$x_{6,6}$	$x_{6,7}$	$x_{6,8}$	$x_{6,9}$	$x_{6,10}$
$x_{7,j}$	$x_{7,1}$	$x_{7,2}$	$x_{7,3}$	$x_{7,4}$	$x_{7,5}$	$x_{7,6}$	$x_{7,7}$	$x_{7,8}$	$x_{7,9}$	$x_{7,10}$
$x_{8,j}$	$x_{8,1}$	$x_{8,2}$	$x_{8,3}$	$x_{8,4}$	$x_{8,5}$	$x_{8,6}$	$x_{8,7}$	$x_{8,8}$	$x_{8,9}$	$x_{8,10}$
$x_{9,j}$	$x_{9,1}$	—	—	—	$x_{9,5}$	$x_{9,6}$	$x_{9,7}$	$x_{9,8}$	$x_{9,9}$	$x_{9,10}$
$x_{10,j}$	$x_{10,1}$	—	—	—	$x_{10,5}$	$x_{10,6}$	$x_{10,7}$	$x_{10,8}$	$x_{10,9}$	$x_{10,10}$
$x_{11,j}$	$x_{11,1}$	—	—	—	$x_{11,5}$	$x_{11,6}$	$x_{11,7}$	$x_{11,8}$	$x_{11,9}$	$x_{11,10}$
$x_{12,j}$	$x_{12,1}$	—	—	—	$x_{12,5}$	$x_{12,6}$	$x_{12,7}$	$x_{12,8}$	$x_{12,9}$	$x_{12,10}$
$x_{13,j}$	$x_{13,1}$	—	—	—	$x_{13,5}$	$x_{13,6}$	—	$x_{13,8}$	$x_{13,9}$	$x_{13,10}$
$x_{14,j}$	— ^b	—	—	—	$x_{14,5}$	—	—	$x_{14,8}$	$x_{14,9}$	$x_{14,10}$
$x_{15,j}$	—	—	—	—	$x_{15,5}$	—	—	$x_{15,8}$	$x_{15,9}$	$x_{15,10}$
$x_{16,j}$	—	—	—	—	$x_{16,5}$	—	—	$x_{16,8}$	$x_{16,9}$	$x_{16,10}$
$x_{17,j}$	—	—	—	—	$x_{17,5}$	—	—	—	$x_{17,9}$	$x_{17,10}$
$x_{18,j}$	—	—	—	—	$x_{18,5}$	—	—	—	$x_{18,9}$	$x_{18,10}$
$x_{19,j}$	—	—	—	—	—	—	—	—	—	$x_{19,10}$

^a $L_2(FD)$, 2nd instar feeding larval stage; L_3 , 3rd instar larval stage; L_4 , 4th instar larval stage; L_5 , 5th instar larval stage; L_6 , 6th instar larval stage; P, pupal stage; A, adult state; E, egg stage; L_1 , 1st instar larval stage; and $L_2(OW)$, 2nd instar overwintering larval stage.

^b — denotes non-existent elements in the matrix which are out of the range of the stage distribution. All such elements were set to zero in the computer simulation.

constants were taken from Cameron et al. (1968) and Régnière (1987). Because of the stage overlapping phenomenon within SBW, a multiple column matrix, X , with 19 rows and 10 columns (19, number of age-classes; 10, number of stages) was generated to describe the age-stage-structure of the SBW population and used as the output form of the simulation model (Table 1). Each column in this matrix represented one stage, while each row represented one age-class. The element, x_{ij} , therefore, represented those individuals at age-class i and stage j .

The model assumed that 2nd instar SBW larvae followed a normal distribution when emerging from overwintering sites in the spring. This assumption was supported by field results reported in Régnière (1987, fig. 5).

As a poikilotherm, the rate of SBW development is directly dependent on temperature. The growth of individuals in the SBW population (or move-

ment of elements from one age-class and stage to the next in the matrix), therefore, was best described by a set of difference equations which calculated growth based on mean daily temperature, $T(K)$, above the minimum temperature required for development for any given stage (C_j). Because the thermal summation of degree-days above the developmental threshold at each stage could result in some of the population advancing only a partial age-class instead of a complete age-class, on any given day, the number of age-classes which the population could grow was defined by:

$$M_j(K) = \text{int} \{ [T_j(K) - C_j] / 10 \} \quad (1)$$

and

$$G_j(K) = \{ [T_j(K) - C_j] / 10 \} - M_j(K) \quad (2)$$

where $M_j(K)$ is the number of whole age-classes grown by those individuals of the j th stage on the k th day, $G_j(K)$ the fractional part of an age-class grown by those individuals of the j th stage on the k th day, $T_j(K)$ the mean daily temperature ($^{\circ}\text{C}$) of the k th day within the j th stage, and C_j the developmental threshold ($^{\circ}\text{C}$) of the j th stage.

Equation (1) calculated the number of complete age-classes the SBW population could grow from the summed degree-days above the developmental threshold. $M_j(K)$ did not exceed three age-classes because greater than 30 degree-days above the threshold temperature (2.5, 2.8 or 4.4°C , depending on the SBW life stage) would have to be accumulated in any one day to reach this level and daily mean temperatures in Canada are usually less than 30°C , even during the summer months. Equation (2) predicted that fraction of the SBW population remaining from Equation (1) which could also continue to grow to the next age-class. The remaining fraction of the SBW population, $1 - G_j(K)$, would remain in the same age-class or would advance only $M_j(K)$ age-classes.

Growth of any insect population is also dependent on the mortality or survival of individuals within that population over time. Thus, to make the model more realistic, life table data (Morris, 1963) were used to divide the survival rate for each stage of SBW, S_j ($j = 1, 2, \dots, n - 1$), into an abiotic survival rate (SN_j) and a biotic survival rate (SP_j). The abiotic survival rate was considered to result from environmental factors, genetic characteristics and/or unhealthy development from poor nutrition. The biotic survival rate was considered to be the sole result of parasites, predators and pathogens. Based on work by Ruesink (1982), the abiotic survival rate was assumed to occur 'between' the life stages while the biotic survival rate was considered to occur 'during' each stage. In general, abiotic factors usually cause mortality as the insect molts, whereas, biotic factors remove individuals from the population during the actual stage of development.

The abiotic survival rate on the k th day, $SN_j(K)$, was defined as:

$$SN_j(K) = SN_j \quad (3)$$

where SN_j is the abiotic survival rate of the j th stage, and was derived from the SBW life table developed in New Brunswick by Morris (1963). Morris (1963) separated larval survival into only two categories, small larval survival (1st to 3rd instar) and large larval survival (4th to 6th instar). In our model, the mean survival rate for small or large larvae from Morris' life table was divided by the number of instars in each category (eg. 3 instars each for small and large larvae) to calculate the abiotic survival for individual larval instars.

The daily biotic survival rate for each SBW stage was dependent on the daily developmental rate of that stage because biotic mortality agents were considered to act throughout each stage, not only at the end of the stage. The developmental rate was derived from the mean daily temperature and number of degree-days required (thermal constant) above the developmental threshold for each stage. Thus, the developmental rate for the j th stage on the k th day, $R_j(K)$, was defined as:

$$R_j(K) = [T_j(K) - C_j]/D_j \quad (4)$$

where D_j is the thermal constant (degree-days) of the j th stage. Because the biotic survival rate on the k th day, $SP_j(K)$, was assumed to occur during each stage, rather than at the end of each stage, it could be defined as:

$$SP_j(K) = SP_j^{R_j(K)} \quad (5)$$

where SP_j is the biotic survival rate of the j th stage.

Four difference equations modelled the growth of the SBW population within the matrix. The first equation described population growth from the last age-class within a stage to the first age-class within the next stage:

$$X_{1,j+1}(K+1) = SP_j(K) SN_j(K) G_j(K) X_{N_j,j}(K) \quad (\text{if } M_j(K) = 0) \quad (6)$$

where N_j is the number of age-classes for the j th stage, and $X_{i,j}(K)$ the number of individuals for age-class i and stage j on the k th day. Such relatively slow development occurred when the mean daily temperature was low ($M_j(K) = 0$) and only a fraction of the individuals ($G_j(K)$) in the population could grow from one age-class to the next. The remaining individuals in that population could not advance because of the low thermal accumulation and had to remain in the same age-class.

The second equation described similar population growth from one stage to the next when the mean daily temperatures were higher:

$$X_{i,j+1}(K+1) = SP_j(K) SN_j(K) \left\{ [1 - G_j(K)] X_{N_j - M_j(K) + i, j}(K) + G_j(K) X_{N_j - M_j(K) + i - 1, j}(K) \right\} \quad (\text{if } 1 \leq i \leq M_j(K)) \quad (7)$$

where $X_{i,j}(K+1)$ is the number of individuals for age-class i and stage j on the $k+1$ th day. Here, because of the relatively high daily temperatures ($1 \leq i \leq M_j(K)$ and ≥ 14.4 degree-days), individuals in the last several age-classes of one stage could develop to any one of the first couple of age-classes in the following stage. The amount of growth from one stage to the next was determined by the cumulative degree-days above the threshold.

The third equation described two types of population growth; individuals in the population which could grow between stages (as in equation 7) and individuals in the population which could grow from the first age-class in one stage to the next age-class(es) in the same stage.

$$X_{i,j}(K+1) = SP_j(K) \left[1 - G_j(K) \right] X_{1,j}(K) + SP_{j-1}(K) SN_{j-1}(K) \times G_{j-1}(K) X_{N_{j-1},j-1}(K) \quad (\text{if } i = M_j(K) + 1) \quad (8)$$

These two types of growth described in equation (8) were determined by the initial age-class from which the individuals started their development ($i = M_j(K) + 1$) and the mean daily temperature ($T(K)$).

The fourth equation described simple population growth between age-classes within one stage:

$$X_{i,j}(K+1) = SP_j(K) \left\{ \left[1 - G_j(K) \right] X_{i-M_j(K),j}(K) + G_j(K) X_{i-M_j(K)-1,j}(K) \right\} \quad (\text{if } M_j(K) + 2 \leq i \leq N_j) \quad (9)$$

In this case, the model only described growth from the second age-class to the last age-class within each stage ($M_j(K) + 2 \leq i \leq N_j$).

When the SBW population developed to the adult stage ($j = 7$), the moths continued to age until their death (the number of age-classes for the adult stage was 12). All moths were considered to have died after age-class 12, which is consistent with female longevity reported in Régnière (1983). It was assumed that female moths mated during their 1st day of life and thus, could oviposit only during age-classes 3 to 11 (Outram, 1971). Based on the results of Sanders and Lucuik (1975), Sanders et al. (1978) and Régnière (1983), the percentage of eggs laid each day in age-class i ($i = 3, 4, \dots, 11$) was assumed to decline from 40, 18, 12, 10, 8, 6, 3, 2, to 1% per day, respectively. The overall oviposition rate was defined as 200 eggs per female with a sex ratio of $\delta : \text{♀}$ 1:1 for the adult population (Morris, 1963; Régnière, 1983).

The elements in column 7 (the adult stage) in matrix X , were calculated by another set of difference equations which predicted the pattern of adult development and daily egg deposition. These equations allowed for three different scenarios according to the age-class of the adult and the mean daily temperature.

The first case allowed for the death of adult moths after age-class 12:

$$X_{i,j}(K+1) = 0 \quad (\text{if } i > N_j) \quad (10)$$

The second case described the slow rate of adult growth and oviposition (by either 0 or 1 age-class per day) when the temperature was low ($M_j(K) = 0$) prior to age-class 12. Here moths aged (progressed through the adult age-classes) by:

$$X_{i,j}(K+1) = \text{sp}_j(K) \left\{ [1 - G_j(K)] X_{i,j}(K) + G_j(K) X_{i-1,j} \right\} \\ (\text{if } M_j(K) = 0) \quad (11)$$

and laid eggs each day such that:

$$X_{1,j+1}(K+1) = G_j(K) \sum_{i=3}^{11} X_{i,j}(K) P_i EF \quad (\text{if } M_j(K) = 0) \quad (12)$$

where P_i is the percentage of eggs laid by the i th age-class (40, 18, 12, 10, 8, 6, 3, 2 to 1%), E the oviposition rate (200 eggs per female moth) and F the sex ratio ($\delta : \text{♀}$ 1:1).

The third case considered the relatively fast rate of adult growth and oviposition (by either 1 or 2 age-classes per day) when the mean daily temperature was high ($M_j(K) \geq 1$) prior to age-class 12. Moths aged by:

$$X_{i,j}(K+1) = \text{sp}_j(K) \left\{ [1 - G_j(K)] X_{i-M_j(K),j}(K) \right. \\ \left. + G_j(K) X_{i-M_j(K)-1,j}(K) \right\} \quad (\text{if } M_j(K) \geq 1) \quad (13)$$

For the egg stage following oviposition, as with larval growth, some of the individuals could advance only a partial age-class instead of a complete age-class, on any given day, and thus, the number of complete age-classes which eggs following oviposition could develop through was defined by:

$$X_{M_j(K),j+1}(K+1) = [1 - G_j(K)] \sum_{i=3}^{11} X_{i,j}(K) P_i EF \quad (\text{if } M_j(K) \geq 1) \\ (14)$$

The fraction of the SBW egg population remaining from equation (14) which could also continue to grow, following oviposition, into the next age-class was defined as:

$$X_{M_j(K)+1,j+1}(K+1) = G_j(K) \sum_{i=3}^{11} X_{i,j}(K) P_i EF \quad (\text{if } M_j(K) \geq 1) \quad (15)$$

Simulation for the best strategy of release

A number of different strategies for inundative release were tested in the simulation by varying the frequency, timing and number of parasites released. Whenever the inundative releases were made in the simulation, the values of the survival rate for SBW egg populations were changed (Fig. 2). These changes were made according to the field data for releases conducted between 1983 and 1986, inclusive, near Hearst, Ontario (84°W; 50°N) (Smith et al., in press). Daily maximum/minimum temperatures were collected annually at this site between mid-June and Mid-August. For days outside the seasonal range (1 March–1 October), values were obtained from Atmospheric Environment Services for Mattice, Ontario (83°W; 50°N). These values were input into the SBW simulation model.

Houseweart et al. (1982) showed that SBW eggs are susceptible to parasitism by *T. minutum* for 5 days at 21°C and 3 days at 27°C. Lawrence and Houseweart (1985) and Smith et al. (1987) demonstrated that under average field conditions, a second generation of *T. minutum* could develop and emerge within ca. 14 days. If released early in the SBW oviposition curve, therefore, this second generation of parasites could still successfully attack susceptible SBW eggs laid at the end of the oviposition period (on average, SBW oviposition occurs during the first 3 weeks of July). In the

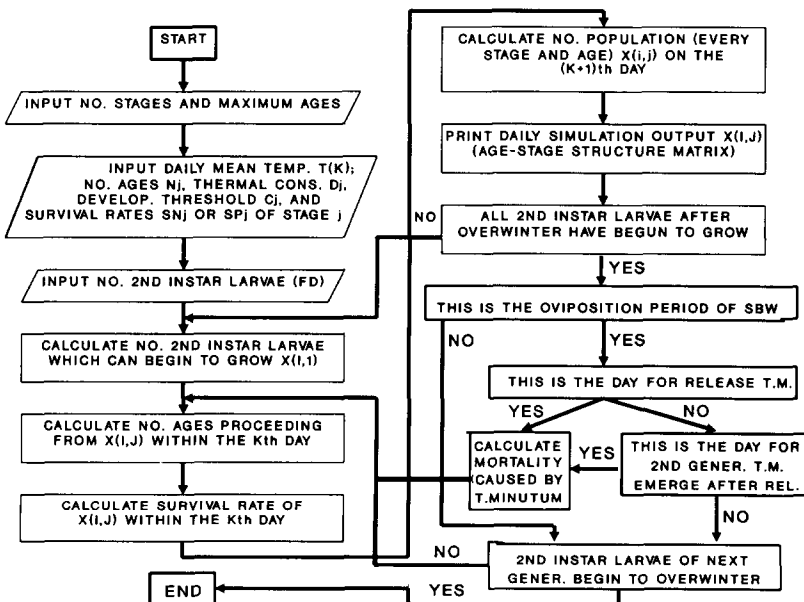


Fig. 2. Procedure for simulation the spruce budworm life system with inundative releases of the egg parasite.

present model, data on the mean developmental rate for strains of *T. minutum* from Smith and Hubbes (1986) were used to obtain the date prior to the end of SBW oviposition on which the 2nd generation of *T. minutum* emerged in the field. If a second generation was possible, the number of females emerging and their impact on SBW eggs was calculated based on: (1) the longevity, fecundity, production of progeny and sex ratio of the first generation (Smith and Hubbes, 1986); and (2) the number of susceptible SBW eggs as predicted by the model.

Frequency. Two frequencies of release were examined, based on information obtained in previous studies (Smith et al., 1987, in press). A 'single release' of *T. minutum* entailed either: (1) the release of 12×10^6 ♀ ♀ parasites per ha in one 24-h period and emergence over 24 h (single 24-h release), or (2) the release of 12×10^6 ♀ ♀ per ha in one 24-h period and emergence over 5 days (single staggered release).

For the 'single staggered release', the daily pattern of emergence from day 1 to day 5 was defined as: (1) Strategy A: increasing from 10, 15, 20, 25, and 30% per day; (2) Strategy B: normally distributed at 10, 20, 40, 20, and 10% per day; or (3) Strategy C: decreasing from 30, 25, 20, 15, and 10% per day. 'Double releases' consisted of two 'single 24-h releases' conducted at different points along the SBW oviposition curve. Parasites were assumed to emerge within a 24-h period following each of these two releases.

Timing. In order to examine the effect of timing of these two types of releases, both were applied at different points over the SBW oviposition period. For the 'single 24-h release', releases of *T. minutum* were made in separate 24-h periods beginning on the 1st day of egg-laying and continuing consecutively, until the 2nd day following the peak deposition of susceptible egg masses. Houseweart et al. (1982) showed that, at field temperatures, *T. minutum* is only capable of parasitizing SBW eggs successfully within the first 4 days of oviposition. Egg masses older than this, therefore, were not considered susceptible and were not included in the model. The dynamics of the model predicted that 4 days would be equivalent to nine age-classes within the egg stage of SBW. 'Double releases' were made as for 'single 24-h releases' by using a series of combinations for the number of days between each 24-h release (1–12 days). For example, the first 24-h release was fixed on a given day and the second 24-h release was shifted from day to day during the oviposition period (Table 2). The given day on which the first release was conducted also changed over the oviposition period as for the 'single 24-h releases'.

Rate. After the best frequency and timing for the two release strategies were established, the rate of release was examined using one year of data

TABLE 2

Timings used to test 'double releases' of *T. minutum* for suppression of spruce budworm in the simulation model

Date of 1st release in July	Date of 2nd release in July												
	13	14	15	16	17	18	19	20	21	22	23	24	25
12	×	×	×	×	×	×	×	×	×	×	×	×	×
13		×	×	×	×	×	×	×	×	×	×	×	×
14			×	×	×	×	×	×	×	×	×	×	×
15				×	×	×	×	×	×	×	×	×	×
16					×	×	×	×	×	×	×	×	×
17						×	×	×	×	×	×	×	×
18							×	×	×	×	×	×	×
19								×	×	×	×	×	×
20									×	×	×	×	×
21										×	×	×	×
22											×	×	×
23												×	×
24													×

(1983). Those rates of release selected for the 'single 24-h release' were 2, 4, 6, 8, 10 and 12×10^6 ♀♀ per ha. Each release rate was set for 22 July because this represented the best timing for a 'single 24-h release'. 'Double releases' were made by examining all possible combinations for each of the two releases at the same rates. As with the 'single 24-h release', the timing for each of the 'double releases' was set by the best strategy derived previously: 21 July for the first release and 24 July for the second release. The percentage of SBW egg masses and eggs which would be parasitized at each rate were derived from Smith et al. (in press).

SIMULATION RESULTS AND ANALYSIS

Simulation of spruce budworm population dynamics

The simulation model of SBW population dynamics developed here made use of mean stage mortalities from some 80 life tables collected in New Brunswick by Morris (1963). To date, this mean life table (table 2.1 in Morris, 1963) is the only one available for the simulation of SBW populations.

To initialize the model and begin a simulation, values were first assigned to each of the state variables X_{ij} ($i = 1, 2, \dots, 19$; $j = 1, 2, \dots, 10$). The initiation of emergence and feeding for overwintering 2nd instar larvae was defined as that day on which the mean daily temperature exceeded the

developmental threshold for that stage (4.4°C). The mean daily temperature, number of ages, thermal constants and developmental thresholds for various stages were also established so that the developmental rates and the number of ages for those individuals of the j th stage which would continue to grow could be calculated.

Once the model was initialized, the dynamic simulation proceeded from day to day according to the accumulation of degree-days from the mean daily temperatures provided. The age-stage-structure matrix (output of the simulation model) was printed for each day. The current simulation began from the emergence of the 2nd instar larvae and stopped when the 2nd instar larvae of the following generation went into overwintering diapause.

A comparison of the observed and simulated SBW populations for Hearst, Ontario in 1985 is shown in Fig. 3. Because only observed data from

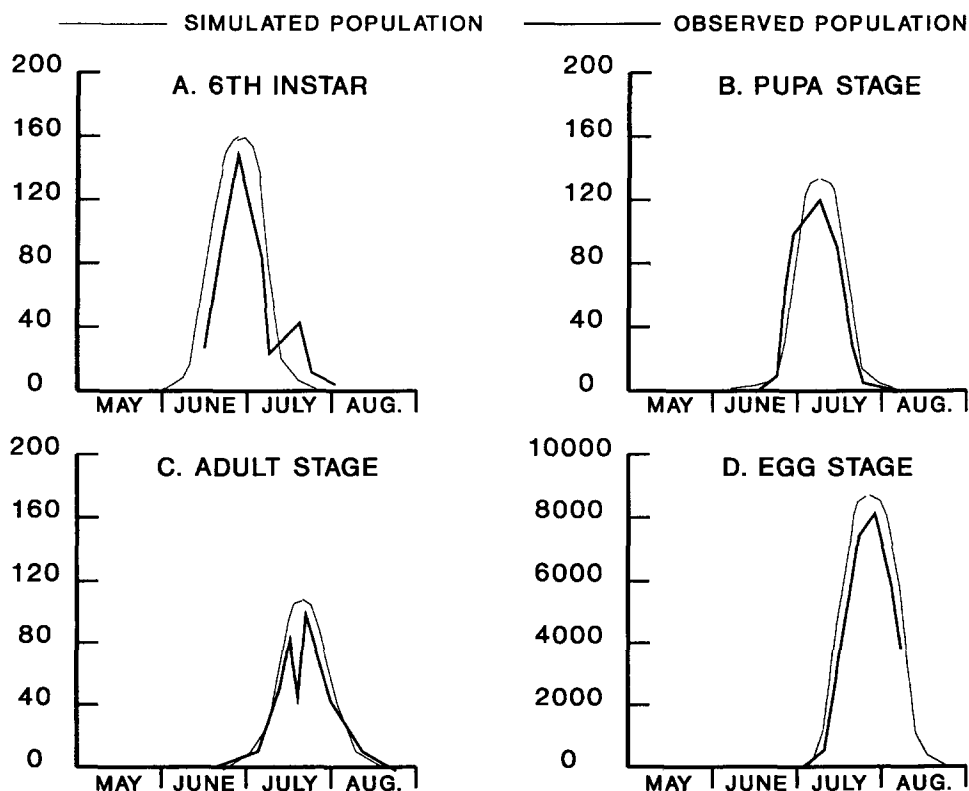


Fig. 3. Comparison of simulation results with observed data for spruce budworm oviposition during 1985 at Hearst, Ontario. Initial population of overwintering 2nd instar spruce budworm assumed to be 800 000 larvae per ha.

19 June to 6 August of that year were available, the comparisons are given for only 6th instar larvae, pupa, adult and egg stages. All simulation results of the stages fit well with the observed data according to the 'timing' and shape of the curves. Although minor differences can be seen between observed and simulated population densities, these may be the result of either sampling errors in the field for observed data or a slight discrepancy in values for the mortalities from the life table used in the simulation; i.e. mean values from Morris's table versus real values from SBW life tables in the Hearst area. Although the work by Morris (1963) represents a classic life table study for SBW, the values were developed in New Brunswick and may not necessarily reflect survival rates for SBW populations in other geographical regions of North America such as Hearst, Ontario.

Simulation for the best strategy of release

In order to compare the different strategies for frequency and timing of parasite release, an initial SBW density of 800 000 2nd instar larvae per ha and a release rate of 12×10^6 ♀♀ *T. minutum* per ha per release was assumed, based on previous field data (Smith et al., 1987). The best strategy was obtained by looking at the resultant SBW larval population and comparing the last two columns of the simulation results; i.e., the density of 1st and 2nd instar larvae for that generation.

Timing. The simulation results for the different timings of a 'single 24-h release' for one year are shown in Table 3. These results suggest that the best timing for a 'single 24-h release' in 1983 would be 14 days after the 1st day of oviposition on 6 July. This date represented the lowest total SBW population density (1st and 2nd instars). Although the model predicted a large number of eggs available on all days between 19 and 23 July inclusive, 20 July was the best date for the 'single 24-h release' because more of the eggs were susceptible to parasitism than on the other days (Table 3).

An interesting result is seen when *T. minutum* is released on 15 and 16 July; both dates show the same density of 1st instar larvae (Table 3). This occurs in the model because, for both release dates, the second generation of *T. minutum* emerges and has an impact on the SBW population on the same day (26 July). Releasing *T. minutum* early in the SBW oviposition curve, therefore, obviously allowed sufficient time for progeny of released parasites to complete development, emerge and oviposit in SBW eggs deposited later in the curve. The number of individuals occurring in the 2nd generation of *T. minutum* from these early releases, however, was limited because there were relatively few SBW eggs available and susceptible to parasitism in the very early part of the oviposition curve.

TABLE 3

Simulation results for different timings of a 'single release' of 12×10^6 ♀♀ *T. minutum* per ha per release for suppression of spruce budworm in Hearst, Ontario during 1983

Date of release	Date 2nd generation <i>T. minutum</i> emerges	Spruce budworm eggs		Simulation results (No. larvae)		
		Available	Susceptible	1st instar	2nd instar	Total ($\times 10^6$)
12 July	23 July	127 439	127 417	81 895	2 184 119	2.27
13 July	24 July	436 335	436 044	26 518	2 084 869	2.11
14 July	25 July	1 072 929	1 071 264	4 793	2 141 648	2.15
15 July	26 July	1 903 703	1 895 754	33 361	2 114 417	2.15
16 July	26 July	2 889 096	2 856 900	33 361	1 756 605	1.79
17 July	27 July	3 860 040	3 753 728	90 558	1 406 391	1.50
18 July	27 July	4 636 092	4 427 252	90 422	1 068 412	1.16
19 July	28 July	5 139 644	4 473 505	126 639	876 302	1.00
20 July	29 July	5 457 085	4 520 052	123 677	810 745	0.93
21 July	29 July	5 549 181	3 671 783	103 926	916 681	1.02

Initial density of 2nd instar overwintering spruce budworm assumed to be 800 000 larvae per ha.

The best timing for a 'single 24-h release' in 1984, 1985 and 1986 is shown in Table 4. The relatively early timing in 1983 compared to the other years was not unexpected because weather conditions were warmer in July 1983

TABLE 4

Best timing for 'single and double releases' of *T. minutum* at 12×10^6 ♀♀ per ha per release for suppression of spruce budworm

Release strategy	Year	Release date		Best simulation results (No. larvae)		
		1st release	2nd release	1st instar	2nd instar	Total ^a ($\times 10^6$)
Single 24-h	1983	20 July	—	123 677	810 745	0.93
	1984	22 July	—	316 339	942 530	1.26
	1985	24 July	—	320 565	869 702	1.19
	1986	25 July	—	291 662	881 549	1.17
Double	1983	18 July	22 July	66 363	342 570	0.41
	1984	20 July	24 July	80 020	363 420	0.44
	1985	22 July	26 July	76 941	412 945	0.49
	1986	23 July	27 July	84 461	429 628	0.52

Initial density of 2nd instar overwintering spruce budworm assumed to be 800 000 larvae per ha.

^a Values below 0.80 represent declining spruce budworm populations (assuming an initial spruce budworm population of 0.80×10^6 larvae per ha).

(monthly mean = 20.6°C) than in the other years (monthly mean = 17.7°C in 1984, 18.3°C in 1985, and 17.6°C in 1986). The best date for release was also earlier in 1984 than in 1985 and 1986 because weather conditions were warmer in the spring of 1984 than in the spring of either 1985 or 1986. This resulted in the earlier emergence of overwintering larvae in 1984 (10 April) than in 1985 or 1986 (18 April), as well as an earlier date for first oviposition in 1984 (2 July) than in 1985 (5 July) and 1986 (6 July).

The best timing for double releases in the years 1983, 1984, 1985 and 1986 is also shown in Table 4. For all years, the time between the 1st and 2nd release was 4 days. As for the 'single 24-h release', the warmer conditions in 1983 resulted in earlier dates for both releases than in the other years.

Frequency. The outcomes from different frequencies for 'single 24-h release', 'single staggered release' and 'double release' and 'double release' were compared to determine the best strategy (Table 5). The results indicate that if *T. minutum* is applied at 12×10^6 ♀♀ per ha per release, in either 'single staggered releases' or 'double releases', SBW populations can be reduced and outbreaks controlled; the final density can be reduced below the original starting density of 0.80×10^6 larvae per ha. A 'single 24-h release', however, will not control the population.

Of the three 'single staggered release' strategies, the best distribution of emergence was Strategy A; increasing the proportion of *T. minutum* emerg-

TABLE 5

Best frequency for releasing 12×10^6 ♀♀ *T. minutum* per ha per release for suppression of spruce budworm

Strategy	Release date		Release rate ($\times 10^6$ ♀♀ per ha)		Simulation results (No.)		
	1st release	2nd release	1st release	2nd release	1st release	2nd release	Total ^a ($\times 10^6$)
Single							
24-h	20 July	—	12	—	123 677	810 745	0.93
Staggered							
A	18 July	—	12	—	95 464	317 762	0.41
B	18 July	—	12	—	106 599	329 502	0.44
C	18 July	—	12	—	107 379	314 698	0.42
Double							
	18 July	22 July	12	12	66 363	342 570	0.41

Initial density of 2nd instar overwintering spruce budworm assumed to be 800 000 larvae per ha.

^a Values below 0.80 represent declining spruce budworm populations (assuming an initial spruce budworm population of 0.80×10^6 larvae per ha).

ing each day following release over the 5 days by 10, 15, 20, 25, and 30% per day, respectively. All three staggered strategies at 12×10^6 ♀♀ per ha produced almost a 50% reduction in the population and, therefore, were twice as effective in reducing SBW populations as a 'double release' at a total of 24×10^6 ♀♀ per ha. Future field studies should concentrate on examining the actual response of SBW populations to such releases.

Rate of release. To determine the best strategy for using *T. minutum* to suppress SBW, the impact of different rates of release were simulated in the dynamic model. Hypothetical releases were made at the best time in one year: 20 July 1983 for the 'single 24-h release', and 18 and 22 July 1983 for the 'double release'. As expected, the model predicted an increasing impact on the SBW population as the rate of release for a 'single 24-h release' increased from 2 to 12×10^6 ♀♀ per ha. As shown previously, however, even at the maximum of 12×10^6 ♀♀ per ha, 'single 24-h releases' of *T. minutum* did not successfully suppress SBW populations. Higher rates may be more effective, although at the present time, the cost of parasite rearing does not make this alternative feasible for SBW control.

With 'double releases', the total number of parasites required to reduce the SBW population (below 800 000 larvae per ha) ranged from 10 to 24×10^6 ♀♀ per ha (Table 6). The best strategy for release with these rates appeared to be 6×10^6 ♀♀ per ha in the first release and 4×10^6 ♀♀ per ha in the second release. This provided a slight reduction in SBW populations of 1% (from 0.80×10^6 to 0.79×10^6 larvae per ha). In order to achieve a 49% reduction in the population (0.41×10^6 larvae per ha), equal to that with Strategy A for a 'single staggered release' of 12×10^6 ♀♀ per ha, a 'double release' totalling 24×10^6 ♀♀ per ha would be required.

TABLE 6

Total number of spruce budworm larvae predicted following increasing rates of 'double releases' of *T. minutum* on 18 and 22 July 1983 in Hearst, Ontario

Rate of 1st release ($\times 10^6$ ♀♀ per ha)	Rate of 2nd release ($\times 10^6$ ♀♀ per ha)					
	2	4	6	8	10	12
2	1.38	1.14	1.05	0.97	0.90	0.85
4	1.11	0.90	0.83	0.76	0.69	0.65
6	1.02	0.79	0.75	0.69	0.62	0.58
8	0.94	0.75	0.69	0.63	0.56	0.52
10	0.84	0.66	0.60	0.55	0.48	0.45
12	0.78	0.61	0.55	0.50	0.44	0.41

Obviously, the impact of inundative release will become greater as the rates of release increase, however, these higher rates will be associated with increasing costs. Reducing the application rate from 24×10^6 ♀ ♀ per ha (eg. Strategy A; 'single staggered release' to 'double release') and retaining the same level of population suppression (0.41×10^6 larvae per ha) could almost halve the total cost. In the future development of inundative releases with *Trichogramma*, it would be most valuable to investigate such findings under field conditions.

DISCUSSION AND CONCLUSIONS

The success of releasing natural enemies such as *Trichogramma* is usually assessed by taking field measurements at one point in time to determine the extent of parasitism in the target stage of the host. This approach often leads to errors in assessment because not all hosts in the population are susceptible at the same time. Percentage parasitism (the ratio of individuals parasitized to the total number of individuals in the population), therefore, may not reflect the true impact of the natural enemy (Van Driesche, 1983). A more accurate assessment would be made by comparing population densities in the same stage of the host between two consecutive generations (e.g. 2nd instar to 2nd instar). A life system simulation model, such as developed here, can be extremely valuable because it makes such comparisons without the associated error of sampling or expense of large-scale field programmes.

Normally, detailed information is needed on the cause-effect relationship between environmental factors and the rates of SBW survival and oviposition, in order to adequately describe SBW population dynamics (Régnière, 1982, 1987). With the life system approach, however, only survival rates of the insect are required because these rates reflect the 'inputs' and 'outputs' of the system as a whole without considering the interacting mechanisms inside the system. Survival rates can be readily obtained from life table data. The benefit to be gained by employing such a general analysis, at the systems level, has been demonstrated in the present paper. Predictions on the potential success of parasite releases or other biological control programmes can be made without detailed cause-effect information on host survival or natural enemy interaction and behaviour under field conditions. Obviously, further refinements in life table data for SBW from the actual release site in northern Ontario will improve the predictability of the model.

The feasibility of using *T. minutum* as a biological control agent in Canada against forest insect pests such as SBW will depend, to a large extent, upon financial considerations (Smith et al., 1987). It is necessary, therefore, to determine the best strategy for release rates, timing and number of releases which will provide the most cost-effective suppression. The

present model has allowed us to evaluate such strategies by means of computer simulation without the prohibitive expense of field studies.

Results from our simulation suggest that, in the future, it will be possible to determine the optimal strategy for inundative release of *T. minutum* for suppression of SBW. Our study has shown that, if properly timed, a 'double release' of parasites will be more effective than a 'single 24-h release' at the same release density. Similar conclusions were reached in developmental studies by Lawrence and Houseweart (1985) and field studies by Smith et al. (1987). Our model also predicts that a 'single staggered release', with increasing rates of emergence, can provide a 49% reduction in SBW populations equivalent to a 'double release' at twice the rate. This type of 'single staggered release', therefore, currently represents the best strategy for using inundative releases of *Trichogramma* and suggests that field studies should be conducted to verify the model predictions.

The present paper concentrates on a life system simulation model for improving inundative releases of the egg parasite, *Trichogramma minutum* against the SBW using life table data. Further development of this model would allow us to explore the potential for integrating parasite releases with other control agents, either simultaneously (within the same year) or sequentially (in consecutive years). It would also enable us to investigate the long-term impact of parasite releases on different levels and phases of the host population and determine the effect of such releases on the host's dynamics over a complete outbreak cycle. The life system approach, therefore, provides a broader context in which effective pest management programmes can be designed.

ACKNOWLEDGEMENTS

The authors thank J. Régnière, R. Fleming and an anonymous reviewer for their comments and suggestions during the preparation of the manuscript. This work was supported through a NSERC grant and COFRDA contract to SMS and a visiting scholarship to MY from the People's Republic of China.

REFERENCES

- Anderson, J.F., 1976. Egg parasitoids of forest defoliating Lepidoptera. In: J.F. Anderson and H.K. Kaya (Editors), *Perspectives in Forest Entomology*. Academic Press, New York, pp. 233–249.
- Blais, J.R., 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.*, 13: 539–547.
- Blais, J.R., 1985. The ecology of the eastern spruce budworm: a review and discussion. pp. 49–59. In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (Editors), *Recent*

- Advances in Spruce Budworm Research. Proc. CANUSA Spruce Budworms Research Symp., 16–20 September 1984, Bangor, ME. Canadian Forestry Service, Ottawa, Ont., 527 pp.
- Cameron, D.G., McDougall, G.A. and Bennett, C.W., 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. *J. Econ. Entomol.*, 61: 857–858.
- Coulson, N.R. and Witter, J.A., 1984. *Forest Entomology: Ecology and Management*. Wiley, 669 pp.
- Houseweart, M.W., Southard, S.G. and Jennings, D.J., 1982. Availability and acceptability of spruce budworm to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *Can. Entomol.*, 114: 657–666.
- Houseweart, M.W., Jennings, D.T. and Lawrence, R.K., 1984. Field releases of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) for suppression of epidemic spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), egg populations in Maine. *Can. Entomol.*, 116: 1357–1366.
- Hughes, R.D., Jones, R.E. and Gutierrez, A.P., 1984. Short term patterns of population change: the life system approach to their study. In: C.B. Huffaker and R.L. Rabb (Editors), *Ecological Entomology*. Wiley, New York, pp. 309–340.
- Lawrence, R.K., and Houseweart, M.W., 1985. Developmental rates of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and implications for timing augmentative releases for suppression of egg populations of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.*, 117: 556–563.
- Morris, R.F. (Editor), 1963. The dynamics of epidemic spruce budworm populations. *Mem. Entomol. Soc. Can.*, 31: 1–332.
- Outram, I., 1971. Aspects of mating in the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.*, 103: 1121–1128.
- Powell, J.A., 1980. Nomenclature of nearctic conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae): Historical review and present status. U.S. For. Serv. Gen. Tech. Rep. PNW-100.
- Régnière, J., 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). *Can. Entomol.*, 114: 811–825.
- Régnière, J., 1983. An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.*, 115: 1371–1382.
- Régnière, J., 1987. Temperature-dependence of eggs and larvae of *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. *Can. Entomol.*, 119: 717–728.
- Royama, T., 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana*. *Ecol. Monogr.*, 51: 473–491.
- Ruesink, W.G., 1982. Analysis and modeling in pest management. In: *Introduction to Insect Pest Management*. R.L. Metcalf and W.H. Luckmann (Editors), Wiley, New York, pp. 353–375.
- Sanders, C.J., 1985. Summary of the discussion group B – What can we learn from historical records? In: C.J. Sanders, R.W. Stark, E.J. Mullins and J. Murphy (Editors), *Recent Advances in Spruce Budworm Research. Proc. CANUSA Spruce Budworms Research Symp.*, 16–20 September 1984, Bangor, ME. Canadian Forestry Service, Ottawa, Ont., p. 145.
- Sanders, C.J. and Lucuik, G.S., 1975. Effects of photoperiod and size on flight activity and oviposition in the eastern spruce budworm (Lepidoptera: Tortricidae). *Can. Entomol.*, 107: 1289–1299.
- Sanders, C.J., Wallace, D.R. and Lucuik, G.S., 1978. Flight activity of female eastern spruce

- budworm (Lepidoptera: Tortricidae) at constant temperatures in the laboratory. Can. Entomol., 110: 627–632.
- Smith, S.M. and Hubbes, M., 1986. Strains of *Trichogramma minutum* Riley. I. Biological and biochemical characterization. J. Appl. Entomol., 101: 223–239.
- Smith, S.M., Hubbes, M. and Carrow, J.R., 1987. Ground releases of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) against the spruce budworm (Lepidoptera: Tortricidae). Can. Entomol., 119: 251–263.
- Smith, S.M., Carrow, J.R. and Laing, J.E. (Editors), in press. Inundative release of the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) against forest insect pests such as the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae): The Ontario project, 1982–1986. Mem. Entomol. Soc. Can.
- Van Driesche, R.G., 1983. The meaning of ‘percent parasitism’ in studies of insect parasitoids. Environ. Entomol., 12: 1611–1622.
- Watt, K.E.F., 1964. The use of mathematics and computers to determine optimal strategy and tactics for a given insect pest control problem. Can. Entomol., 96: 202–220.