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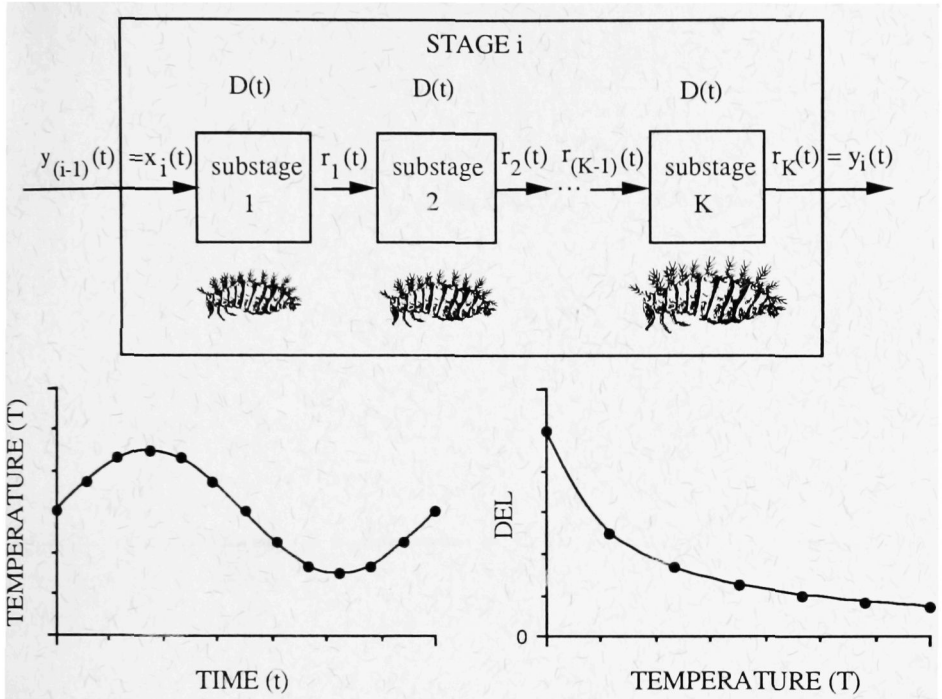
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Yuqing Fan, Francis A. Drummond, and Eleanor Groden



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Simulating the Development
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ABSTRACT

A computer model was developed to simulate and predict the phenology of Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, populations on dry beans, *Phaseolus vulgaris* L. Time-varying distributed developmental rates of the egg, four larval instars, and pupal stages were simulated with degree day models, based on a standardized cumulative probability distribution function from a range of constant temperature experiments. Predictions from the simulation model provided a good fit to the observed constant temperature data and field experiments. Using temperature data in the form of daily maximums and minimums, the model can be used to predict the occurrence of immature MBB stages under field conditions, when the frequency distribution of egg mass recruitment is known (i.e., from sampling). It is also possible to incorporate mortality of the population by modifying the delay subroutine, and to simulate insect consumption by adding a consumption subroutine.

KEY WORDS: Insecta, *Epilachna varivestis*, degree day, simulation, distributed developmental rates.

INTRODUCTION

The Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, was first found in Maine in 1930. Since 1944, it has been found in all bean-growing areas of the state (Hawkins 1944). Now it appears to be a sporadic pest in Maine. In 1988, a severe infestation was found in a commercial dry bean farm in Sidney, Maine, and in 1989 the only heavy infestation found was in a commercial green bean field in Belgrade, Maine.

Predicting the occurrence of developmental stages is a crucial factor in Integrated Pest Management (IPM) decision making. Economic damage is often heaviest during certain developmental stages, and efficient use of insecticides and biological control agents requires forecasts of pest phenology for well-timed applications. In the literature, there have been a growing number of studies on modeling the distributed developmental times of pest insect populations in order to predict the overlapping occurrences of developmental stages. Distributed developmental time models are more refined than average developmental time models in that they can be used to predict the variation in phenology exhibited by insect populations. A number of distributed model forms have been developed that are based on the non-linear relationship between developmental rate and temperature using data from constant temperature studies (Stinner et al. 1975; Sharpe et al. 1977; Wagner et al. 1984; and Drummond et al. 1985). Distributed models based on linear degree day relationships have received less attention (Smith et al. 1984). Dennis et al. (1986) proposed a method of using the logistic distribution in describing distributed development from field observations of western spruce budworms, *Choristoneuria occidentalis* Freeman.

Studies by Fan et al. (1991a) showed that predictions of the mean developmental time of MBB by the linear degree day model are better than those by the non-linear biophysical model under fluctuating high temperatures and field conditions. The same results were also observed by Taylor and Shields (1990) with the armyworm, *Pseudoletia unipuncta* (Haworth), and by Roltsch et al. (1990) with the western grape skeletonizer, *Harrisina brillians*. Hochberg et al. (1986) compared four phenology models (degree day, Gauss, bivariate linear, and bivariate quadratic models) in predicting the occurrence of the pea aphid, *Acyrtosiphon pisum*, and the blue alfalfa aphid, *Acyrtosiphon kondoi*. They found that though the most complex models fit the constant temperature developmental data best, the degree day model gave the best prediction of field data. This does not mean, however, that there are no limitations to

the degree day model. Its applications and limitations have been discussed in detail by Wang (1960), Baskerville and Emin (1969), Pruess (1983), and Higley et al. (1986).

In the present paper we present a computer simulation model for the immature stages of MBB on dry beans, *Phaseolus vulgaris* L., based on the linear degree day model and time-varying distributed delay, using data from a range of constant temperature experiments.

METHODS

Model

The basic requisite of the model is that average insect developmental rate is linearly related to ambient temperature and, therefore, can be described with the degree day model. The insect "age" is proportional to accumulated degree days. The amount of developmental time (in degree days) for an individual to complete the i^{th} stage can be expressed as:

$$\text{TDD}_i = \int (T, 0) \{ \text{Max}[0, \text{Temp}(t) - t_i] \} dt$$

Where:

TDD_i is degree days required for an individual to complete the i^{th} developmental stage;

Max takes 0 degree day when $[\text{Temp}(t) - t_i]$ is less than 0;

$\text{Temp}(t)$ is the average ambient temperature at time t ;

t_i is the developmental threshold of the i^{th} stage;

T is the time required for an individual to pass through the i^{th} stage of development;

dt is the time increment in calculating the degree day.

In order to calculate degree days with daily maximums and minimums, diurnal fluctuations were simulated with a sine function, and degree days were calculated with a sine wave approximation method (Baskerville and Emin 1969; Allen 1976). When both daily temperature maximum (T_{max}) and minimum (T_{min}) are greater than t_i , daily degree day (DD):

$$\text{DD} = T_{\text{bar}} - t_i$$

Where:

$$T_{\text{bar}} = T_{\text{max}} + T_{\text{min}}/2$$

When both T_{max} and T_{min} are less than t_i , then:

$$\text{DD} = 0.$$

When T_{max} is greater than t_i and T_{min} is less than t_i , then:

$$DD = 1/2\pi[A \cdot \cos(\theta) + (\pi/2 - \theta)(T_{bar} - t_i)].$$

Where:

$$A = T_{max} - T_{min};$$

$$\theta = \arcsin(t_i - T_{bar}/A).$$

(see appendix for FORTRAN 77 subroutine DEGDAY).

Due to inherent differences among individuals in a population, insects reared under identical conditions develop at different rates, which means different TDD_i requirements. Within a population the proportion of insects in stage i or beyond by time t is:

$$P_i(t) = f_i(ADD_i).$$

Where:

ADD_i is DD accumulated up to time t ;

f_i is a cumulative distribution function of the i^{th} stage development.

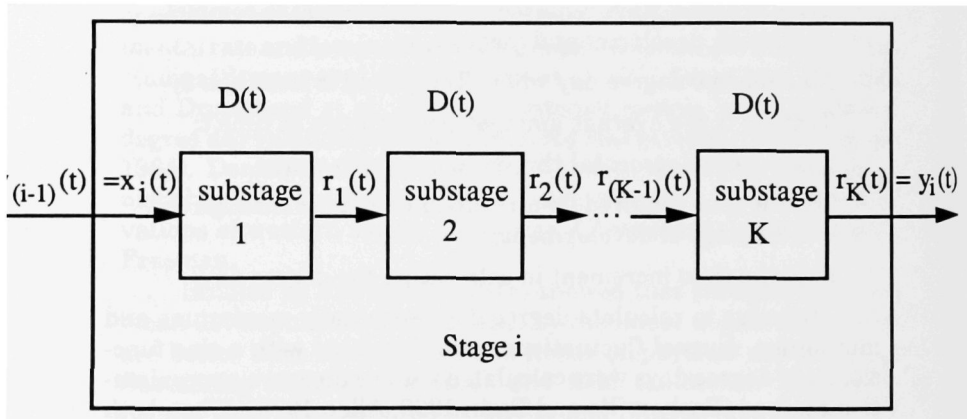


Figure 1. A K^{th} order time-varying distributed delay. $x_i(t)$ is the input to the delay process of the i^{th} stage and the output of previous stage $y_{(i-1)}(t)$ at time t ; $y_i(t)$ is the output of the i^{th} stage and the input of the next stage $x_{(i+1)}(t)$ at time t ; $D(t)$ is a time varying delay parameter, defined as DEL/K (DEL is the total maturation delay, in this case it equals TDD_i/DD_i , where DD_i is degree days accumulated between time t and $t-1$) at time t ; K is the number of substages (i.e., discrete subunits or developmental stages of the same age duration within an insect life stage, such as a pupal stage) in the delay process; and $r_k(t)$ is the array of intermediate rates.

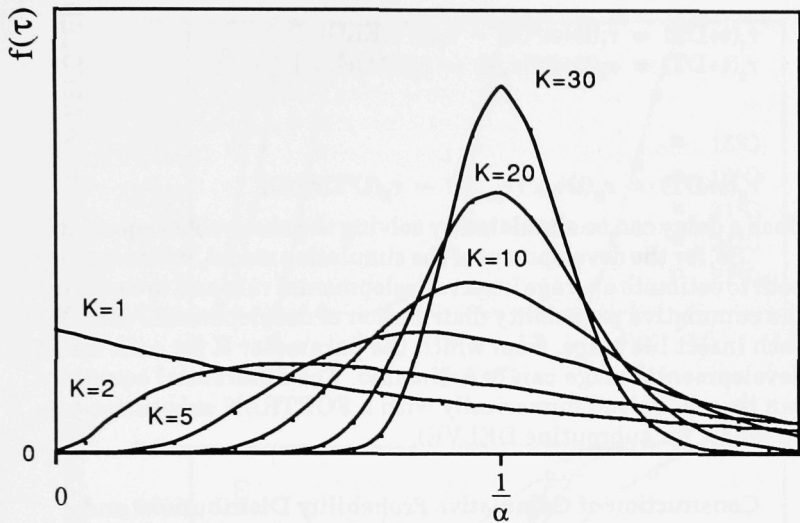


Figure 2. The Erlang family of density functions. An entity (t) (i.e., an insect cohort) entering the delay process has a probability $f(\tau)$ of leaving the delay (i.e., the insect stage).

The time-varying distributed delay described by Manetsch and Park (1977) was used to simulate the f_i distribution function. In a K^{th} order time varying distributed delay model, a single developmental stage is divided into K subclasses or substages ("Boxcars"), as shown in Fig. 1. Mathematically, K specifies a member of the Erlang family of density functions describing the transit times of individual entities (τ) in a particular model (Fig. 2). DEL determines the mean (α) of the probability density function. This is the average developmental time of a cohort or population of insects. The Erlang density function is given as:

$$f(\tau) = (\alpha K)^K (t)^{K-1} \exp(-\alpha K t) / (K-1)!$$

Where:

$$\alpha = 1/\text{DEL}$$

Manetsch and Park (1977) showed that the Erlang density functions is equivalent to a set of K^{th} order linear differential equations. If we assume that

DT = the time increment being used in the simulation;

DELP = the past value of DEL;

A = DT*K/DEL; and

DELD = $1 + ((\text{DEL} - \text{DELP}) / (\text{DT} * K))$, then,

$$r_1(t+DT) = r_1(t) + A^*(x) - r_1(t) * DELD]$$

$$r_2(t+DT) = r_2(t) + A^*[r_1(t) - r_2(t) * DELD]$$

$$r_k(t+DT) = r_k(t) + A^*[r_{(k-1)}(t) - r_k(t) * DELD]$$

Such a delay can be simulated by solving the above set of equations.

So, for the development of the simulation model, it is necessary both to estimate average insect developmental rate and to construct the cumulative probability distribution of developmental rates for each insect life stage, from which the parameter K for each insect developmental stage can be estimated. The differential equations can then be solved numerically with a FORTRAN subroutine (see appendix for subroutine DELVE).

Construction of Cumulative Probability Distributions and Parameter Estimation of the Model

Cumulative probability distributions of insect developmental times for a certain stage are displaced in time (in calendar days) because of strong temperature effects on developmental rate (Fig. 3A). According to the linearity theory of the degree day model, when the times are converted to DDs, the distributions at all temperatures become equivalent (Fig. 3B). Ideally, the distribution on a degree day scale would have identical shapes, and the developmental times of individuals in a population under either constant or variable temperatures could be predicted by using a rate summation (numerical integration) based on the accumulation of DDs. In practice, frequency distributions based on DDs have similar but rarely identical shapes at all intermediate temperatures. The error variance might be due to inadequate sample size (especially when trying to estimate the tails of distributions), violation of assumptions of the linear temperature-developmental rate relationship, or the effects of other factors, such as unstable growth chamber performance, or differential food quality.

The equivalent shape concept of Sharpe et al. (1977) and Curry et al. (1978a,b) is used here as a base to standardize the frequency distributions, as illustrated with the MBB fourth instar developmental data. For each temperature (1) a cumulative frequency distribution is constructed for each stage by adding up the frequencies in successive class intervals (a zero frequency is estimated and added to the lower end of the distribution) (Fig. 3A); (2) next, the times (DD) when 1, 10, 20, 30, . . . , 90, and 100% of the insect cohort complete development are calculated by linear interpolation. These estimates are referred to as tau distributions following the ter-

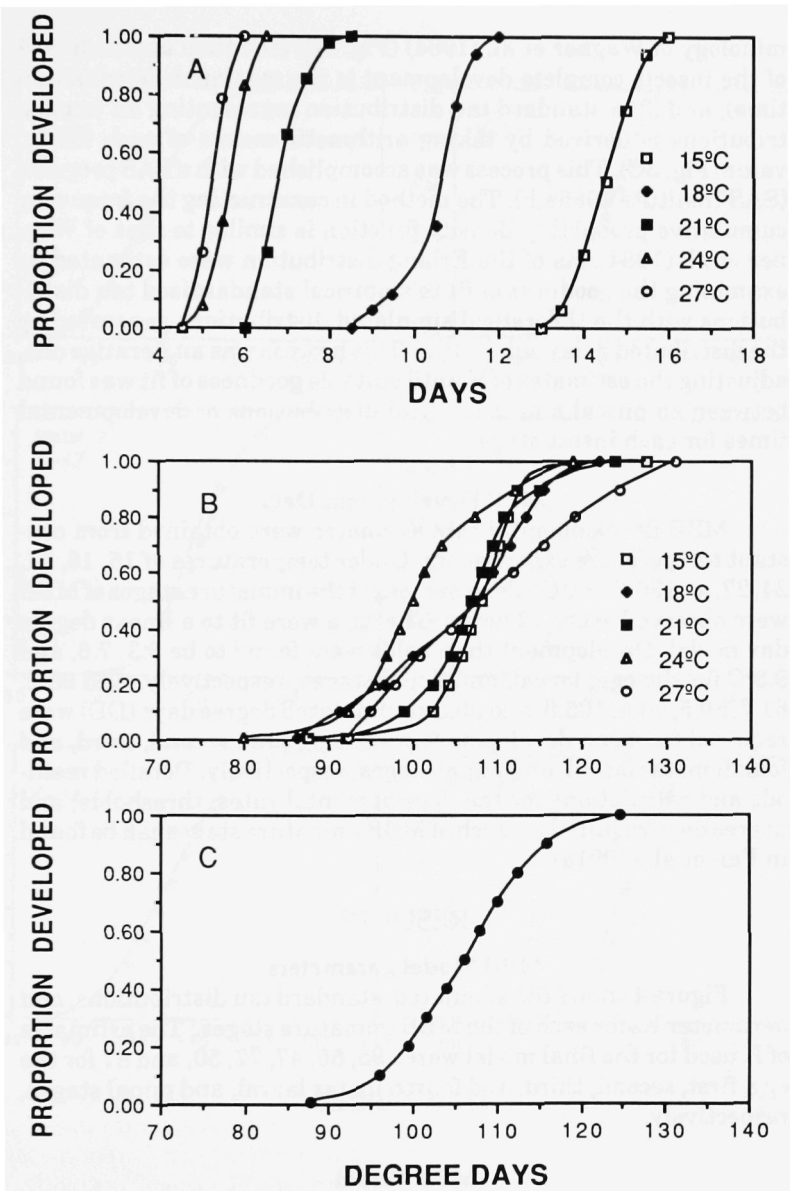


Figure 3. Cumulative probability distributions of MBB fourth instar: (A) developmental times in calendar days; (B) developmental times in degree days at 1, 10, 20, ..., 90, and 100% developed; (C) standardized mean times in degree days.

minology of Wagner et al. (1984) (Fig. 3B) (the time at which 50% of the insects complete development is the median developmental time); and (3) a standard tau distribution representing all tau distributions is derived by taking arithmetic means of each tau (τ) value (Fig. 3C). This process was accomplished with a SAS program (SAS Institute 1985a,b). The method in constructing the frequency cumulative probability density function is similar to that of Wagner et al. (1984). Ks of the Erlang distribution were estimated by examining the goodness of fit to empirical standardized tau distributions with the theoretical simulated distributions generated by the distributed delay subroutine. This process was an iterative one, adjusting the estimates of K until suitable goodness of fit was found between empirical and theoretical distributions of developmental times for each insect stage.

MBB Development Data

MBB developmental rate estimates were obtained from constant temperature experiments. Under temperatures of 15, 18, 21, 24, 27, and 30°C ($\pm 1^\circ\text{C}$), development of the immature stages of MBB were observed every 12 hours. The data were fit to a linear degree day model. Development thresholds were found to be 8.3, 7.6, and 9.3°C for the egg, larval, and pupal stages, respectively. And 98.2, 61.7, 50.5, 60.6, 105.9, and 90.3 accumulated degree days (DD) were required for mean development of the egg, first, second, third, and fourth instar larval, and pupal stages, respectively. Detailed methods and calculations for the developmental rates, thresholds, and degree days required for each of MBB immature stages can be found in Fan et al. (1991a).

RESULTS

MBB Model Parameters

Figure 4 shows the simulated, standard tau distributions, and parameter Ks for each of the MBB immature stages. The estimates of K used for the final model were: 95, 55, 47, 72, 50, and 87 for the egg, first, second, third, and fourth instar larval, and pupal stages, respectively.

MBB Model

A complete simulation model (available upon request, specify Macintosh or IBM format diskette) was developed by directing the output of the previous stage as the input for the next stage. It was written in ANSI FORTRAN 77 and runs on a Macintosh computer.

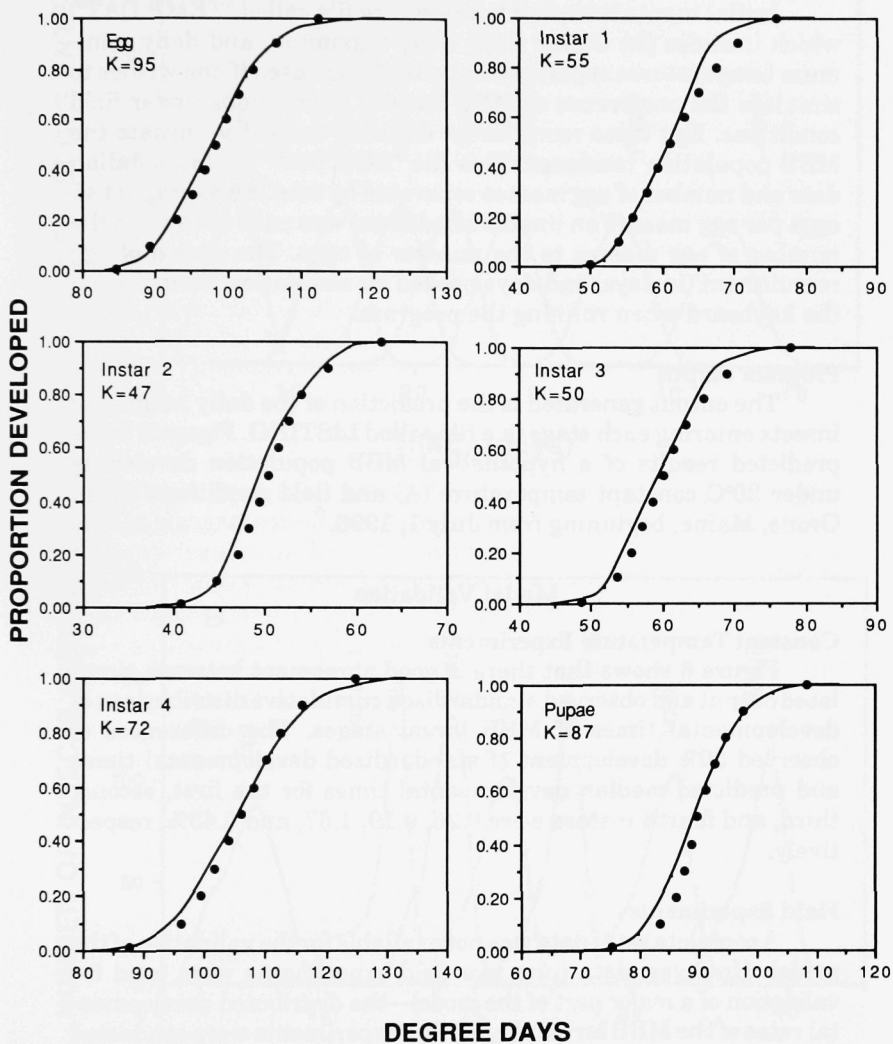


Figure 4. Standardized cumulative probability distributions (solid circles) and distributions simulated with time varying distributed delay model (curves) for all MBB immature stages and the parameter K 's.

Program inputs

Initial inputs include a temperature file called "TEMP.DAT", which includes the Julian date, daily maximum, and daily minimum temperatures separated by tabs. This is used if one wishes to simulate the occurrence of MBB natural populations under field conditions. Egg mass recruitment data are needed to initiate the MBB population incidence. This file "EGG.DAT" contains Julian date and number of egg masses separated by tabs. An average of 45 eggs per egg mass (Fan unpublished data) was used to convert the number of egg masses to the number of eggs. The period of egg recruitment (in days) and days needed for simulation is input from the keyboard when running the program.

Program output

The output generated is the prediction of the daily number of insects entering each stage in a file called LISTING. Figure 5 is the predicted results of a hypothetical MBB population developing under 20°C constant temperature (A) and field conditions (B) in Orono, Maine, beginning from July 1, 1990.

Model Validation

Constant Temperature Experiments

Figure 6 shows that there is good agreement between simulated output and observed standardized cumulative distributions of developmental times of MBB larval stages. The differences of observed 50% development of standardized developmental times and predicted median developmental times for the first, second, third, and fourth instars were 0.26, 0.19, 1.67, and 0.43%, respectively.

Field Experiments

A complete set of data was not available for the validation of the model. However, data from two field experiments were used for validation of a major part of the model—the distributed developmental rates of the MBB larval stages. The experiments were conducted in the summers of 1989 and 1990 on two cropping systems (conventional and low input practices, see Fan [1991]) of dry beans (*P. vulgaris* cv. Maine yellow eye) at the University of Maine Sustainable Agriculture Research Farm.

In 1989, one plant in each plot was covered with a 0.3 x 0.3 x 0.6 m cage and inoculated with 6 to 10 newly hatched first instar larvae. In 1990, 4 plants in each plot were caged individually and inoculated with 5, 10, 15, or 20 newly hatched first instar larvae.

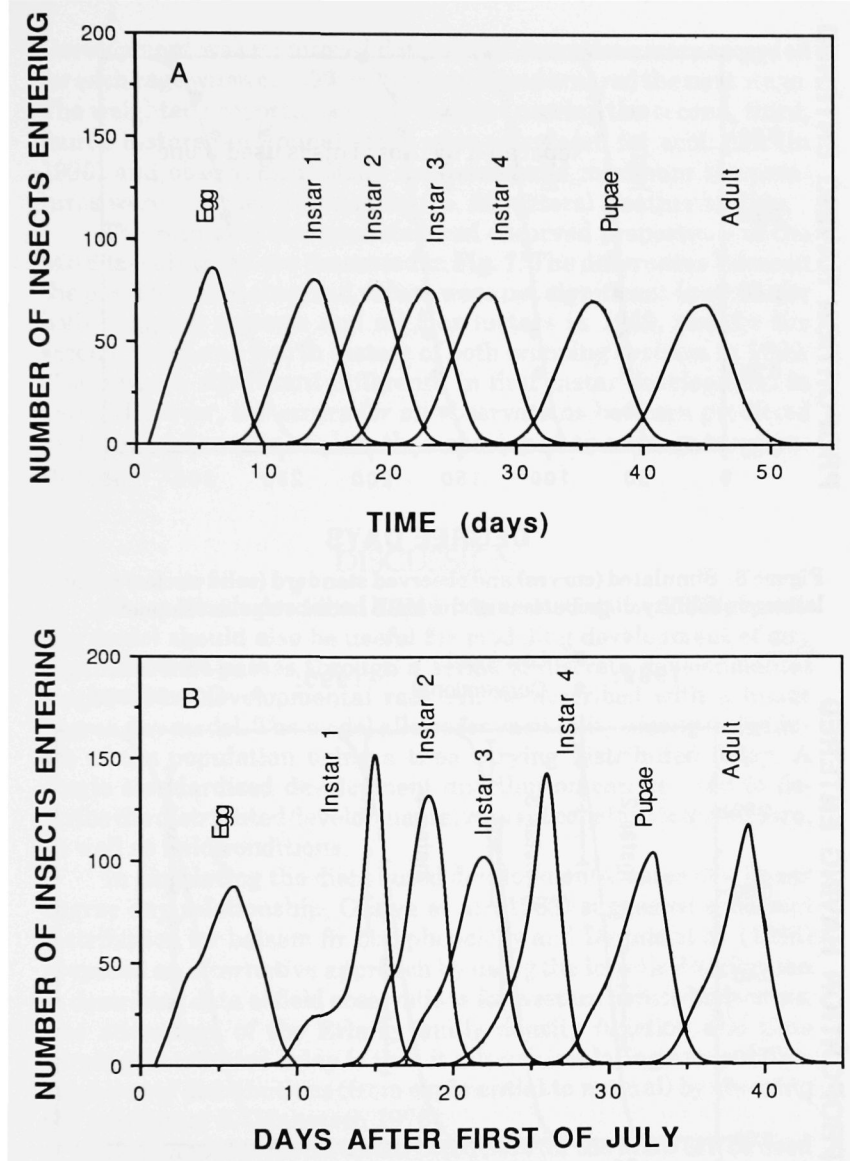


Figure 5. Simulations of the development of a MBB population under constant 20°C (A) and field conditions (B) of Orono, Maine, beginning from July 1, 1990.

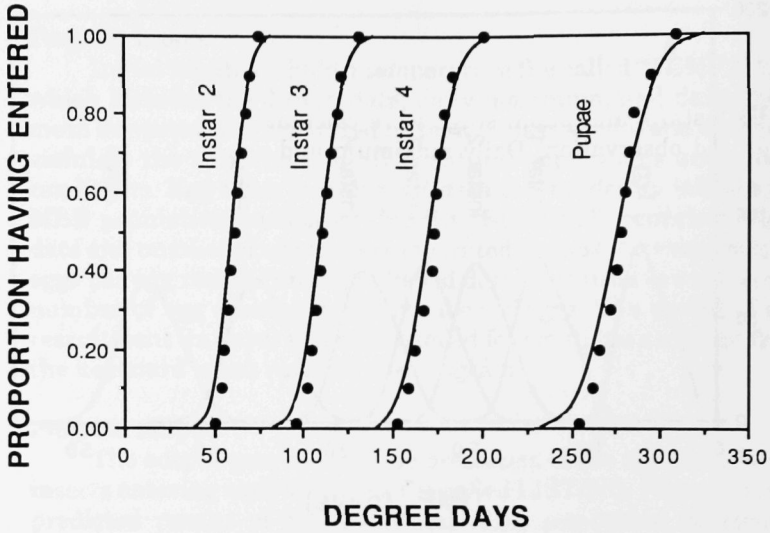


Figure 6. Simulated (curves) and observed standard (solid circles) cumulative probability distributions of the MBB larval stage development.

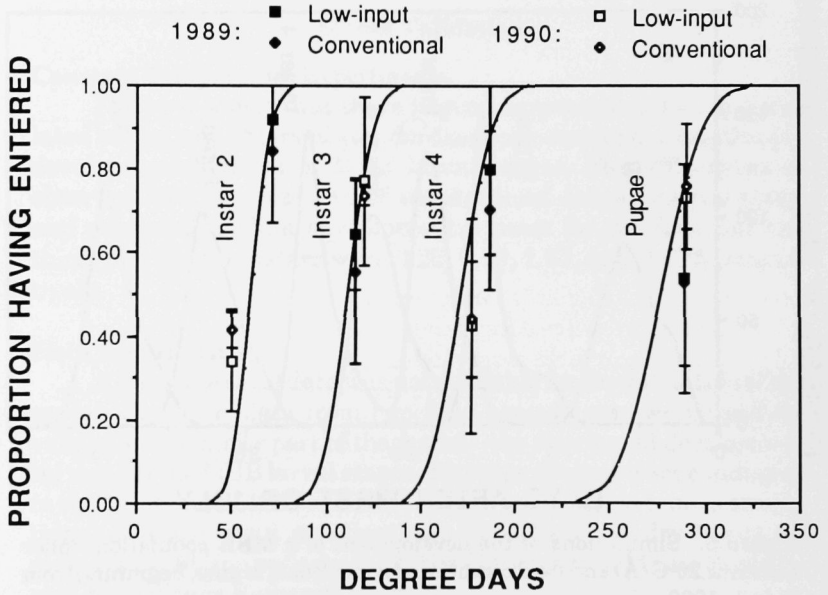


Figure 7. Simulated cumulative probability distributions (curves) of MBB larval stage development and observed proportions (with standard deviations) of a MBB cohort entering the next stage or beyond under field conditions in the conventional and low-input production systems of dry beans in 1989 and 1990.

Development was monitored daily and observations were recorded for each cage when ca. 50% of the insects had entered the next stage. The weighted proportions of the insects entering the second, third, fourth instars, and pupal stage were calculated for each plot (in 1990) and observation. Daily maximum and minimum temperatures were recorded at a nearby (ca. 50 meters) weather station.

The results of the predicted and observed proportions of the MBB larval stages are presented in Fig. 7. The differences between the predicted and observed values were not significant ($\alpha=0.05$) for both cropping systems and all four instars in 1989, and for the second, third, and fourth instars of both cropping systems in 1990. There was a significant difference in first instar development in 1990. However, the errors for all observations between predicted and observed results are less than one day at an average temperature of 27°C.

DISCUSSION

The methods described here for constructing the MBB phenology model should also be useful for modeling development of any organism that passes through a series of discrete developmental stages when developmental rate can be described with a linear degree day model. The model allows for variability among individuals of the population using a time-varying distributed delay. A single standardized development distribution can be used to describe the distributed developmental rates at constant temperature, as well as field conditions.

In simulating the distributed developmental rates of a linear degree day relationship, Osawa et al. (1983) suggested a normal distribution for balsam fir bud phenology and Dennis et al. (1986) proposed an alternative approach by using the logistic distribution in describing data of field observations for western spruce budworms. The advantage of the Erlang family density function and time varying distributed delay is that it allows simulating many different types of distributions (from exponential to normal) by choosing the parameter K (Manetsch 1976).

The computer model constructed here for the MBB can be used to simulate and predict the occurrence of the immature MBB stages on dry beans under field conditions, when the egg recruitment distribution is known. Though the complete model has not been evaluated with a natural MBB population, the major part of the model, which simulates the distributed development of MBB larval stages, has been validated with field data from two cropping systems

of dry bean production for two years, and has been shown to give accurate predictions for the development of cohorts of MBB larval stages.

It is also possible to incorporate mortality of the population into the model by modification of the delay subroutine (DELVF). Insect consumption can be simulated by adding a consumption subroutine. With the modifications the model has been used to evaluate the effect of within stage survival and feeding patterns for simulating foliage consumption (Fan et al. 1991b).

In summary, we have presented a method for simulating the distributed development of the immature MBB stages, using data from a range of constant temperature studies. We developed a computer model for the prediction of MBB phenology on dry beans.

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APPENDIX

SUBROUTINE DEGDAY (BASE, TH, TL, DD)

C FORTRAN subroutine DEGDAY for calculating daily degree
C day (DD) from maximum and minimum temperatures.

C Variables:

C BASE : Development threshold
C TH : Daily maximum temperature
C TL : Daily minimum temperature
C DD : Daily degree day

DD=0

TBAR=(TH+TL)/2.

A=TH-TL

IF (BASE-TH) 5, 5, 6

6 DD=0.

RETURN

5 IF (BASE-TL) 7, 7, 8

7 DD=TBAR-BASE

RETURN

8 HPIE=1.570796

TPIE=6.283181

X=(BASE-TBAR)/A

THETA=ASIN(X)

DD=((TBAR-BASE)*(HPIE-THETA)+A*COS(THETA))/TPIE

RETURN

END

SUBROUTINE DELVF (VIN, VOUT, R, STRG, DEL, DELP, DT, K)

C FORTRAN subroutine DELVF for solving the Kth order differential
 C equations to move the insects from one development life stage to the
 C next development stage.

C Variables:

C VIN : Number of insects entering the delay process
 C VOUT : Number of insects leaving the delay process
 C R : Array of intermediate rates
 C STRG : Number of insects staying in the delay
 C DEL : Daily maturation delay
 C DELP : DEL of the previous day
 C DT : Time increment of the model
 C K : Number of substages

REAL R(1:K)

OMIT=0.0001

V=VIN

FK=FLOAT(K)

DELD=1.+(DEL-DELP)/(DT*FK)

A=DT*FK/DEL

DELP=DEL

DO 1 I=1,K

DR=R(I)

R(I)=DR+A*(V-DR*DELD)

IF (R(I) .LE. OMIT) R(I)=0.

1 V=DR

SR=0.

DO 2 I=1,K

SR=SR+R(I)

2 CONTINUE

STRG=SR*DEL/FK

VOUT=R(K)

RETURN

END