A Temperature-Dependent Model for Fall Armyworm Development[1,2]

CARL S. BARFIELD,[3] E. R. MITCHELL,[4] AND S. L. POE[5]

Department of Entomology and Nematology, University of Florida, and USDA, Insect Attractants Laboratory, Gainesville 32611

ABSTRACT

The influence of temperature on egg-to-adult developmental times and rates of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), was studied in the laboratory at a variety of constant and variable temperatures. Mean total developmental time ranged from 66.6 days (15.6°C) to 18.4 days (35.0°C). Male and female development times were not significantly different.

Means and standard deviations of fall armyworm developmental rates (= times^{-1}) were inputs into a previously derived absolute reaction rate model designed to generate a set of kinetic constants usable in predicting developmental times. The distribution of cohort developmental times was compared to predictions from an existing stochastic cohort model and was found to be in reasonable agreement at all temperatures tested.

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is an annual pest infesting a sequence of cropping systems from a source of overwintering pupae that emerge in southern Florida and portions of the Gulf Coast (Chittenden 1901, Luginbill 1928). It is a major pest of field corn, sweet corn, pasturegrass, and peanuts in the southeastern United States. While a relatively large amount of research has been completed on host plant resistance (Starks et al. 1967, Leuck and Perkins 1972, Leuck 1970) and chemical control (Cantu and Wolfenbarger 1972, Roberts 1965) of this species, little attention has been given to the life cycle, particularly temperature-dependent development. Luginbill (1928) gave developmental times for *S. frugiperda* stages but lacked both the range and precision of temperature controls necessary to model the development process.

We were interested in deriving a usable developmental model for fall armyworm populations as an integral part of a total pest management program designed for control of this species in corn and peanuts. Placing both insect and host plant in proper temporal relationship was of major concern. Meeting this need demanded that we first conduct a thorough study of *S. frugiperda* development over a wide range of constant and variable temperatures likely to be encountered by this insect in nature. The present study was designed to construct a temperature-dependent developmental model for the fall armyworm based on the concepts and ideas presented in the bio-physical, absolute reaction rate model of Sharpe and DeMichele (1977) and the extension of that model to cohort populations by Sharpe et al. (1977).

Use of these 2 models would occur in 4 distinct phases. First, constant temperature development rates (and their respective standard deviations) would serve as inputs to the absolute reaction model (Sharpe and DeMichele 1977). Output from this model would consist of a set of kinetic constants useful in describing the developmental process in *S. frugiperda*. Second, these constants would become inputs into a stochastic cohort model (Sharpe et al. 1977) designed to predict the distribution of development times under any temperature regime. Third, laboratory data on development times of *S. frugiperda* at controlled variable temperatures would be compared to model predictions at those temperatures. Finally, "real world" data on developmental periods of *S. frugiperda* on corn and peanuts would be collected and compared to model predictions based on in-field temperature data. This sequence of events would be followed by a comparison, if the model were validated, of different types of temperature data (e.g., daily min/max vs. hourly micro-temperatures of leaves, soil, etc.) and the relative accuracy of each when used in the *S. frugiperda* model.

MATERIALS AND METHODS

Fall armyworm cultures were maintained at the USDA, Insect Attractants Laboratory, Gainesville, Fla., where immatures were reared on artificial diet according to the general techniques of Burton (1967). A series of tests was conducted over a wide range of constant and variable temperatures by isolating cohort individuals into 1-oz medicine cups partially filled with diet and recording the egg-to-adult development times.

For each described test, egg masses were collected from oviposition cages where eggs had been deposited on tissue paper during the previous scotoperiod. Oviposition cages were maintained at 26.7°±1°C and 75% RH. Egg masses were removed from the tissue paper, placed in diet cups, and transferred to the appropriate test environment. These eggs were observed daily until hatch, when 100 first instars were isolated individually into diet cups and returned to the respective test chambers. Data were recorded on larval and pupal mortality and on total development times.

Spodoptera frugiperda egg-to-adult development times were recorded under 3 types of temperature regimes:

1. Constant temperatures of 15.6, 18.3, 21.1, 23.9, 26.7, 29.4, 32.2, 35.0 and 37.8°C. Each test

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[3] Presently, Ass't. Res. Scientist, Entomol. and Nematol., Univ. of Florida, Gainesville, Fla. 32611.

[4] USDA, Insect Attractants Lab, Gainesville.

[5] Assoc. Prof., Entomol. and Nematol., Univ. of Florida.

Table 1.—Daily min/max temperature (°C) for 4 variable temperature regimes utilized in studying *S. frugiperda* development. Each utilized a photoperiod of 14L: 10D.

	Random 1		Random 2		Summer		Spring[a]	
Day	Min	Max	Min	Max	Min	Max	Min	Max
1	22.8	33.3	28.9	33.8	22.2	33.9	8.3	21.7
2	21.9	32.8	17.8	33.3	22.2	34.7	8.9	21.4
3	18.3	30.8	24.4	32.8	22.5	34.2	8.9	21.1
4	16.7	35.6	25.0	36.1	22.2	33.9	8.3	21.1
5	13.9	24.2	22.2	37.2	22.8	34.2	8.9	21.7
6	15.6	28.3	14.4	27.8	22.2	34.2	9.4	22.2
7	11.1	30.6	19.7	30.6	22.8	33.9	10.0	22.2
8	15.6	28.3	24.4	32.2	22.2	34.2	10.0	22.2
9	21.7	32.8	17.8	33.1	22.2	35.0	10.0	22.2
10	18.3	27.2	23.9	29.7	23.1	35.0	10.0	22.8
11	17.2	35.0	24.4	36.9	23.1	34.4	8.9	22.8
12	13.9	23.9	18.1	27.8	23.3	34.7	8.9	22.8
13	15.3	28.1	14.4	30.3	22.8	34.4	8.9	22.8
14	11.4	30.8	20.0	37.2	23.1	33.9	8.9	22.8
15	15.6	28.3	20.6	33.9	22.2	34.4	10.0	22.2
16	22.2	32.8	18.3	33.9	22.5	35.0	8.9	22.8
17	18.3	27.8	24.4	30.3	22.2	34.4		
18	17.2	35.3	25.0	37.2	22.2	33.6		
19	13.6	24.2	18.3	26.7	22.2	33.9		
20	15.8	28.3	14.2	30.0	23.1	35.0		
21	11.7	31.1	19.7	36.9	23.3	35.0		
22	15.6	28.3	21.7	33.3	23.1	35.0		
23	22.2	32.8	17.5	32.5	23.1	35.6		
24	18.9	27.8	23.9	29.4	23.1	35.0		
25	17.2	35.6	24.4	36.7	22.8	34.4		
26	12.8	22.8	17.8	27.5	22.8	34.4		
27	14.4	27.2	13.9	29.7	22.2	34.4		
28	10.6	30.0	19.4	36.4	22.8	34.4		
29	12.8	26.1	20.0	30.6	22.5	34.4		
30	21.1	31.7	17.5	33.9	22.8	35.0		
31	17.8	26.7	25.0	30.6				
32	17.2	35.0	25.3	37.2				
33	13.3	24.4	17.2	27.5				
34	15.6	28.3						
35	11.7	31.7						
36	13.3	27.2						
37	22.2	32.8						
38	18.3	27.2						
39	17.2	35.8						
40	13.9	24.4						
41	15.6	28.3						
42	11.7	31.1						
43	12.2	26.7						
44	21.9	33.3						
45	17.8	27.8						

[a] No eggs hatched at this regime; fungus covered eggs after 16 days.

maintained a photoperiod of 14L:10D and the respective constant temperature ± 1°C.

2. A day/night regime using a 14L:10D photoperiod with 32.2°C during photophase and 21.1°C during scotophase.
3. Four cam-controlled variable temperature regimes simulating (see Table 1):
   a. avg temperatures during "spring" at Gainesville, Fla. (roughly, fluctuations between 21° and 8°C).
   b. avg temperatures during "summer" at Gainesville, Fla. (roughly, fluctuations between 34° and 22°C).
   c. 2 temperature regimes (called "Random") which employed widely fluctuating temperatures reaching both temperature extremes for *S. frugiperda*. These regimes were used to check the accuracy of the derived kinetic constants by utilizing many temperatures lying outside the linear portion of the temperature-development curve for this species.

RESULTS

Analysis of the developmental data on *S. frugiperda* indicated that the models of Sharpe and DeMichele (1977) and Sharpe et al. (1977) could be utilized to describe the effects of temperature on the development of this insect. A summary of the developmental data is given in Table 2. Egg-to-adult development times ranged from slightly over 66 days (15.6°C) to about 18 days (35.0°C). There were no significant differences in male and female developmental times. The lower developmental threshold for egg development (i.e., that temperature at which eggs were just able to develop into larvae) was found to occur between 15.6° and 18.3°C.

Developmental rate (= time^{-1}) data obtained for *S. frugiperda* are also shown in Table 2. Percent deviation (ratio of the standard deviation to mean development rate) in developmental rates averaged ca. 5% and was relatively constant independent of temperature or sex. Such constant percent deviation was required in order to utilize the model of Sharpe et al. (1977) and had been demonstrated to be true for the boll weevil, *Anthonomus grandis* Boheman, and the cotton fleahopper, *Pseudatomoscelis seriatus* Reuter (Sharpe et al. 1977). This constant variability also had been confirmed for the braconid, *Bracon mellitor* Say (Barfield et al. 1977).

The Stochastic Model.—A detailed description of the derivation of this model is given by Sharpe et al. (1977). Briefly, the model will account for: (1) the skew in emergence times observed in most poikilothermic organisms and (2) the upper and lower areas of non-linear development along the temperature-development response curve. The stochastic model has the general form:

$$r(T) = \frac{\epsilon_c \, T \, e^{\phi - H_A^{\ddagger}/RT}}{1 + e^{(\Delta S_L - \Delta H_L/T)/R} + e^{(\Delta S_H - \Delta H_H/T)/R}} \quad (1)$$

where, r(T) = mean development rate at absolute temperature T,

ϵ_c = relative concentration of development factors (gene activators and/or biochemical catalysts and regulators); random variable with mean = 1.0 and standard deviation ρ,

R = the universal gas constant,

$H_A^{\ddagger}$ = enthalpy of activation of the developmental process (cal/mole),

Table 2.—Summary of constant temperature developmental data for cohorts of *S. frugiperda* reared on artificial diet and at a photoperiod of 14L:10D.

Temp (°C)	No. individuals		Sex	Development times (days)		Development rates (days^{-1})		% deviation
	Initial	Surviving		Mean	SD	Mean	SD	[σ/R(T)]
15.6	>100	0	M&F	—[a]	—	—	—	—
18.3	100	21	M	66.5	2.79	.015	.001	07
		47	F	66.6	4.04	.015	.001	07
21.1	100	20	M	53.3	2.07	.019	.001	05
		35	F	52.3	2.36	.019	.001	05
23.9	100	38	M	39.0	2.19	.026	.001	04
		44	F	37.8	2.27	.027	.002	07
26.7	100	49	M	29.6	1.37	.034	.001	03
		40	F	28.1	0.88	.036	.001	03
29.4	100	40	M	22.1	1.27	.045	.003	07
		31	F	22.5	0.85	.045	.002	04
32.2	100	41	M	19.3	0.91	.052	.002	04
		44	F	19.7	0.80	.051	.002	04
35.0	100	22	M	18.5	0.98	.054	.003	06
		31	F	18.4	1.26	.055	.004	07
37.8	100	0	M&F	—[b]	—	—	—	—

[a] No egg hatch at this regime.
[b] No adult emergence at this regime (all died as larvae).

ΔS_L = change in entropy of low temperature inactivation (cal/mole − °K),

ΔH_L = change in enthalpy of low temperature inactivation (cal/mole),

ΔS_H = change in entropy of high temperature inactivation (cal/mole − °K),

ΔH_H = change in enthalpy of high temperature inactivation (cal/mole),

ϕ = the life stage constant.

Thus, the model describes the developmental process in terms of 8 constants (7 derived from the data): R, the 6 constants of equation (1) and ρ, the ratio of $\sigma/r(T)$ (see Table 2). These quantities, estimated from constant temperature studies, were used to predict the probability distribution of development times for cohorts of *S. frugiperda* reared under variable temperatures.

The constants for the *S. frugiperda* model were determined using the data in Table 2 and the nonlinear regression techniques of Marquardt (1963) (see Sharpe and DeMichele 1977, Barfield et al. 1977). Those constants (Table 3) were used in the stochastic cohort model to determine the probability distribution of adult emergence times under each variable temperature regime.

Variable Temperature Development.—Adult eclosion times for *S. frugiperda* cohorts reared under the day/night and "summer" variable temperature regimes are depicted in Fig. 1. Histogram plots illustrate the percentage of adults emerging as a function of days from oviposition. The solid lines depict the probability of emergence according to model predictions. There appears to be reasonable agreement between model and observed data at these temperature regimes. These particular regimes represent "typical" temperatures experienced in the corn and peanut growing areas near Gainesville, Fla., during a given growing season.

The model employs 3 sets (= total of 6) of kinetic constants: 2 for the low temperature, non-linear portion of the development curve, 2 for the linear portion, and 2 for the high temperature, non-linear portion. An independent check of each of these pairs of constants is most desirable in evaluating their accuracy. One method of doing this is to utilize non-realistic widely fluctuating temperatures, including brief periods within 1 of the 2 extreme non-linear regions of the study species. As the temperatures enter 1 of the 3 regions, the pair of constants derived for that region dominate model development. If the

Table 3.—Developmental constants for *S. frugiperda* derived from a nonlinear regression fit of constant temperature development rates.

	Constants	Value	Units
Kinetic	$\ddagger H_A$	11,822.57	cal/mole
	S_H	295.08	cal/mole − °K
	H_H	90,678.50	cal/mole
	S_L	−19.59	cal/mole − °K
	H_L	−6603.414	cal/mole
Life Stage (egg-to-adult)	ϕ_{EA}	12.254	time^{-1}
	ρ_{EA}	0.0507	—

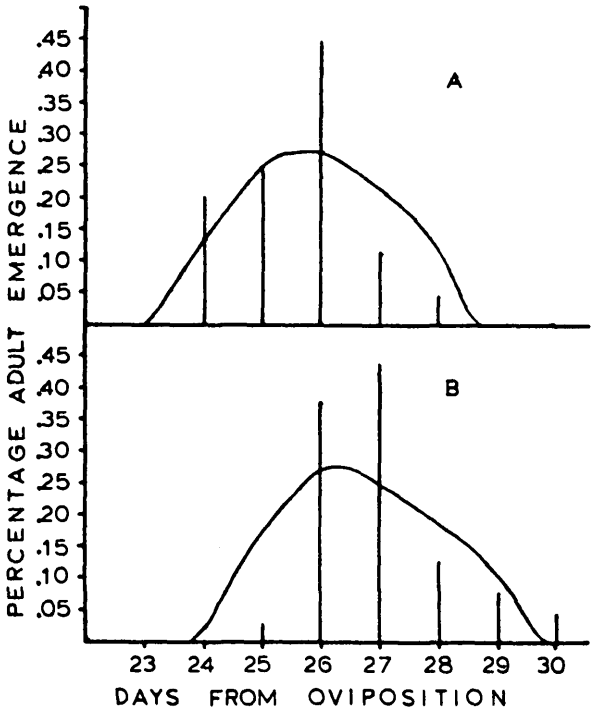

FIG. 1.—Histogram plot and model predicted distribution (curve) of *S. frugiperda* adult eclosion times at (A) day/night temperature regime using 32.2°C during photophase and 21.1°C during scotophase and (B) variable temperatures simulating those "typical" at Gainesville, Fla. during "Summer." Both (A) and (B) maintained a photoperiod of 14L:10D.

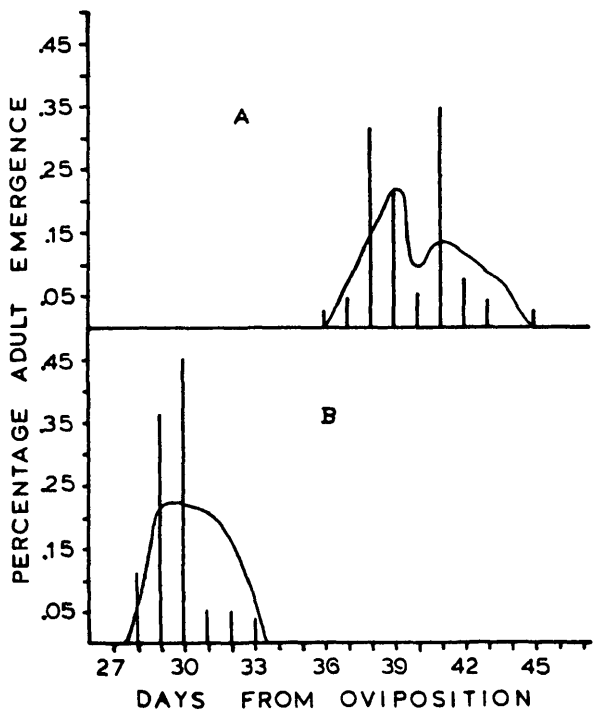

FIG. 2.—Histogram plot and model predicted distribution (curve) of *S. frugiperda* adult eclosion times at 2 "Random", widely fluctuating temperature regimes (see Table 1). (A) maintained less amplitude in temperature fluctuation than did (B). Both maintained photoperiods of 14L:10D.

model can still predict reasonably well the emergence times, more confidence is gained in the derived kinetic constants.

Fig. 2 depicts results of studies conducted under 2 "Random" temperature regimes. Daily min/max values for these regimes are given in Table 1. Despite the wide fluctuations in temperature, there is still reasonable agreement between model and observed data. "Random 1" tended to fluctuate as did the observed data, while "Random 2" was somewhat at odds with the model during days 30–32. This was not too surprising as Sharpe (pers. comm.) has found that for cohorts of less than 100 insects [using *Heliothis zea* (Boddie)] the model and observed skew are sometimes at odds (see Barfield et al. 1977). However, means and ranges of adult eclosion times are also useful in comparing model and observed data. These type data are quite useful in designing pest management strategies where the probable onset, mid-point and last occurrence of specific pests in the field are vitally important. An overall comparison of the *S. frugiperda* model and observed data is given in Table 4. Both means and ranges of model predictions and observed data are in good agreement.

DISCUSSION AND CONCLUSIONS

Our results tend to show that developmental data collected on *S. frugiperda* are usable in the generalized development models of Sharpe and DeMichele (1977) and Sharpe et al. (1977). There was reasonable agreement between model predictions and developmental data at 4 variable temperature regimes, 2 of which utilized many temperatures in the extreme range of this species.

Spodoptera frugiperda populations annually infest a variety of plant systems from the Gulf Coast northward and westward (Luginbill 1928). Any pest management program designed to combat this pest would require an effective tool for predicting its de-

Table 4.—Comparison of model and observed *S. frugiperda* development times at several variable temperature regimes.

Temperature regime	No. of observations	Observed mean (days)	Predicted mean (days)	Observed range (days)	Predicted range (days)
32.2/21.1°C	67	25.5	26.1	24–28	23–29
"Summer"[a]	87	26.9	28.8	25–30	24–29.5
"Random 1"[a]	90	39.6	40.2	36–45	36–44.5
"Random 2"[a]	71	29.7	30.5	28–33	28–34
"Spring"[a]	0[b]	—	—	—	—

[a] See Materials and Methods for details.
[b] No eggs hatched at this regime.

velopmental periods. This, for example, might be important in forewarning scouts when to intensify sampling schedules to detect economically important infestations, in timing insecticide applications to optimize the killing efficiency, or in aiding in the prediction of larval feeding periods, adult flights, etc.

The natural ecosystems inhabited by *S. frugiperda* are, at best, extremely complicated. The present model utilizes only temperature to predict developmental periods. While temperature is no doubt a major factor influencing *S. frugiperda* development, other factors (e.g., nutritive value of host plant) undoubtedly play some role, although Roberts (1963) showed no significant difference in mean egg-to-adult development time of *S. frugiperda* reared on corn, cowpea, gain sorghum, lima beans, millet, or peanuts. Future refinements of the present model must include the effects of other key factors affecting *S. frugiperda* in the sequence of host plant communities it infests annually.

An economically feasible pest management program may not be able to utilize a sophisticated, in-field environmental monitoring network for each field under a given management program (see Fulton and Haynes 1977). Also, data cannot be collected over, say, some 30–40 day period and used to predict *S. frugiperda* development for cohorts developing (and inflicting damage) during that same period. The applicability of localized temperature data vs. regional data will, at some time, have to be addressed prior to any regional use of the present developmental model. A 1st step in this direction may be a comparison of localized micro-temperatures with local and regional averages for daily min/max for their ability to predict accurately field development of *S. frugiperda.*

In conclusion, the present model appears adequate for describing the effects of temperature on *S. frugiperda* development. Carefully designed field tests will allow further validation of the present model and will illuminate areas in the host plant/*S. frugiperda* system demanding closer attention before the model can be integrated into a total pest management program for this insect.

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