Validation of a Physiological Day Equation: Development of the Mexican Bean Beetle on Snap Beans and Soybeans

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ABSTRACT

A physiological day equation proposed by Waddill et al. (1976) of the form $PD = 1/24\ \{[.55(TMAX-TMIN)+TMIN]-THT+[.15(TMAX-TMIN)+TMIN]-THT\}$ where $TMAX$ = Maximum Temperature, $TMIN$ = Minimum Temperature and THT = Developmental Threshold, predicted development of the larvae of the Mexican bean beetle, *Epilachna varivestis* Mulsant, on soybeans and snap beans with only ca. a 2% error. This sine curve based equation incorporates geographical location coefficients, and predictions were accurate enough for acceptable simulation limits, especially with fluctuating temperatures such as those that occur in the field. Predictions by the equation were improved when temperatures did not approach the physiological limits of beetle development.

The total number of days required for larvae to mature on snap beans (*Phaseolus*) and soybeans was 16.5 and 23.5, respectively. Extension of Mexican bean beetle developmental time when soybeans were utilized as food may have serious implications when compiling biological data for computer simulations.

In many pest management programs current emphasis is on the development of computer simulations for instructive and predictive purposes. One such computer simulation of the Mexican bean beetle, *Epilachna varivestis* Mulsant, on soybeans is currently being constructed and refined (Waddill et al. 1976). An important submodel of this simulation is the relationship between temperature and development. The most general assumption is that development of organisms follows a time scale which is temperature dependent. Implicit in the concept is the assumption that the insect developmental velocity (percent development per unit time) is proportional to heat quantity input above a threshold limit. Various mathematical formulae have been used to express the developmental velocity, but the most useful is the logistic curve of Pearl and Reed (1920). Davidson (1944) showed the near linearity of the velocity curve between the upper and lower limits, and also the alteration of the rate and mortality as the temperature nears the limits.

In efforts to more accurately simulate natural conditions with reference to developmental rates, fluctuating temperature regimes have been used (Eubank et al. 1973). Sigmoid curve equations based on constant temperatures that determine developmental rates for each instar can be used for predicting development at fluctuating temperatures, but the process is time consuming. Stinner et al. (1974) developed a Fortran algorithm for accomplishing the summation of temperature effects at 2- or 3-h intervals and predicting rates at fluctuating temperatures.

Another method of predicting the effect of temperature on biological processes is heat accumulation expressed in degree-days, which has been used in various forms for almost 2½ centuries (Wang 1960). Arnold (1960) used daily maximum and minimum temperatures to circumvent extended calculations of the area beneath the temperature curve and above the threshold temperature to determine cumulative degree-day values. He based the method on the mathematical similarity of the daily temperature cycle and the trigonometric sine curve. Baskerville and Emin (1969) extended Arnold's method by adding a Fortran program and providing formulae to account for temperature cycles above and below upper and lower threshold temperatures. Allen (1976) presented 6 formulae for temperature cycle combinations, some exceeding upper and lower threshold temperatures. This Fortran program was based on a sine curve, and considered the 1st daily minimum not necessarily the same as the 2nd daily minimum. Hence, 2 half-day computations were necessary to determine degree days for a single day.

In the interests of program time, bulk, and simplicity, a new equation has been formulated for the relationship between temperature and development. Waddill et al. (1976) developed an equation that is based on the sine curve and calculates physiological days from daily maximum and minimum temperatures.

This study is concerned with the validation of

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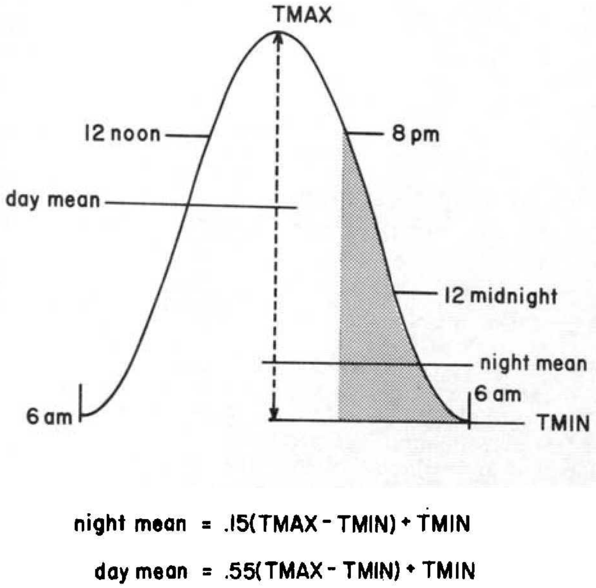

FIG. 1.—Sine wave representation of the daily temperature cycle. Correction coefficients are used to determine the proportional distance between the range of day and night time temperature means.

this physiological day equation of development of the Mexican bean beetle on soybeans and snap beans.

Methods and Materials

The daily temperature cycles were recorded by a revolving drum hydrothermograph. Weather data were used to calculate physiological days by the following formula (Waddill et al. 1976):

$$PD = \frac{1}{24}\{[.55(TMAX - TMIN) + TMIN] - THT + [.15(TMAX - TMIN) + TMIN] - THT\}$$

where TMAX = daily maximum temperature; TMIN = daily minimum temperature; and THT = developmental threshold. In this case 15°C was used as the developmental threshold (unpublished data). The equation depicts a linear relationship between development and temperature, and the physiological days predicted are the results of the cumulated area beneath the temperature curve and the threshold temperature. The area can be measured directly by a planimeter, but has been commonly measured indirectly through the averaging of daily high and low temperatures. However, considering the time spent at each temperature during the daily rise and fall, correction coefficients have been added to evaluate a 'true' mean for day and night temperature curves. The true mean temperature is distinguished from averaging the high and low temperature and is the mean temperature considering the duration of time at each temperature of a daily curve (Fig. 1).

The daytime coefficient (0.55) was determined in the following manner: (1) temperatures for each h of daytime were summed and divided by the number of h during the daylight h over several seasons; then (2) regression analysis of the avg daytime temperatures against the daytime portion of the physiological day equation (TMAX−TMIN+TMIN) times the coefficient values which maximized the correlation coefficient. The coefficient for the nighttime portion of the equation was determined by the same method.

The coefficients used can vary for geographic locations that would normally modify the shape of the temperature cycle. These coefficients for Clemson University Edisto Experiment Station, Blackville, SC, were set at 55% of the difference between the maximum and minimum temperatures for the curve depicting daytime temperatures and 15% for the night temperature curve. Because the equation is based on a mean day and night temperature of 27°C, a day in which the day and night means are 27°C, the equation prediction will be one physiological day. For days averaging less than 27°C, the physiological day would be expressed as a fraction of a day.

Physiological days were calculated for each day and were accumulated for each stadium of the Mexican bean beetle. Since the physiological day equation is based on a sine curve temperature cycle and location correction coefficients, predictions for constant and alternating temperature regimes must be determined in a different manner. Temperatures at which larvae were reared were placed in the equation and the fraction of a physiological day was found. This fraction was then multiplied by the hours needed for development at 27°C. The results were then added (or the portion substracted if the fraction were over 1) to the hours needed at 27°C.

Mexican bean beetle egg masses were collected from 'Coker 136' soybeans and brought to the laboratory. Upon hatching, 1st instars were placed in plastic petri dishes and supplied with fresh soybean leaflets. A moistened cotton ball was placed over the end of the leaflet petiole to prevent rapid desiccation. After the 1st molt, 2nd instars were placed singly in individual petri dishes and given fresh leaflets daily until pupation. All larvae used for constant temperature experiments were maintained in rearing chambers at 27°, 22°, and 17°C each varying ± 2°C, with 50–65% RH, and 14:10 L:D. For experiments dealing with alternating temperatures, sets of larvae were transferred after 8 h from a rearing chamber at 32°±2°C, 40–50% RH, and constant light to 3 other chambers. They were then held for 16 h at 27°, 22°, or 17°C with an L:D of 6:10. Larvae were checked at 12-h intervals and records of molting and mortality were made.

Two 10-oz styrofoam Kool Kups® were modified to form small cages to observe larvae for field experiments (Fig. 2). For cage construction, the top 1 inch was cut away from a cup and covered with Saran® screening. The bottom of a 2nd cup was cut away and likewise covered with screening.

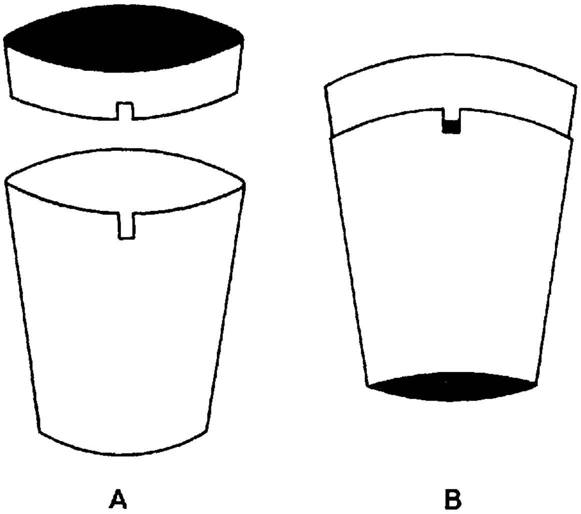

FIG. 2.—Cup-cage used to contain Mexican bean beetle larvae in the field. A—cage parts separated to show screened top and notches to allow attachment to petiole. B—cage parts together to form completed cage.

The 2 portions were then notched to accommodate the leaf petiole. The tapered portion of the top part was pressed tightly into the bottom part which formed a cage to enclose a soybean leaf. The light weight cages could be easily attached to the plants and the tight fitting parts held the cage snugly to the soybean leaf petiole. The screened bottom prevented water accumulation.

Newly hatched larvae were collected from fields of 'Bragg' (1975) and Coker 136 (1976) soybeans, and snap beans (1976). First-stage larvae were placed in groups in a single cup-cage until the 1st molt; they were then transferred singly to individual cup-cages. Larvae were checked at 12-h intervals and moved to fresh leaves when necessary. All field and laboratory experiments were conducted at the Clemson University Edisto Experiment Station, Blackville, SC.

Results and Discussion

The physiological day equation predictions for each instar reared in the field on Bragg and Coker 136 soybeans approximated those days needed for development at constant 27°C on soybeans in the laboratory (Table 1). The total days needed at the constant temperature for development was 23.0 days. The predicted physiological days needed totaled 23.4 and 23.6 on Bragg and Coker 136, respectively. The error of the predicted development time was ½ day longer which was ca. 2%. Individual larvae were observed to have 1 shortened stadium length, but appeared to compensate the next stage by having a longer developmental time. These small inherent variations are expected in biological experiments, but the equation predictions were within ½ day of observed stadia lengths in the laboratory. Thus, the sine curve based equation, the location correction coefficients, and the estimated threshold temperature for the bean beetle were accurate enough for acceptable simulation limits.

The equation for calculating physiological days has several advantages over others (Stinner et al. 1974, Allen 1976) that have been developed. With this single equation and inputs of the daily maximum and minimum temperatures, the daily contribution to development is easily calculated. The correction coefficients add a dimension that compensates for the alteration of the temperature cycle due to geographical location. These coefficients can be reasonably estimated by examination of temperature curves of the region. Thus, with this relatively simple equation, the only remaining factor that must be determined is the developmental threshold temperature. The results of these experiments indicate the value of this equation in computer simulations.

Although the physiological day equation primarily is to be used for calculations involving the daily temperature cycle, predictions were made for constant temperature regimes (Table 2). A mean error of 6% was found for predictions at constant 22°C, and a mean error of 20% for predictions at constant 17°C. The observed laboratory data indicated that

Table 1.—Mean number of days needed for development of Mexican bean beetle larvae in the laboratory at 27°C on soybeans compared with calculations from the physiological day equation[a] on 2 varieties of soybeans in the field.

			Equation predictions			
	Laboratory reared on 27°C		Field reared on Bragg soybeans		Field reared on Coker 136 soybeans	
Stadia	N	Mean±SD	N	Mean±SD	N	Mean±SD
1st	100	3.64±0.22	100	3.90±0.41	60	3.51±0.24
2nd	84	3.51±0.62	94	3.30±0.45	54	3.21±0.41
3rd	81	3.91±0.67	79	3.91±0.49	48	4.47±0.74
4th	77	7.02±0.68	69	7.41±0.73	46	7.63±0.79
Pupa	74	4.92±0.47	57	4.93±0.72	43	4.98±0.47

[a] $PD = 1/24 \{ [.55(TMAX - TMIN) + TMIN] - 15 + [.15(TMAX - TMIN) + TMIN] - 15 \}$.

Table 2.—Mean number of days needed for development of Mexican bean beetle larvae in the laboratory at constant temperatures compared with calculations from the physiological day equation.[a]

	Laboratory reared at 27°C		Laboratory reared at 22°C			Laboratory reared at 17°C		
Stadia	N	Mean±SD	N	Mean±SD	Equation prediction	N	Mean±SD	Equation prediction
1st	100	3.64±0.22	100	5.28±0.43	5.39	70	8.64±0.82	7.16
2nd	84	3.51±0.62	86	4.47±0.57	4.91	60	7.17±0.84	6.63
3rd	81	3.91±0.67	81	5.11±0.55	5.48	55	9.83±2.17	7.39
4th	77	7.02±0.68	76	9.29±0.79	9.82	48	16.79±2.09	13.36
Pupa	74	4.92±0.47	75	6.45±0.42	6.89	44	13.67±0.65	10.30

[a] $PD = 1/24\ \{[.55(TMAX - TMIN) + TMIN] - 15 + [.15(TMAX - TMIN) + TMIN] - 15\}$.

Mexican bean beetle larvae, like other insects, have a sigmoid developmental curve over a range of constant temperatures. The large error found at 17°C was due to the temperatures which approached the developmental threshold.

Larval development was measured in alternating temperature regimes that roughly simulate the daily rise and fall of temperatures (Table 3). First instar survival after two 8-h periods at 32°C was only 3%, so the experiment was restarted with 2nd instars. These averaged only 14% mortality with the highest (20%) occurring in the 32°–17°C regime. Equation predictions approximated developmental times for 2 regimes, 32°–27°C and 32°–22°C, and had the largest error in the last 2 stadia. The greatest error occurred with the 32°–17°C regime and reached as high as 12% for some stadia. A portion of the error in this last regime was due to the nearness of 17°C to the threshold temperature (15°C) and the possibility that 32°C was near the upper threshold. Both temperatures would then retard development. Since the equation is linear and not sigmoid, the lengthened development near the upper and lower thresholds could not appear in the predictions. Also, the possibility exists that the 8 h at 32°C in the other 2 regimes (32°–27°C and 32°-22°C) contributed to the error in those predictions.

Results from experiments using the physiological day equation with constant and alternating temperatures in the laboratory were not as precise as those obtained from field observations. The simplicity of the equation, in regards to computer time, and its accuracy, 2% error in the prediction of the total development time, illustrate the equation's usefulness in computer simulations of development time in the field for the Mexican bean beetle.

Results from field experiments to show the difference in development lengths on snap beans and Coker 136 soybeans are presented in Fig. 3. Physiological days were calculated by the equation. The total number of days required for larvae to mature on snap beans and soybeans was 16.5 and 23.6, respectively. Kogan (1972) found similar results in laboratory experiments at 27°C where larvae reared through the 4th stadium on snap beans and soybeans took 14 and 18.3 days, respectively. Those fed 'Harosoy' and 'Clark' soybeans weighed less and consumed more leaf material. He concluded that the lack of necessary amounts of nutrients was the major reason for differences in developmental times.

The extended development on soybeans by the Mexican bean beetle is only one problem encountered when compiling biological information for computer simulations. Data from experiments must be suitable for conversion into the particular form required by simulation languages. The relationship between temperature and development is one such area that normally requires transformation. Many

Table 3.—Mean number of days needed for development of Mexican bean beetle larvae in the laboratory at alternating temperatures compared with calculations from the physiological day equation.[a]

	Temperature regime			Temperature regime			Temperature regime		
	8 h at 32°C 16 h at 27°C			8 h at 32°C 16 h at 22°C			8 h at 32°C 16 h at 17°C		
Stadia	N	Mean±SD	Equation prediction	N	Mean±SD	Equation prediction	N	Mean±SD	Equation prediction
1st[b]	—	—		—	—		—	—	
2nd	60	3.35±0.49	3.07	40	3.90±0.44	3.89	40	4.89±0.59	4.95
3rd	56	3.95±0.40	3.36	34	4.82±0.46	4.34	32	7.18±0.88	5.52
4th	52	7.40±0.99	6.03	33	8.65±0.81	7.79	30	11.03±1.64	9.89
Pupa	51	5.09±0.59	4.23	28	6.17±0.60	5.46	24	9.09±0.69	6.94

[a] $PD = 1/24\ \{[.55(TMAX - TMIN) + TMIN] - 15 + [.15(TMAX - TMIN) + TMIN] - 15\}$.
[b] First instars were killed by the exposure to 16 h at 32°C.

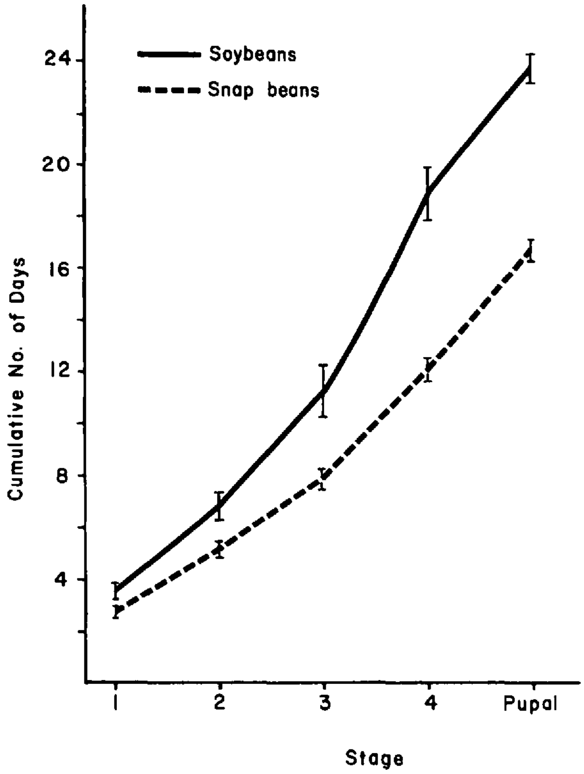

FIG. 3.—Comparison of the cumulative physiological days needed for development of Mexican bean beetle larvae on Coker 136 soybeans and snap beans in the field. Vertical lines denote standard deviations.

of the earlier workers chose chronological days as a means of expressing development. This is inadequate for computer simulations. The physiological day equation discussed and evaluated here easily solves problems with development by: (1) simplification of calculations, and (2) production of accurate predictions. With this equation, development is based on a temperature standard that can vary for individual species. For the Mexican bean beetle, the equation used 27°C as the standard temperature. The equation predictions are expressed in fractions of days that are easily accumulated and are easily used in simulations that increment on a daily basis.

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