Temperature-Dependent Development of Mexican Bean Beetle (Coleoptera: Coccinellidae) Immatures on Snap Bean and Soybean Foliage[1]

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ABSTRACT Developmental periods and survival were determined for immature stages of the Mexican bean beetle at constant temperatures of 11, 15, 20, 25, and 30°C. Rearings were conducted on greenhouse-grown snap bean foliage, greenhouse-grown soybean foliage, and field-grown soybean foliage. Comparisons between rearings on greenhouse snap bean and greenhouse soybean foliage indicated that larval developmental periods for individual instars did not differ between host plants, but larval survival was different depending on temperatures. Comparisons between rearings on greenhouse and field soybean foliage indicated no differences in larval developmental periods or survival. The constant temperature developmental rates for eggs and larvae permitted satisfactory simulation of egg and larval development under changing temperature regimes in the laboratory. For each stage, a fitted equation for the developmental rate - temperature relationship on snap bean and on soybean foliage was determined.

The Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, has become an important defoliator of soybeans, *Glycine max* (L.) Merrill, in the Middle Atlantic region. Formerly, it was only a pest of *Phaseolus*, which includes snap and lima beans. In an effort to manage the MBB in a manner that would not disrupt the populations of other soybean arthropods, the eulophid wasp, *Pediobius foveolatus* (Crawford), was imported from India and released in the eastern United States (Angalet et al. 1968). Since the parasite did not overwinter in that region, a program involving snap bean nurse plots for concentrating the MBB and colonizing the parasite was developed and implemented on a statewide basis in Maryland (Stevens et al. 1975). Since 1980, the USDA has supported a regional program for biological control of the MBB on soybeans with this parasite. Evaluation of the ongoing program was a high priority, and one approach taken was to construct a computer simulation model for MBB and *P. foveolatus* populations in both snap bean nurse plots and commercial soybean fields. This paper reports and compares the temperature-dependent development and survival of all immature stages of the MBB over an extended range of temperatures on both snap bean and soybean foliage as was required for this modeling effort.

Materials and Methods

Host Plant and Insect Material

Snap bean foliage, *P. vulgaris* L. (var. Burpee Stringless) was grown in the greenhouse under natural light conditions in College Park, MD. This was the variety used in nurse plots throughout Maryland. Seed was planted in Promix BX®, a soilless mix containing the necessary macro- and micronutrients.

Soybean foliage was obtained from plants (1) grown in the same potting mix in the same greenhouse and (2) from a commercial soybean field in Queenstown, MD. Essex, the most popular variety in Maryland, was grown in the greenhouse. Foliage was obtained when plants were in the reproductive stages R1-R5 (Fehr et al. 1971) with three to six nodes/main stem. Field-grown soybean foliage was obtained from plants (var. James) in reproductive stages R2-R6 with 10 to 11 nodes/main stem. Both the greenhouse and field soybeans were full season determinate varieties, and the foliage was collected when the plants were in approximately the same developmental stages.

For all studies, MBB adults were obtained from the Maryland Department of Agriculture where immatures were reared continuously on snap bean foliage at 25°C and a photoperiod of 16:8 (L:D). That colony had been founded from field-collected adults within six months of this study.

Experimental Rearing Conditions

Immature stages were reared individually in 250 ml paper cartons with clear plastic lids. Eggs were incubated as clusters. The leaf in each carton was kept viable by placing the end of the petiole into a water vial. Leaves were changed as needed to maintain a continuous food supply for the larvae. Each carton was checked daily, the developmental stage was recorded, and newly eclosed adults were sexed.

Eggs were obtained daily from a freely mating caged population of MBB adults incubated at 20–25°C and photoperiods of 15:9 to 16:8 (L:D). Adults were provided with only snap bean or soybean foliage as was required by each study. Newly emerged 1st instar larvae and newly molted larvae of other instars were obtained daily from eggs and larvae incubated under similar conditions with the appropriate host plant material. These were used to supplement the rearings as needed.

Experimental rearing conditions included five constant temperatures: 11, 15, 20, 25, and 30°C with photoperiods of 14:10 to 16:8. Relative humidities were

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kept as high as possible by placing open pans of water in all incubators and by enclosing rearing cartons in clear plastic bags containing moist paper towels.

Eggs from MBB adults fed only snap bean foliage were incubated at all five temperatures. Developmental times were observed for at least 40 individuals at each suitable temperature. For comparison, eggs from adults fed only soybean foliage were incubated at 25°C. More than 200 developmental times were observed at that temperature.

First through 4th instar larvae were reared on greenhouse snap bean foliage at all five temperatures and on greenhouse soybean foliage at the four higher temperatures. Development was recorded for the resulting prepupae and pupae. For most of these stages at most of these temperatures, developmental times were obtained for at least 20 individuals. For comparison, 1st through 4th instar larvae were reared at 25°C on field-grown soybean foliage. Development was recorded for the resulting prepupae and pupae as well.

From the records for each individual, the developmental period for each stage was determined for that temperature and plant material. For each stage under each set of rearing conditions, the median developmental period (50th percentile) was determined as a measure of the location of the distribution of developmental times. The 10th and 90th percentile periods were determined as measures of the variation in developmental times among individuals under those conditions. Ten percent of the developmental periods are as short or shorter than the 10th percentile period. Percentage survival through each stage was calculated by dividing the number surviving through the stage by the starting number and multiplying the result by 100%. Since survival and developmental time data were not always derived from the same individuals, both samples sizes were determined and reported.

Statistical Comparison of Developmental Periods and Percentage Survival

Developmental periods and percentage survival were compared separately for feeding (1st, 2nd, 3rd, and 4th instar larvae) and nonfeeding (prepupa and pupa) immature stages because host plant differences were expected to be more pronounced for the feeding stages. Comparisons were made (1) between rearings on greenhouse snap bean and greenhouse soybean foliage and (2) between greenhouse soybean and field soybean foliage. The following linear regression approach was used. Developmental period percentiles and survival were paired by instar and temperature. The values for one plant material were regressed on those for the other. The slope and y-intercept were tested for difference from one and zero, respectively. A significant t value for either parameter indicated a difference between the plant materials. All slopes and intercepts were tested at the 1% level of significance. If no significant difference was found between two rearings, then the regression value (r^2) was determined. Values for greenhouse soybean were regressed on those for greenhouse snap bean and similarly for field soybean on greenhouse soybean. The three developmental percentiles were compared separately for the greenhouse plant materials but had to be analyzed together for the field material because only one temperature had been used. There were not enough pairs of data to permit regression for nonfeeding stages on greenhouse versus field soybean.

Fitting Developmental Rate - Temperature Equations

For each stage reared at more than one temperature on greenhouse snap bean and greenhouse soybean foliage, the median developmental rate at each temperature on each host plant was calculated from the median developmental period for that temperature according to: developmental rate (%/day) = $\frac{1}{\text{developmental period (days)}} \times 100\%$. For each stage on each host plant, a developmental rate - temperature equation was fitted to yield developmental rate (y) as a function of temperature (x). The data was transformed to linearize the relationship and least squares linear

Table 1. Developmental periods and hatch at constant temperatures for Mexican bean beetle eggs from adults fed greenhouse snap bean and soybean foliage

Temp (°C)	Developmental period (days) 10th percentile	50th percentile	90th percentile		Hatch (%)	
			Snap bean			
11	—[a]	—[a]	—[a]	(0)[b]	0.0	(323)[c]
15	16	16	17	(61)	21.0	(290)
20	6	7	8	(72)	41.4	(174)
25	4	5	7	(575)	79.7	(778)
30	4	4	4	(42)	12.3	(341)
			Soybean			
25	4	5	6	(204)	41.4	(493)

[a]Too few developmental times were obtained to permit computation of this percentile.
[b]No. in parentheses are the numbers of developmental times obtained.
[c]No. in parentheses are the starting numbers for hatch determination.

Table 2. Developmental periods and survival of 1st instar larvae through pupae of the Mexican bean beetle at constant temperatures on greenhouse snap bean foliage

Stage	Temp (°C)	Developmental period (days) 10th percentile	50th percentile	90th percentile		Survival (%)	
1st-instar larva	11	11	16	16	(11)[a]	21.6	(51)[b]
	15	8	9	11	(53)	71.6	(74)
	20	5	5	6	(50)	82.0	(61)
	25	3	4	4	(98)	86.2	(116)
	30	3	3	4	(21)	58.3	(36)
2nd-instar larva	11	—[c]	13	—[c]	(5)	45.5	(11)
	15	7	7	9	(43)	81.1	(53)
	20	3	4	5	(48)	96.0	(50)
	25	3	3	4	(97)	98.0	(101)
	30	2	2	3	(59)	96.7	(61)
3rd-instar larva	11	—[c]	14	—[c]	(3)	50.0	(6)
	15	7	9	10.5	(25)	59.5	(42)
	20	3	4	5	(46)	97.9	(47)
	25	3	4	5	(99)	97.1	(104)
	30	2	3	4	(52)	91.2	(57)
4th-instar larva	11	—[c]	21	—[c]	(8)	80.0	(10)
	15	10	13	15	(30)	85.7	(35)
	20	5	7	8	(39)	92.9	(42)
	25	3	5	6	(83)	96.7	(90)
	30	3	5	7	(40)	80.0	(50)
Prepupa	11	—[c]	—[c]	—[c]	(0)	0.0	(6)
	15	3	4.5	7	(28)	93.3	(30)
	20	2	3	4	(39)	100.0	(39)
	25	1	2	3	(80)	96.6	(87)
	30	1	2	2	(32)	80.0	(40)
Pupa	15	14	15	16	(26)	96.3	(27)
	20	7	7	9	(38)	97.4	(39)
	25	4	5	7	(77)	96.4	(84)
	30	3	4	6	(27)	84.4	(32)

[a]No. in parentheses are the numbers of developmental times obtained.
[b]No. in parentheses are the starting numbers for survival determination.
[c]Too few developmental times were obtained to permit computation of this percentile.

regression was used to fit a straight line. The regression equation was then transformed back to the original units. Since the temperature ranges used in each study encompassed different segments of the theoretical developmental rate temperature - relationship described by Logan et al. (1976), the fitted equations differed in form according to the data and were either linear, exponential, or sigmoid (Davidson 1944). To provide a visual measure of goodness of fit, each equation was plotted through the original set of developmental rate - temperature data.

Validity of Constant Temperature Developmental Rates under Changing Temperature Conditions

The constant temperature developmental rates for eggs and larvae on snap bean foliage were used to simulate immature development under changing temperature conditions in the laboratory. Four cohorts of newly deposited eggs (243 total) were placed in separate cartons. The incubation temperature for each cohort was changed daily by moving the respective carton to a different incubator. Each cohort was exposed to a different random sequence of the five temperatures: 11, 15, 20, 25, and 30°C. All stages were counted daily and maintained on greenhouse snap bean foliage. Rearing was terminated after 22 days when 50% or more of each cohort had attained the 4th instar. For each cohort, the total number of days required for at least 50% of that cohort to reach the 1st, 2nd, 3rd, and 4th instars was determined. Thus, the observed phenological data consisted of a set of 16 time periods (for the four cohorts and four stages/cohort).

The development of each cohort was then simulated by using (1) the median developmental rates observed for each stage at each of the five constant temperatures and (2) the known sequence of incubation temperatures for each cohort. Starting with the egg stage, the total percentage of development completed by the median individual in the cohort by the end of a given day was calculated by adding the product of the median developmental rate (%/day) for eggs at that temperature and the one elapsed day to the total percent accumulated up to that day. When the total reached 100%, 50% of the simulated cohort was considered to have attained the 1st

Table 3. Developmental periods and survival of 1st instar larvae through pupae of the Mexican bean beetle at constant temperatures on greenhouse soybean foliage

Stage	Temp (°C)	Developmental period (days) 10th percentile	50th percentile	90th percentile		Survival (%)	
1st-instar larva	15	8	10	14	(32)[a]	100.0	(32)[b]
	20	5	5	8	(35)	83.3	(42)
	25	4	4	4	(26)	78.8	(33)
	30	2	4	5	(69)	93.2	(74)
2nd-instar larva	15	7	7	9	(32)	100.0	(32)
	20	3	4	7	(33)	94.3	(35)
	25	2	3	4	(60)	89.6	(67)
	30	2	3	5	(95)	77.9	(95)
3rd-instar larva	15	8	9	12	(31)	96.9	(32)
	20	4	5	7	(32)	97.0	(33)
	25	3	4	6	(48)	82.8	(58)
	30	3	5	7	(52)	70.3	(74)
4th-instar larva	15	12	14	18	(28)	90.3	(31)
	20	7	8	9	(31)	96.9	(32)
	25	4	6	9	(33)	76.7	(43)
	30	5	7	10	(27)	51.9	(52)
Prepupa	15	2	4	5	(21)	75.0	(28)
	20	2	3	4	(30)	88.2	(34)
	25	1	2	3	(31)	93.9	(33)
	30	1	1	2	(17)	63.0	(27)
Pupa	15	9	14	15	(15)	71.4	(21)
	20	7	9	10	(30)	100.0	(30)
	25	4	5	6	(28)	90.3	(31)
	30	4	4.5	5	(10)	58.8	(17)

[a]No. in parentheses are the numbers of developmental times obtained.
[b]No. in parentheses are the starting numbers for survival determination.

Table 4. Developmental periods and survival of 1st instar larvae through pupae of the Mexican bean beetle at constant 25°C on field-grown soybean foliage

Stage	Developmental period (days) 10th percentile	50th percentile	90th percentile		Survival (%)	
1st-instar larva	5	6	6	(37)[a]	93.0	(43)[b]
2nd-instar larva	3	4	6	(34)	100.0	(34)
3rd-instar larva	3	5	7	(44)	97.8	(45)
4th-instar larva	6	7	9	(13)	90.5	(42)
Prepupa	—[c]	2	—[c]	(9)	86.8	(38)
Pupa	—[c]	5	—[c]	(4)	88.9	(27)

[a]No. in parentheses are the numbers of developmental times obtained.
[b]No. in parentheses are the starting numbers for survival determination.
[c]Too few developmental times were obtained to permit computation of this percentile.

instar. Development accumulations were then restarted using the median developmental rates for 1st instar larvae. In this way, the number of days required for 50% of the simulated cohort to reach the 1st, 2nd, 3rd, and 4th instar was calculated.

The observed number of days was then paired with the simulated number of days required to reach each of these four stages within each cohort and the observed values were regressed on the simulated ones for the four cohorts combined. The null hypothesis for valid simulation of the observed phenology was a slope equal to one and y-intercept equal to zero (Mellors and Helgesen 1983). The slope and intercept were tested at the 1% level of significance.

A further simulation was conducted to test the suitability of an overall assumption of linearity for all the

developmental rate - temperature relationships. This analysis was done because the developmental rate equations had been fitted according to forms suggested by the data and were not all fit as straight line relationships. From the median developmental rates for each stage at two well-spaced intermediate temperatures (15 and 25°C), the median developmental rates for the other three temperatures (11, 20, and 30°C) were calculated by assuming that the developmental rates had a straight line relationship with temperature. The two temperatures, 15 and 25°C, are commonly used in insect developmental studies. The development of each cohort was then simulated using (1) the two observed and three calculated median developmental rates for each stage and (2) the known sequence of incubation temperatures. The results for the four cohorts combined were subjected to the same regression test for simulation validity.

Results and Discussion

Development and Survival on Different Host Plants

The constant temperature developmental periods and survival of eggs from MBB adults fed only snap bean or soybean foliage are presented in Table 1. At 25°C, egg development times differed little between the two adult food sources suggesting that the egg development times for snap beans at other temperatures might be representative of eggs deposited by adults fed only soybean foliage. However, egg survival differed between snap bean and soybean fed adults. Egg survival for snap bean fed adults decreased greatly with temperature above and below 25°C. No egg survival occurred at 11°C suggesting that this temperature might be below the developmental threshold. Developmental periods and survival of 1st through 4th instar larvae, prepupae, and pupae on greenhouse snap bean and greenhouse soybean foliage are presented in Tables 2 and 3. Statistical comparisons of developmental periods over temperatures for 1st through 4th instar larvae indicated that neither 10th, 50th, nor 90th percentile periods differed between host plants ($t \geq -0.1002$ and ≤ 1.820 for both slope and intercept; 14 df; $r^2 = 0.888$ to 0.944 for each percentile), but survival was significantly different ($t \geq 4.600$ or ≤ -4.623; 14 df). At 25 and 30°C, survival on soybean was lower than that on snap bean but the opposite trend occurred at 15 and 20°C.

In Barney and Rock's (1975) comparison of 15 soybean varieties with lima beans, survival was lower on soybeans; however, they observed greater development times on greenhouse-grown soybean vs lima bean foliage. Bernhardt and Shepard (1978) found longer development times on field-grown soybean versus snap bean foliage. The lack of significant development time differences probably occurred because we compared developmental times for individual stages, whereas, other authors compared total development time from egg hatch to pupation. For example, Barney and Rock found an average difference of about four days between rearings on foliage of lima bean and commercial soybean varieties at 27°C or only about a one day difference per instar in development time. Differences of this magnitude are evident for some stages in Tables 2 and 3 as well.

For the prepupal and pupal stages produced on greenhouse snap bean and soybean foliage, statistical comparisons of developmental periods over temperatures indicated that neither the 50th nor 90th percentile periods nor survival differed between host plants ($t \geq -1.714$ and ≤ 1.446; 5 df; $r^2 = 0.657$ to 0.956 for each parameter), but that the 10th percentile period was significantly different ($t = 4.086$; 6 df). At 15°C, the 10th percentile period was shorter on soybeans than on snap beans, not longer as might have been expected. Although the prepupal and pupal stages do not feed, there was no evidence of increased development time or decreased survival on soybeans compared to snap beans. The percentage female for adults from pupae produced on greenhouse snap bean and soybean foliage averaged 49.7 and 48.8 for total rearings of 171 and 82 adults.

The developmental periods and survival of 1st through 4th instar larvae, prepupae, and pupae on field-grown soybean foliage at 25°C are presented in Table 4. For the feeding stages (1st through 4th instar), statistical comparisons between rearings on greenhouse and field soybean foliage indicated no difference in developmental period ($t \geq -1.120$ and ≤ 3.144; 10 df; $r^2 = 0.847$) or survival ($t \geq -1.642$ and $t \leq 2.637$; 2 df; $r^2 = 0.907$). For the nonfeeding stages, the median developmental periods and percentage survival were nearly the same for these two sources of soybean foliage as well (Tables 3 and 4). Therefore, the results of the rearings on greenhouse soybean foliage at other temperatures may be representative of development and survival on field-grown soybean foliage. Comparisons of total larval development times at 26–27°C on commercial varieties of greenhouse-grown (Barney and Rock 1975) vs. field-grown (McAvoy and Smith 1979) soybean foliage also indicate at best only small differences between the reported values of 16.27 to 16.78 and 17.1 days, respectively.

The fitted developmental rate - temperature equations and observed median developmental rate data points are plotted together in Figs. 1 and 2, respectively, for rearings on greenhouse snap bean and soybean foliage. For many of the stages, the data suggested nonlinear developmental rate - temperature relationships. Between host plants, the functional forms for a stage often differed because small nonsignificant differences in developmental periods corresponded to visible differences in developmental rates.

Validity of Constant Temperature Developmental Rates

Statistical comparisons between the observed development of the combined four cohorts and their simulated development based on constant temperature developmental rates indicated no difference ($t \geq -0.7719$ and ≤ 2.259; 14 df; $r^2 = 0.965$). However, when straight line developmental rate - temperature relationships were assumed for all stages, observed and simulated phenologies were different ($t = 3.678$; 14 df). Although the developmental rate - temperature relationships for the

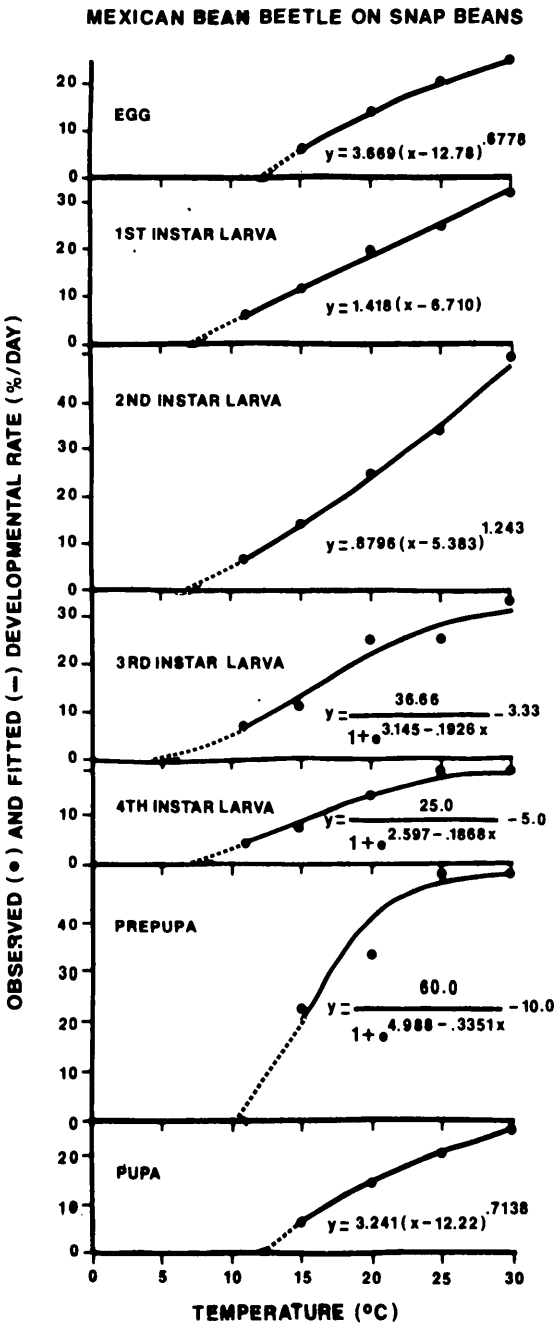

FIG. 1. Observed median developmental rate data points at constant temperatures and fitted equations for Mexican bean beetle immatures on greenhouse snap bean foliage.

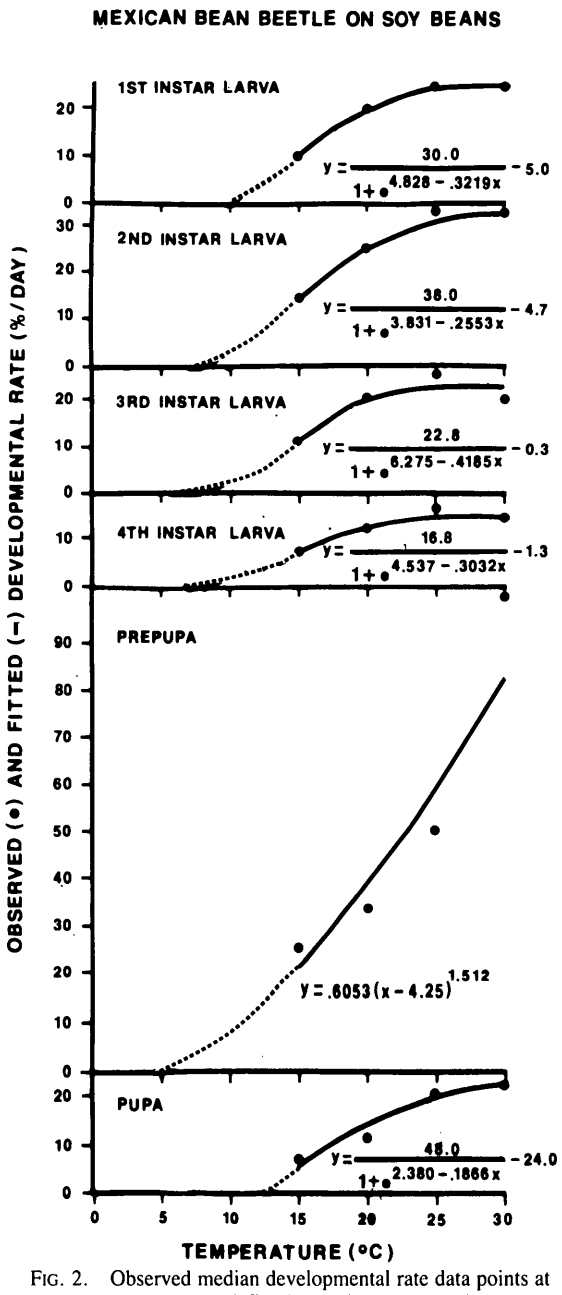

FIG. 2. Observed median developmental rate data points at constant temperatures and fitted equations for Mexican bean beetle immatures on greenhouse soybean foliage.

egg through 3rd instar show only small deviations from linearity, the cumulative effect of these differences was significant. Therefore, degree day and other linear development models may not be as accurate as nonlinear approaches in simulating the development of MBB immatures under these temperature conditions. However, linear approximations to MBB developmental rate relationships have been satisfactory for forecasting MBB phenology under other temperature conditions (Bernhardt and Shepard 1978, Waddill et al. 1976).

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