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**Laboratory Studies on the
Development, Longevity, and Fecundity
of Six Lepidopterous Pests
of Cotton in Arizona**

Technical Bulletin No. 1454

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**Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE
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Laboratory Studies on the Development, Longevity, and Fecundity of Six Lepidopterous Pests of Cotton in Arizona

By R. E. Fye and W. C. McAda

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Contents

	Page
Summary.....	1
Introduction.....	1
Methods.....	2
Bollworm.....	5
Tobacco budworm.....	20
Beet armyworm.....	30
Cabbage looper.....	39
Saltmarsh caterpillar.....	48
Pink bollworm.....	57
Discussion.....	70
Literature cited.....	72

Laboratory Studies on the Development, Longevity, and Fecundity of Six Lepidopterous Pests of Cotton in Arizona

By R. E. FYE, *research entomologist*, and W. C. MCADA, *agricultural research technician, Entomology Research Division, Agricultural Research Service*

SUMMARY

Development of the following insects may be predicted from the proportion of development (reciprocal units of development) in a 2-hour period at mean substrate temperatures between 20° and 35° C.: The bollworm (*Heliothis zea* (Boddie)), the tobacco budworm (*H. virescens* (F.)), the beet armyworm (*Spodoptera exigua* (Hübner)), the cabbage looper (*Trichoplusia ni* (Hübner)), and the saltmarsh caterpillar (*Estigmene acrea* (Drury)). The reciprocal units of development may be estimated using simple regression equations with the logarithm of temperature as the independent variable. When mean temperatures above 38° were included in the temperature regimes, the development was slowed. Reciprocal units of development for the pink bollworm (*Pectinophora gossypiella* (Saunders)) were better predicted using an asymptotic regression equation with the logarithm of temperature as the independent variable. High temperatures reduced longevity and lowered fecundity of all species.

INTRODUCTION

During the study and development of biological control organisms, a thorough acquaintance with the development and behavior of the target species is essential. Determining the relationship of development, longevity, and fecundity to temperature input is necessary (1) to develop the best rearing system for the parasites, predators, or pathogens, (2) to develop 'predictive capability' for the age stratification of the target population, and (3) to determine the effect of temperature extremes on both the host and the control organisms.

This study was conducted to establish the relationship of development, longevity, and fecundity to temperature flux for the bollworm (*Heliothis zea* (Boddie)), the tobacco budworm (*H. virescens* (F.)), the beet armyworm (*Spodoptera exigua* (Hübner)), the cabbage looper (*Trichoplusia ni* (Hübner)), the saltmarsh caterpillar (*Estigmene acrea* (Drury)), and the pink bollworm (*Pectinophora gossypiella* (Saunders)).

METHODS

The insects for study were from the cultures of the Cotton Insects Biological Control Laboratory, Tucson, Ariz., and were of Arizona origin. All species were in culture for 1 to 4 years without introduction of wild stock.

The rearing methods used in the study were similar to those described by Patana (18).¹ The ovipositing females were held for several hours at the experimental temperatures before the eggs were collected. In the oviposition cages were strips of paper toweling. They were readily removed, cut into small pieces bearing the desired number of eggs, and placed in plastic petri plates. The eggs were collected at 2-hour intervals for at least a 14-hour period. They were then held at the test temperatures and checked frequently.

When hatching commenced, the eggs were checked at 2-hour intervals to determine when the first-instar larvae emerged. As they emerged they were counted and transferred two or three per cup to individual coffee creamers containing lima bean medium (Patana 18 and Shorey 21). The larvae were checked at 24-hour intervals and the changes of instar were noted. As the instars changed, the larvae were dusted with various colors of fluorescent pigment so the subsequent instar change could be readily determined. As the larvae developed, the dates when the instar changes occurred were noted until the larvae pupated. The pupae were held until the adults emerged and the time involved was recorded. Thus the entire development cycle was observed.

The emerging moths were paired and the fecundity of individual females was determined by placing the pairs in 1-quart cages. The moths were fed a 5-percent honey solution. Strips of paper toweling were placed in the cages and changed daily, along with the plastic bag liner of the oviposition cage. Thereby the oviposition of the individual females was recorded daily. The time of death was noted and from these records the longevity was calculated.

The experimental temperatures utilized in the study were 20°, 25°, 30°, and 33° C. One set of cabinets was maintained at constant temperatures $\pm 1^\circ$. In a second set of cabinets, temperatures with the approximate mean of the constant temperatures over a 24-hour period were programmed into cam-controlled environmental chambers in sequences similar to those normally occurring within the cotton canopy in Arizona cottonfields. A representative sequence of the programmed temperatures is presented in table 1. The relative humidity was maintained above the 50-percent level.

¹ Italic numbers in parentheses refer to Literature Cited, p. 72.

TABLE 1.—Temperatures for study of bollworm development

Period	20° C.			25° C.			30° C.			33° C.		
	Mean tem- perature	RUD ¹	Degree- 2 hour >13.3° C. ²	Mean tem- perature	RUD	Degree- 2 hour >13.3° C.	Mean tem- perature	RUD	Degree- 2 hour >13.3° C.	Mean tem- perature	RUD	Degree- 2 hour >13.3° C.
<i>Constant</i>	° C.	Number	Number	° C.	Number	Number	° C.	Number	Number	° C.	Number	Number
Each 2 hours-----	20.0	0.0019	6.7	25.0	0.0029	11.7	30.0	0.0038	16.7	33.0	0.0042	19.7
Daily-----	20.0	.0228	80.4	25.0	.0348	140.4	30.0	.0456	200.4	33.0	.0504	236.4
<i>Programed</i>												
0001-0200-----	17.8	.0014	4.5	22.8	.0025	9.5	27.2	.0033	13.9	30.9	.0039	17.6
0201-0400-----	14.4	.0004	1.1	21.7	.0023	8.4	27.2	.0033	13.9	27.2	.0033	13.9
0401-0600-----	10.6	.0000	0	18.9	.0016	5.6	24.4	.0028	11.1	23.3	.0026	10.0
0601-0800-----	13.6	.0001	.3	18.9	.0016	5.6	25.6	.0030	12.3	28.3	.0035	15.0
0801-1000-----	20.3	.0020	7.0	25.0	.0029	11.7	29.4	.0037	16.1	33.6	.0043	20.3
1001-1200-----	23.6	.0027	10.3	30.3	.0038	17.0	32.8	.0042	19.5	35.9	.0046	22.6
1201-1400-----	25.9	.0031	12.6	33.1	.0042	19.8	35.6	.0045	22.3	37.8	.0048	24.5
1401-1600-----	27.2	.0033	13.9	34.7	.0044	21.4	36.7	.0047	23.4	39.4	.0050	26.1
1601-1800-----	28.0	.0034	14.7	34.4	.0044	21.1	37.0	.0047	23.7	40.6	.0052	27.3
1801-2000-----	26.1	.0031	12.8	32.0	.0041	18.7	37.2	.0047	23.9	38.9	.0050	25.6
2001-2200-----	21.7	.0023	8.4	27.2	.0033	13.9	32.8	.0042	19.5	34.7	.0044	21.4
2201-2400-----	19.2	.0017	5.9	23.6	.0027	10.3	27.2	.0033	13.9	32.2	.0041	18.9
Total-----		.0235	91.5		.0378	163.0		.0464	213.5		.0507	243.2

¹ RUD=reciprocal units of development for 2-hour periods.

² Threshold temperature from the regression equation: $\hat{y} = -0.0119 + 0.0106 (\log t)$. (\hat{y} = estimate of RUD; t = mean substrate temperature from the regression equation: $\hat{y} =$ substrate temperature (°C.) for each 2-hour period.)

The data were reduced to reciprocal units of development (RUDs) for 2-hour periods by dividing one (the total development period of the insects in these stages) by the number of 2-hour periods determined at each constant temperature. These RUDs represented the proportion of the development in a 2-hour period at the constant temperatures. The RUDs for each constant temperature were graphed (fig. 1) against the logarithm of the development temperature, and simple linear regression analysis was performed. The resulting regression equation estimates the RUDs for all temperatures between 20° and 33° C. for each 2-hour period.

For the programed regimes the RUDs for each 2-hour period were

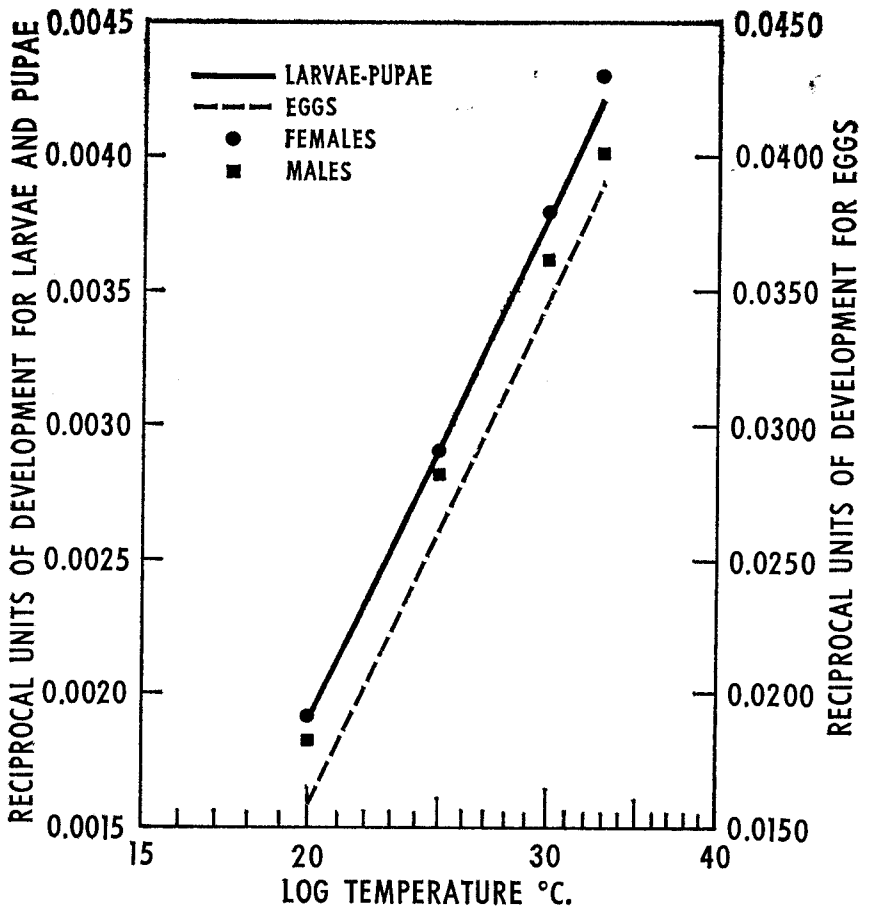


FIGURE 1.—Regression lines for reciprocal units of development of eggs and larvae-pupae of the bollworm on the logarithm of temperature (° C.).

calculated from the regression equations. The accumulated units represent the percent of development of half the population at any given time in the development period.

The threshold temperature for the linear part of the curve was estimated from the regression equation. From these thresholds the degree ($^{\circ}$ C.)-2-hour periods were determined by the degree-day method, i.e., the mean temperature for each period was calculated and the threshold temperature subtracted. The remainders were summed and compared for each desired stage of development. The remainders or effective temperature input for each 2-hour period will hereafter be designated as "degree-2 hour $>$ threshold temperature" or "degree-2-hour period."

BOLLWORM

The temperature regimes and the associated reciprocal units of development (RUDs) for the bollworm study are given in table 1 and the development data are summarized in table 2.

A comparison of the summation of RUDs with the heat input of degree-2 hour $>13.3^{\circ}$ C. indicated that the former technique provided a more accurate estimate of development. Actually degree-2-hour period may be utilized as X axis for a regression analysis with the RUD on the Y axis. A straight line with a high coefficient of determination results is as accurate as the RUDs. Such a regression takes into account the varying velocity of the physiological reactions at the changing temperatures but places the researcher in the same position as utilizing the RUD technique. However, the RUD furnishes a useful direct estimate of percent of development.

The summation of the RUDs for the programed regimes utilizing representative canopy temperatures shows that the RUD is useful for analyzing the temperature input of changing temperatures. Comparison of the RUD summations and the summation of the degree-2-hour periods again indicates that the RUD technique is superior to the degree-2-hour period input in estimating the development of the bollworm.

The breakdown of the development period into instars is presented in table 3. The bollworm commonly has five instars although many times the sixth and occasionally a seventh instar are necessary.

At all constant and programed temperatures, the males required slightly longer to develop than the females. The slightly lower calculated thresholds and the extended development period of the male indicate that the physiology of the female may proceed faster than that of the male.

TABLE 2.—*Egg and larval-pupal development of bollworm at various constant and programmed temperatures*

Temperature (° C.)	Constant temperatures					Programmed temperatures				
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >13.3° C.²	Insects	Σ RUD	Σ degree-2 hour >13.3° C.²	
				Units	Summation 1					
EGG STAGE										
20	161	Days	Number	Number	Number	Number	Number	Number	Number	Number
25	97	---	65.2	0.0155	1.010	372	168	1.033	362	
30	111	---	38.4	.0257	.987	411	191	1.040	508	
33	132	---	29.1	.0341	.992	457	230	.976	480	
		---	26.2	.0385	1.009	490	142	1.178	589	
MALE LARVAL-PUPAL STAGE										
20	63	46.7	560	0.0018	0.991	3,755	65	0.973	3,788	
25	36	27.8	334	.0028	.935	3,903	57	1.214	5,232	
30	63	23.1	277	.0036	.986	4,625	56	1.053	4,846	
33	63	20.4	245	.0040	.975	4,826	53	1.176	5,642	

FEMALE LARVAL-PUPAL STAGE

20	70	45.2	543	0.0019	1.021	3,634	70	0.942	3,669
25	19	26.8	322	.0029	.943	3,762	54	1.138	4,906
30	52	22.1	265	.0038	1.007	4,428	60	1.007	4,633
33	41	19.7	236	.0043	1.003	4,657	51	1.133	5,448

¹ Based on estimates from regression equations (fig. 1):

Eggs: $\hat{y} = -0.1223 + 0.1059 (\log t)$

Males: $\hat{y} = -0.0115 + 0.0102 (\log t)$

Females: $\hat{y} = -0.0123 + 0.0109 (\log t)$

where

\hat{y} = estimate of RUD

t = mean substrate temperature (° C.) for each 2-hour period

² Calculated thresholds (° C.):

Eggs----- 14.3

Males----- 13.2

Females----- 13.5

TABLE 3.—Development periods of bollworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar		5th instar	
	Larvae Number	Period Days	Larvae Number	Period Days	Larvae Number	Period Days	Larvae Number	Period Days	Larvae Number	Period Days
<i>Constant</i>	20: ♂	65 4.0±0.4	65 2.7±0.5	65 3.1±0.6	65 3.8±0.8	65 9.0±2.7	65 3.8±0.8	65 3.9±.8	65 9.5±3.0	65 9.0±2.7
	20: ♀	72 4.1±.4	72 2.7±.5	72 3.1±.5	72 3.1±.5	72 3.9±.8	72 9.5±3.0	72 3.9±.8	72 9.5±3.0	72 9.5±3.0
	25: ♂	39 3.0±0	39 2.1±.3	39 2.1±.3	39 2.1±.3	39 2.0±.4	39 3.3±1.4	39 2.0±.4	39 3.3±1.4	39 3.3±1.4
	25: ♀	20 3.0±0	20 2.0±0	20 2.0±0	20 2.0±0	20 1.9±.5	20 3.1±1.1	20 1.9±.5	20 3.1±1.1	20 3.1±1.1
	30: ♂	68 2.1±.3	68 1.9±.3	68 1.9±.3	68 1.2±.4	68 2.1±.8	68 5.3±1.1	68 2.1±.8	68 2.1±.8	68 5.3±1.1
	30: ♀	56 2.2±.4	56 1.8±.4	56 1.8±.4	56 1.3±.4	56 1.9±.4	56 5.3±.9	56 1.9±.4	56 1.9±.4	56 5.3±.9
<i>Programed</i>	20: ♂	72 2.0±.1	72 1.1±.3	72 1.5±.5	72 1.5±.5	72 4.6±1.6	72 1.5±.5	72 1.5±.5	72 4.6±1.6	72 4.6±1.6
	20: ♀	47 2.0±0	47 1.1±.3	47 1.7±.5	47 1.7±.5	47 4.8±1.3	47 1.7±.5	47 1.7±.5	47 4.8±1.3	47 4.8±1.3
	25: ♂	72 3.7±.5	72 2.7±.5	72 2.7±.5	72 3.1±.4	72 3.9±1.0	72 7.8±2.6	72 3.1±.4	72 3.9±1.0	72 7.8±2.6
	25: ♀	72 3.7±.5	72 2.7±.5	72 2.7±.5	72 3.1±.4	72 3.9±.9	72 7.7±2.3	72 3.1±.4	72 3.9±.9	72 7.7±2.3
	30: ♂	70 3.2±.6	70 2.1±.3	70 2.1±.3	70 2.3±.6	70 2.6±.6	70 7.1±2.4	70 2.3±.6	70 2.6±.6	70 7.1±2.4
	30: ♀	62 3.1±.3	62 2.1±.4	62 2.1±.4	62 2.3±.5	62 2.6±.5	62 6.8±1.9	62 2.3±.5	62 2.6±.5	62 6.8±1.9

	6th instar			7th instar			Pupal stage				Total	
	Larvae	Period		Larvae	Period		Pupae	Period	Adults	Period	Number	Days
	Number	Days		Number	Days		Number	Days	Number	Days	Number	Days
30: ♂	62	2.0±0	1.7±.4	62	1.4±.5	62	1.9±.4	62	1.9±.4	62	5.2±1.3	
♀	64	2.0±0	1.9±.3	64	1.2±.4	64	2.0±.3	64	2.0±.3	64	5.4±1.0	
33: ♂	59	2.2±.4	1.6±.5	59	1.5±.5	59	1.9±.6	59	1.9±.6	59	4.8±1.6	
♀	59	2.1±.3	1.8±.4	59	1.4±.6	59	1.8±.6	59	1.8±.6	59	4.6±1.7	
<i>Constant</i>												
20: ♂	15	11.3±1.6									63	21.5±1.2
♀	15	10.8±1.2									70	19.8±1.2
25: ♂	33	3.5±1.3									35	11.9±.7
♀	19	3.9±1.9	1		3.0						19	11.2±.7
30: ♂	1	5.0±0									63	10.7±.6
♀											52	9.6±.6
33: ♂	15	4.5±1.0									63	9.0±.8
♀	5	5.0±.7									41	8.4±2.0

TABLE 3.—*Development periods of bollworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued*

Temperature (° C.) and sex	6th instar		7th instar		Pupal stage		Total	
	Laivae	Period	Larvae	Days	Pupae	Period	Adults	Period
20: <i>Programed</i>	Number	Days	Number	Days	Number	Days	Number	Days
	22	10.1±1.1	---	---	65	17.5±0.8	65	41.4±2.5
	21	9.2±2.2	---	---	70	16.3±.8	70	40.1±2.4
25:	17	7.6±1.2	1	9.0	57	13.7±1.2	57	32.1±2.5
	9	7.3±2.1	1	9.0	54	12.4±1.1	54	30.1±2.2
30:	6	4.7±1.0	---	---	56	10.1±1.4	56	22.7±1.2
	2	7.5±5.0	---	---	60	9.2±.5	60	21.7±1.3
33:	14	4.1±1.9	1	6.0	53	10.1±.7	53	23.2±1.7
	16	6.1±1.7	---	---	51	9.2±.8	51	22.4±1.6

The summation of the length of each instar exceeds the overall total larval and pupal development in the final column of table 3. However, this is explained by the large standard deviations associated with the mean length of the various larval instars and pupal stages. Generally the summation of time with the smallest standard deviation is associated with the periods with the smallest standard deviations in the various instars and pupal stage. The variance in data in table 3 represents the genetic, physiological, and biological variation that may occur in an insect population as well as minor differences in technique.

The relationship of RUDs to the age stratification of the larval and pupal population is presented for a constant and a programmed mean temperature of approximately 20° C. in table 4. Comparisons of the results show that the RUDs are reasonably accurate in determining the age stratification of a population. The development in the programmed regime was considerably faster; however, the RUDs accumulated more rapidly (table 1). Comparisons of the summations of the RUDs in the constant and programmed regimes indicate that a similar percentage of the population was in each instar at any given summation. Overall it is evident that the breakdown of the development into 2-hour periods may be a convenient way to analyze the age stratification of a population.

The results at both a constant and a programmed 25° C. indicated the input of RUDs was fairly well correlated with the age stratification. Comparison of the results with those at 20° indicated a marked similarity of the age stratifications at any given summation of RUDs in the two regimes. In the later larval instars some differences resulted because a few individuals attained the seventh instar. However, the final emergence of the adults when associated with the summation of RUDs was similar.

The results at constant and programmed temperatures of 30° C. showed an abbreviated development period as compared with the development periods at 20° and 25°, and a marked similarity of the age stratification with the summation of RUDs was evident. None of the larvae attained the seventh instar and only a few achieved the sixth instar.

Development periods at constant and programmed temperatures of 33° C. were similar to those at 30° and time spent in each instar was relatively brief. The age stratification was also well correlated with the input of RUDs. However, at 33° more larvae had sixth instars and a single individual attained the seventh instar in the programmed temperature regime. Thus there is reasonable indication that the number of instars is associated with the conditions of development. Fewer

TABLE 4.—*Living bollworm larvae, pupae, and adults on specific day when reared at a constant and programed 20° C.*

Day after hatch	RUD ¹	Larvae in designated instar						Pupae	Emerg- ed adults
		1	2	3	4	5	6		
CONSTANT TEMPERATURE									
		<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
1	0. 0228	100. 0							
2		100. 0							
3	. 0684	100. 0							
4		93. 4	6. 6						
5	. 1140	8. 8	91. 2						
6			100. 0						
7	. 1596		59. 9	40. 1					
8			8. 8	91. 2					
9	. 2052		. 7	98. 5	0. 7				
10				57. 7	42. 3				
11	. 2508			19. 0	81. 0				
12				2. 9	94. 2	2. 9			
13	. 2964				87. 6	12. 4			
14					46. 0	54. 0			
15	. 3420				22. 6	75. 2	2. 2		
16					8. 8	86. 9	4. 4		
17	. 3876				2. 2	86. 9	10. 9		
18						86. 9	13. 1		
19	. 4332					83. 2	16. 8		
20						81. 8	18. 2		
21	. 4788					81. 0	19. 0		
22						78. 8	19. 7	1. 5	
23	. 5244					70. 8	21. 2	8. 0	
24						55. 9	20. 6	23. 5	
25	. 5700					30. 1	20. 6	49. 3	
26						22. 2	18. 5	59. 3	
27	. 6156					9. 6	14. 8	75. 6	
28						5. 9	11. 2	82. 9	
29	. 6612					3. 0	9. 0	88. 1	
30						1. 5	6. 7	91. 8	
31	. 7068					. 7	5. 2	94. 0	
32							4. 5	95. 5	
33	. 7524						3. 0	97. 0	
34							1. 5	98. 5	
35	. 7980						1. 5	98. 5	
36							. 8	99. 2	
37	. 8436							100. 0	
38								100. 0	
39	. 8892							100. 0	
40								100. 0	

TABLE 4.—*Living bollworm larvae, pupae, and adults on specific day when reared at a constant and programed 20° C.*—Continued

Day after hatch	RUD ¹	Larvae in designated instar						Pupae	Emerged adults
		1	2	3	4	5	6		
CONSTANT TEMPERATURE—continued									
		Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
41	. 9348							100. 0	
42								94. 7	5. 3
43	. 9804							88. 8	11. 3
44								75. 1	24. 8
45	1. 0260							54. 9	45. 1
46								46. 7	53. 3
47	1. 0716							31. 6	68. 4
48								25. 6	74. 4
49	1. 1172							21. 1	78. 9
50								14. 3	85. 7
51	1. 1628							12. 8	87. 2
52								7. 5	92. 5
53	1. 2084							4. 6	95. 4
54								3. 8	96. 2
55	1. 2540							3. 0	97. 0
56								2. 3	97. 7
57	1. 2996							2. 3	97. 7
58								. 8	99. 2
59	1. 3452							. 8	99. 2
60								. 8	99. 2
61	1. 3908								100. 0
PROGRAMED TEMPERATURE									
1	0. 0235	100. 0							
2		100. 0							
3	. 0705	100. 0							
4		65. 3	34. 7						
5	. 1175	2. 8	97. 2						
6			100. 0						
7	. 1645		37. 5	62. 5					
8			2. 1	97. 9					
9	. 2115			97. 2	2. 8				
10				40. 3	59. 7				
11	. 2585			8. 3	91. 7				
12				. 7	91. 0	8. 3			
13	. 3055				82. 6	17. 4			

See footnote at end of table.

TABLE 4.—*Living bollworm larvae, pupae, and adults on specific day when reared at a constant and programed 20° C.—Continued*

Day after hatch	RUD ¹	Larvae in designated instar						Pupae	Emerg- ed adults
		1	2	3	4	5	6		
PROGRAMED TEMPERATURE—continued									
		<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
14					40.3	59.7			
15	.3525				16.0	83.3	0.7		
16					2.8	90.3	6.9		
17	.3995				2.1	81.9	16.0		
18						76.4	23.6		
19	.4465					72.2	27.8		
20						72.2	27.8		
21	.4935					70.1	29.2	0.7	
22						59.7	29.8	10.5	
23	.5405					39.2	29.4	31.5	
24						21.1	26.1	52.8	
25	.5875					8.5	23.9	67.6	
26						4.3	19.1	76.6	
27	.6345					2.2	13.1	84.6	
28						1.5	9.5	89.0	
29	.6815					.7	4.4	94.9	
30							2.2	97.8	
31	.7285						.7	99.3	
32								100.0	
33	.7755							100.0	
34								100.0	
35	.8225							100.0	
36								100.0	
37	.8695							99.3	0.7
38								96.2	3.8
39	.9165							83.7	16.3
40								62.2	37.8
41	.9635							43.7	56.3
42								28.9	71.1
43	1.0105							18.5	81.5
44								14.0	86.0
45	1.0575							11.1	88.9
46								5.2	94.8
47	1.1045							4.5	95.5
48								1.4	98.6
49	1.1515								100.0

¹ Accumulated reciprocal units of development

instars are necessary under ideal conditions, but at very low or very high temperatures the number of instars is increased. Based on the number of instars, the data indicate that a constant 30° was the ideal rearing temperature in this study.

In the programed regime of 30° and 33° C. the high temperatures of approximately 38° and 40°, respectively, apparently resulted in some adverse effects. However, the summation of the RUDs in table 1 for the programed regimes indicates that the deleterious effects were not extensive. In fact, removal of the RUDs for the single period in each day in excess of 40° returns the summation to approximately 1. Therefore the upper functional threshold of the bollworm is apparently in the 38°-40° range.

Mortality of up to 20 percent of larvae and evident in pupae in the programed regimes mainly reflected the mortality in the pupal stage and commonly occurred at the time of pupation. Apparently in the programed regimes the pupation started at such a time that an upper or a lower functional threshold was reached during the process and the pupation was suspended. When the regime returned to temperatures of normal physiological activity, the pupation process was not completed. As a result, many of the prepupae attained only partial pupation and none survived. These individuals were particularly prevalent at high temperatures.

The accumulated percentage of bollworms ovipositing is presented in table 5. At all temperatures there was a preoviposition period of at

TABLE 5.—*Accumulated bollworms ovipositing at 4 programed temperatures*¹

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
1.....	0	0	0	0
2.....	16.1	0	0	0
3.....	58.1	2.9	0	18.9
4.....	77.4	28.6	32.4	54.0
5.....	90.3	57.1	51.3	86.5
6.....	100.0	82.8	70.3	97.3
7.....		91.4	83.7	97.3
8.....		97.1	94.5	97.3
9.....		100.0	100.0	97.3
10.....				97.3
11.....				100.0

¹ Based on number of moths in table 6.

least 1 day and 2 to 3 days at the higher temperatures. The data suggest that the higher temperatures may affect preoviposition as an interference either with the physiological activity of the female moths or with the mating process. At the higher temperatures a few moths had preoviposition periods of 8 to 10 days, and these individuals in a population would greatly accelerate the overlapping of generations. The overlapping phenomena would be accentuated during periods of high temperatures when extended preoviposition accompanies accelerated development.

The longevity and fecundity of the bollworm in the programmed regimes are given in table 6. The males lived from an average of 11 days at 33° C. to 17 days at 20°. The females had a slightly longer lifespan with a mean of 15.4 days at 30° and 33° and 21.7 days at 20°. As in the development cycles, the variation among the individuals was great.

The fecundity of the females was also highly variable. The mean ranged from 449 eggs at 30° C. to 1,774 eggs at 20°. Thus the fecundity was greatly reduced at the higher temperatures. The variation between individuals was also greater at 30° and 33° with the standard deviation nearly equal to the mean number of eggs laid. Assuming that the number of eggs laid at 20° best approaches the potential of the females, it is evident that the higher temperatures reduced the fecundity by one-half or more.

Projecting this to field conditions we may then conclude that the field populations at high temperatures may result from a small part of the actual potential of the females of the population. The failure of the females to realize their potential at high temperatures, coupled with an increased sterility of the eggs laid (Fye and Poole 6), would partially account for the dearth of bollworms in irrigated areas of the Southwestern United States until cotton or other host crops have

TABLE 6.—*Longevity and fecundity of bollworm at 4 programmed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	31	17. 2±7. 2	31	21. 7±9. 4	1, 774±937
25.....	37	19. 5±7. 3	37	19. 7±6. 1	1, 047±654
30.....	32	11. 9±4. 6	37	15. 4±4. 6	449±378
33.....	35	10. 9±4. 4	37	15. 4±5. 9	766±715

modified the environment sufficiently to permit a better utilization of the fecundity potential and an improved egg hatch.

Generally fecundity was a function of longevity (tables 7 and 8). At all temperatures 96 to 100 percent of the eggs had been laid when 70-percent mortality of the females had occurred, and 99 to 100 percent of the eggs had been laid when mortality of the females was 90 percent. At all temperatures 90 percent of the eggs had been laid when 50-percent mortality had occurred. Thus most of the females laid their eggs fairly rapidly in the first 2 weeks after emergence.

Utilization of RUDs to compare temperature input to the longevity of the females after emergence indicates that the adult life of the females is approximately 70 percent of that of the larval-pupal development period. At 20° C. the females lived only approximately half of the equivalent of the larval and pupal development period.

The threshold temperature of 13.3° C. for the bollworms from the Tucson, Ariz., culture was slightly higher than that of 12.6° determined by Mangat and Apple (16) for their Wisconsin culture. The Wisconsin bollworms also required a longer development period at 18.3° C. but a shorter time at 23.9° than did the Arizona culture.

Lukefahr and Martin (14) found that the male bollworm from a Brownsville, Tex., strain lived on an average for 10.9, 9.7, and 8.6 days and the females for 12.4, 11.5, and 11.1 days when the larvae were fed the Berger (2) diet, corn, and cotton squares, respectively. The longevity of the Brownsville strain was similar to that of the Arizona strain reared at 30° and 33° C., but it was appreciably shorter at 25°. The fecundity of the Brownsville bollworms was 934, 429, and 465 eggs per female when the larvae were fed the Berger (2) diet, corn, and cotton squares, respectively. These fecundity means are well within the range of the standard deviations for the fecundity of the Arizona strain held at 25°, 30°, and 33° (table 6).

Likewise the fecundity of bollworms from College Station, Tex., fed the wheat germ diet (Adkisson et al. 1) was 702, 649, 628, and 668 per female in four tests conducted by Chauthani and Adkisson (5) at 26.8° C. Thus the fecundity of the Brownsville, College Station, and Tucson strains appears to be similar at these study temperatures. However, the potential fecundity was apparently better realized at 20°.

Lukefahr and Martin (15), Guerra and Ouye (8), Shaver and Lukefahr (19), and Guerra et al. (9) fed larvae the Berger (2) diet and used a temperature range of 26.7° to 29° C. They found the larval period of a Brownsville strain of the bollworm to be 12.7, 17, 13.9, and 19 days, respectively. Chauthani and Adkisson (5) using the wheat germ diet found the larval period of a College Station strain to be 15.9, 17.9, and 18.3 days in their tests. Thus the larval periods of the Texas strains and the Arizona strain appeared to be similar.

TABLE 7.—*Accumulated eggs laid by bollworm at 4 programed temperatures*

Days after emergence	Eggs laid at indicated mean temperature (° C.)			
	20	25	30	33
1.....	Percent 0	Percent 0	Percent 0	Percent 0
2.....	0	0	0	0
3.....	<. 1	2. 3	0	. 2
4.....	<. 1	4. 7	. 5	2. 2
5.....	. 2	8. 8	2. 6	14. 6
6.....	1. 3	15. 7	5. 3	31. 4
7.....	4. 7	24. 8	9. 9	46. 2
8.....	9. 1	33. 6	17. 6	56. 6
9.....	16. 1	42. 1	30. 3	66. 0
10.....	23. 0	50. 3	43. 4	73. 8
11.....	31. 0	59. 3	56. 4	78. 6
12.....	38. 7	67. 5	66. 8	82. 3
13.....	46. 8	74. 9	77. 8	85. 6
14.....	53. 9	80. 8	85. 7	89. 7
15.....	61. 2	85. 3	91. 4	92. 5
16.....	66. 4	88. 6	94. 4	94. 7
17.....	71. 5	91. 6	97. 4	97. 1
18.....	75. 3	94. 0	98. 3	98. 7
19.....	80. 2	95. 9	99. 3	99. 3
20.....	82. 8	96. 7	99. 8	99. 7
21.....	85. 7	97. 4	100. 0	99. 9
22.....	88. 3	97. 8	-----	100. 0
23.....	90. 7	98. 1	-----	-----
24.....	92. 6	98. 3	-----	-----
25.....	94. 1	98. 5	-----	-----
26.....	95. 2	98. 6	-----	-----
27.....	96. 1	98. 9	-----	-----
28.....	96. 8	99. 0	-----	-----
29.....	97. 4	99. 3	-----	-----
30.....	97. 8	99. 5	-----	-----
31.....	98. 1	99. 7	-----	-----
32.....	98. 6	99. 7	-----	-----
33.....	98. 9	99. 8	-----	-----
34.....	99. 1	99. 9	-----	-----
35.....	99. 4	99. 9	-----	-----
36.....	99. 6	100. 0	-----	-----
37.....	99. 9	-----	-----	-----
38.....	99. 9	-----	-----	-----
39.....	100. 0	-----	-----	-----

TABLE 8.—*Accumulated mortality of bollworm at 4 programed temperatures*

Days after emergence	Mortality at indicated mean temperature (° C.)							
	20		25		30		33	
	♂	♀	♂	♀	♂	♀	♂	♀
	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
1			0	0	3.2	0	0	0
2			0	0	6.4	0	0	0
3	2.8		0	0	6.4	0	2.9	0
4	5.7		0	0	6.4	0	8.6	0
5	5.7		0	0	6.4	2.7	20.0	2.6
6	8.6		2.8	0	6.4	2.7	25.7	5.3
7	8.6	3.0	2.8	0	16.1	5.4	25.7	13.2
8	14.3	6.0	2.8	2.8	19.3	8.1	25.7	18.4
9	17.1	18.1	2.8	2.8	29.0	8.1	31.4	18.4
10	17.1	21.2	5.6	2.8	32.2	10.8	45.7	23.7
11	22.9	21.2	8.3	5.6	41.9	16.2	51.4	36.8
12	31.4	24.2	19.4	5.6	48.3	27.0	62.8	36.8
13	37.1	30.3	30.6	11.1	54.8	29.7	65.7	42.1
14	37.1	33.3	33.3	19.4	64.5	43.2	74.2	50.0
15	40.0	33.3	36.1	22.2	83.8	62.1	88.5	52.6
16	42.9	33.3	38.9	30.6	83.8	64.8	91.4	55.2
17	42.9	33.3	41.7	36.1	87.0	72.9	97.1	57.9
18	51.4	33.3	44.4	41.7	93.5	72.9	97.1	68.4
19	54.3	39.4	50.0	55.6	96.7	81.0	97.1	76.3
20	62.9	39.4	55.6	63.9	100.0	83.7	100.0	76.3
21	68.6	45.5	58.3	66.7		89.1		78.9
22	77.1	45.5	69.4	75.0		89.1		89.4
23	80.0	45.5	72.2	80.6		94.5		94.7
24	85.7	51.5	77.8	86.1		100.0		97.3
25	85.7	57.6	80.6	91.7				97.3
26	88.6	66.7	86.1	91.7				97.3
27	94.3	69.7	88.9	91.7				100.0
28	94.3	75.7	88.9	91.7				
29	97.1	81.8	88.9	91.7				
30	97.1	81.8	91.7	94.4				
31	100.0	84.8	91.7	94.4				
32		84.8	91.7	94.4				
33		87.8	91.7	94.4				
34		87.8	91.7	94.4				
35		93.9	97.2	94.4				
36		93.9	100.0	97.2				
37		96.9		97.2				
38		96.9		100.0				
39		100.0						

Guerra and Ouye (8) and Guerra et al. (9) in rearing studies at 26.7° C. found pupal periods for the Brownsville strain of 12 and 14 days. Thus the pupal period for the Arizona strain (table 3) appeared to be slightly shorter than for the Texas strain.

The same workers also reported an adult lifespan for the Texas bollworms of 14 and 16 days, which was similar to the longevity of the females of the Arizona strain but was somewhat longer than the longevity of the males. Thus the Texas and Arizona strains appeared to be similar in regard to their development period except for a slightly protracted pupal period for the Texas strain.

TOBACCO BUDWORM

The observed egg and larval-pupal development periods of the tobacco budworm are presented in table 9. The RUDs gave a better estimate of the development time than did the degree-2 hour $>13.2^{\circ}$ C. The data for the constant temperatures were particularly consistent. However, in the programed regime both the egg and larval-pupal stages were shorter than would be expected using both analytical techniques. These data indicate that the physiological systems of the immature stages of the tobacco budworm are more efficient at the lower temperatures. Keister and Buck (13) suggested that at higher temperatures an autotoxication of some physiological systems occurs with an attending decrease in the velocity of the reaction. Therefore the more rapid development at 20° may be attributable to such a phenomenon.

The development times for several instars of the tobacco budworm in table 10 indicate broad variance for the various periods. However, the variance associated with the total development was not proportionately as great. At the lower temperatures one additional instar was commonly required by the larvae to complete development. The extra instar was more frequent in the male insects than in the female and the males required an additional 1 to 2 days to complete development. Because of the broad variance for the several stages the totals were slightly less than the sum of the instar and pupal periods.

In the 20° C. constant regime the development of the insects was closely associated with the calculated RUDs. The broad spread of the percentages reflected the genetic plasticity of the population in the constant and programed regimes. However, the calculated RUDs did not provide as accurate an estimate of the development in the programed as in the constant temperature regime. The occurrence or absence of autotoxication was previously suggested as a possible

TABLE 9.—Egg and larval-pupal development of tobacco budworm at various constant and programed temperatures

Temperature (° C.)	Constant temperatures					Programed temperatures			
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >13.2° C.†	Insects	Σ RUD	Σ degree-2 hour >13.2° C.†
				Units	Summation †				
EGG STAGE									
20	164	Days	Number	Number	Number	Number	Number	Number	Number
25	93	---	64.5	0.0159	1.024	374	118	0.662	264
30	72	---	37.3	.0263	.979	403	384	.994	441
33	93	---	28.0	.0347	.973	442	126	.999	470
		---	26.1	.0392	1.023	543	114	1.141	562
MALE LARVAL-PUPAL STAGE									
20	60	49.5	594	0.0017	1.010	3,920	71	0.928	3,852
25	40	29.4	353	.0027	.953	4,092	49	1.224	5,566
30	54	25.4	305	.0035	1.007	5,060	42	1.116	5,432
33	40	21.1	253	.0039	.987	4,963	19	1.121	5,696

See footnotes at end of table.

TABLE 9.—Egg and larval-pupal development of tobacco budworm at various constant and programed temperatures—Con.

Temperature (° C.)	Constant temperatures				Programed temperatures				
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >13.2° C. ²	Insects	Σ RUD	Σ degree-2 hour >13.2° C. ²
				Units	Summation ¹				
20-----	Number	Days	Number	Number	Number	Number	Number	Number	
25-----	51	46.6	559	1.062	3,914	49	0.858	3,565	
30-----	28	28.0	336	.941	4,032	35	1.162	5,287	
33-----	53	24.4	293	1.055	4,978	46	1.054	5,131	
	49	20.5	246	.984	4,920	53	1.092	5,548	

FEMALE LARVAL-PUPAL STAGE

¹ Based on estimates from regression equations:
 Eggs: $\hat{y} = -0.1236 + 0.1072 (\log t)$
 Males: $\hat{y} = -0.0113 + 0.0100 (\log t)$
 Females: $\hat{y} = -0.0110 + 0.0099 (\log t)$

² Calculated thresholds (° C.):
 Eggs----- 14.2
 Males----- 13.4
 Females----- 13.0

where \hat{y} = estimate of RUD
 t = mean substrate temperature (° C.) for each 2-hour period

explanation for this variable development. In addition, there may be some physiological momentum, which carried over from the higher temperatures in the regime into the subsequent periods in which cooler temperatures occur. If this was the case, the adverse effects of the high temperatures in the programed regimes at 25°, 30°, and 33° nullified this momentum.

The calculated RUDs effectively estimated the development in the 25°, 30°, and 33° C. constant regimes but overestimated it in the programed regimes. Since the programed regimes included temperatures that were probably above the upper functional threshold temperature of the insects, it was apparent that these high temperatures have a deleterious effect on the development of the insects. In estimating the development above 35°, consideration must be given to a development slowdown. Incompletely pupated individuals, particularly in the higher programed temperatures, indicated that the extreme temperatures may also have caused a cessation of pupation and that once slowed the insect did not regain sufficient physiological momentum to complete pupation.

The ovipositing females required a minimum 2-day preoviposition period (table 11), and most individuals oviposited by the fifth or sixth day. However, as in the case of development, a few individuals were delayed in ovipositing.

The longevity and fecundity data from the programed regimes are included in table 12. Assuming that the oviposition at 20° C. reflected the potential fecundity of the females, it was evident that the higher temperatures in the more extreme regimes drastically reduced the fecundity. In the hotter regimes this decrease amounted to approximately two-thirds of the total potential. The longevity was similarly reduced and the relationship between longevity and fecundity was evident. However, the cumulative data of the total eggs (table 13) laid by the tobacco budworm indicated that from 85 to 98 percent of the eggs were laid within 15 days after the emergence of the female. The higher percentages of eggs were oviposited sooner in the hotter regimes, but individuals with prolonged oviposition periods were more evident in the cooler regimes.

The mortality data in table 14 reflect a shorter lifespan for the males and extended longevity for certain individuals. A comparison with table 13 shows that most females died shortly after oviposition was completed.

Lukefahr and Martin (15), Guerra and Ouye (8), Guerra et al. (9), and Shaver and Lukefahr (19) rearing a Brownsville, Tex., strain of the tobacco budworm on the diet developed by Berger (2) at 26.7° C. found larval periods of 13, 17, 18, and 12.8 days, which were similar

TABLE 10.—Development periods of tobacco budworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar		
	Larvae Number	Period Days	Larvae Number	Period Days	Larvae Number	Period Days	Larvae Number	Period Days	
<i>Constant</i>	20: ♂	61	4.6±0.6	61	2.7±0.8	61	3.1±0.7	61	3.7±0.7
	♀	52	4.6±.5	52	2.6±.6	52	3.0±.4	52	3.8±.8
	♂	41	3.1±.3	41	2.0±.2	41	2.0±.2	41	2.0±.4
	♀	28	3.1±.3	28	2.0±0	28	1.8±.4	28	2.2±.4
33:	♂	55	2.9±.3	55	1.4±.5	55	1.7±.5	55	2.0±.4
	♀	55	2.9±.3	55	1.4±.5	55	1.7±.4	55	1.8±.4
	♂	45	2.0±.2	45	1.5±.5	45	1.4±.5	45	1.3±.5
	♀	55	2.0±.1	55	1.5±.5	55	1.4±.5	55	1.4±.7
<i>Programed</i>	20: ♂	72	3.9±.4	72	2.9±.3	72	3.0±.4	72	3.9±.7
	♀	50	3.7±.5	50	2.8±.4	50	2.8±.5	50	3.9±.5
	♂	56	3.5±.5	56	2.0±0	56	2.0±0	56	2.5±.7
	♀	42	3.4±.5	42	2.0±0	42	2.0±0	42	2.5±.6

TABLE 10.—*Development periods of tobacco budworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued*

Temperature (° C.) and sex	5th instar		6th instar		Pupal stage		Total	
	Larvae Number	Period Days	Larvae Number	Period Days	Pupae Number	Period Days	Adults Number	Period Days
20: ♂	72	8.8±1.6	5	9.6±1.5	71	18.6±.5	71	41.6±2.1
	50	8.6±1.0	1	10.0±0	49	16.4±1.1	49	38.5±1.7
25: ♂	56	7.5±1.1	1	8.0±0	49	16.2±.9	49	33.9±1.7
	42	7.2±1.1	2	8.0±1.4	35	14.8±.9	35	32.2±1.7
30: ♂	45	6.2±1.2	3	7.0±4.0	42	11.7±1.7	42	25.3±2.0
	50	6.1±1.1	---	---	46	10.5±.8	46	23.9±1.5
33: ♂	36	5.4±1.0	1	6.0±0	19	11.1±.4	19	23.3±.7
	59	5.4±.6	---	---	53	10.3±.6	53	22.7±1.0

Programed

to the 14 days at 25° in this study. Chauthani and Adkisson (5) rearing a College Station, Tex., strain on the wheat germ diet developed by Adkisson et al. (1) reported a larval development period of 15.7 days. These authors found that the longevity of the moths in their studies ranged from 13 to 14 days, which was slightly less than the longevity of the moths in this study.

Chauthani and Adkisson (5) found the fecundity of the tobacco budworm moths to be 512, 491, 398, and 323 eggs per female in four studies, and Lukefahr and Martin (14) observed a fecundity of 418 eggs per female. These data fall within the confidence limits of the mean fecundity determined for the Arizona strain. Thus the Texas and Arizona strains appeared to be similar except for longevity.

TABLE 11.—*Accumulated tobacco budworms ovipositing at 4 programed temperatures*

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
1.....	0	0	0	0
2.....	0	0	0	0
3.....	20.0	5.7	3.0	29.4
4.....	71.4	37.1	42.4	91.2
5.....	88.6	88.6	69.7	100.0
6.....	97.1	94.3	93.9	-----
7.....	97.1	94.3	93.9	-----
8.....	100.0	100.0	97.0	-----
9.....	-----	-----	97.0	-----
10.....	-----	-----	97.0	-----
11.....	-----	-----	100.0	-----

TABLE 12.—*Longevity and fecundity of tobacco budworm at 4 programed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	37	25.1 ± 8.8	37	25.1 ± 7.0	1,626 ± 460
25.....	35	19.6 ± 5.9	35	20.7 ± 6.2	963 ± 435
30.....	33	14.6 ± 4.9	33	16.9 ± 4.9	370 ± 287
33.....	34	11.6 ± 3.1	34	15.7 ± 5.7	495 ± 329

TABLE 13.—*Accumulated eggs laid by tobacco budworm at 4 programed temperatures*

Days after emergence	Eggs laid at indicated mean temperature (° C.)			
	20	25	30	33
	Percent	Percent	Percent	Percent
1	0	0	0	0
2	0	0	0	0
3	.3	.3	.1	.3
4	3.0	4.7	5.0	6.6
5	13.0	14.8	11.6	19.0
6	24.1	26.7	23.9	32.1
7	34.7	38.2	40.2	47.1
8	45.1	47.8	55.4	59.8
9	54.5	57.1	65.9	70.6
10	61.7	64.8	75.9	77.7
11	68.8	70.6	84.8	83.7
12	73.9	75.1	89.4	88.9
13	78.4	78.9	91.6	92.5
14	82.0	82.8	94.3	95.4
15	85.6	86.6	95.3	97.5
16	87.9	89.4	96.4	98.7
17	89.7	91.4	97.1	99.8
18	91.7	92.8	97.5	99.8
19	93.0	93.6	98.1	99.9
20	94.4	95.0	98.7	99.9
21	95.4	95.9	99.5	99.9
22	96.4	97.0	99.8	100.0
23	97.1	97.7	99.9	-----
24	97.7	98.5	100.0	-----
25	98.0	99.0	-----	-----
26	98.2	99.3	-----	-----
27	98.6	99.5	-----	-----
28	98.7	99.6	-----	-----
29	98.8	99.7	-----	-----
30	99.0	99.8	-----	-----
31	99.1	100.0	-----	-----
32	99.4	-----	-----	-----
33	99.5	-----	-----	-----
34	99.5	-----	-----	-----
35	99.6	-----	-----	-----
36	99.7	-----	-----	-----
37	99.8	-----	-----	-----
38	99.9	-----	-----	-----
39	99.9	-----	-----	-----
40	99.9	-----	-----	-----
41	100.0	-----	-----	-----

TABLE 14.—*Accumulated mortality of tobacco budworm at 4 programed temperatures*

Days after emergence	Mortality at indicated mean temperature (° C.)							
	20		25		30		33	
	♂	♀	♂	♀	♂	♀	♂	♀
	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	0	0	0	5.9	0	6.1	5.6
4	0	0	0	0	5.9	0	12.1	8.3
5	0	2.9	0	0	5.9	0	24.2	8.3
6	0	2.9	0	0	5.9	0	24.2	8.3
7	0	2.9	0	2.8	8.8	0	24.2	8.3
8	0	2.9	2.8	2.8	8.8	0	27.3	11.1
9	0	2.9	5.6	5.6	8.8	0	33.3	13.9
10	0	2.9	8.3	5.6	14.7	2.9	39.4	19.4
11	2.7	2.9	8.3	5.6	26.5	14.3	42.4	19.4
12	5.4	5.9	8.3	8.3	29.4	20.0	51.5	25.0
13	5.4	8.8	8.3	11.1	38.2	22.9	57.6	27.8
14	5.4	11.8	8.3	11.1	47.1	34.3	72.7	30.6
15	5.4	14.7	22.2	13.9	58.8	48.6	75.8	36.1
16	10.8	20.1	36.1	22.2	70.6	54.3	81.8	50.0
17	16.2	20.1	38.9	33.3	76.5	62.9	84.8	55.6
18	16.2	23.5	41.7	33.3	76.5	68.6	84.8	72.2
19	18.9	29.4	50.0	33.3	79.4	71.4	93.9	75.0
20	29.7	29.4	63.9	47.2	85.3	80.0	100.0	77.8
21	29.7	32.4	63.9	58.3	91.2	80.0	-----	83.3
22	35.1	32.4	72.2	66.7	97.1	85.7	-----	86.1
23	40.5	35.3	77.8	75.0	100.0	94.3	-----	88.9
24	45.9	35.3	80.6	77.8	-----	94.3	-----	94.4
25	51.4	47.1	88.9	80.6	-----	94.3	-----	97.2
26	56.8	64.7	88.9	80.6	-----	94.3	-----	100.0
27	62.2	64.7	88.9	83.3	-----	94.3	-----	-----
28	78.4	67.6	91.7	86.1	-----	94.3	-----	-----
29	78.4	76.5	97.2	94.4	-----	97.1	-----	-----
30	83.8	82.4	97.2	97.2	-----	100.0	-----	-----
31	83.8	82.4	97.2	97.2	-----	-----	-----	-----
32	83.8	85.3	97.2	97.2	-----	-----	-----	-----
33	89.2	85.3	97.2	97.2	-----	-----	-----	-----
34	91.9	88.2	97.2	97.2	-----	-----	-----	-----
35	91.9	88.2	97.2	97.2	-----	-----	-----	-----
36	94.6	91.2	100.0	100.0	-----	-----	-----	-----
37	97.3	91.2	-----	-----	-----	-----	-----	-----
38	97.3	91.2	-----	-----	-----	-----	-----	-----
39	97.3	91.2	-----	-----	-----	-----	-----	-----

Table 14.—*Accumulated mortality of tobacco budworm at 4 programed temperatures—Continued*

Days after emergence	Mortality at indicated mean temperature (° C.)							
	20		25		30		33	
	♂	♀	♂	♀	♂	♀	♂	♀
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
40.....	97.3	91.2	-----	-----	-----	-----	-----	-----
41.....	97.3	94.1	-----	-----	-----	-----	-----	-----
42.....	97.3	94.1	-----	-----	-----	-----	-----	-----
43.....	97.3	97.1	-----	-----	-----	-----	-----	-----
44.....	100.0	97.1	-----	-----	-----	-----	-----	-----
45.....		100.0	-----	-----	-----	-----	-----	-----

BEET ARMYWORM

The results in table 15 indicate that the regression equations for the development of the egg and the larval-pupal stages of the beet armyworm gave good estimates under constant temperatures. The most apparent differences were at the lower temperatures with development at 20° C. constant temperature being underestimated and overestimated at 25°. However, the 6- to 7-percent differences represent only about a day and a half error in the overall estimate of the larval-pupal period. In the programed regimes the regression equations both underestimated and overestimated the time of development and the underestimate was particularly obvious at 20°. The improved efficiency at lower temperatures has been discussed previously in regard to the *Heliothis* species. Generally the RUDs gave a better approximation of development than did the 2-hour >14° periods.

The development periods for each instar are presented in table 16. Generally the beet armyworm larvae had five instars, but certain individuals required six. The development periods were more rapid at the warmer temperatures, and rapid development was particularly evident in the constant-temperature regimes. However, when sustained temperatures in excess of 35° C. were included in programed regimes, the development period was longer. The high temperatures apparently exceeded the upper functional threshold of certain undetermined physiological systems of the beet armyworm.

At a constant and a programed 20° C. the summation of the estimated RUDs tended to underestimate the development. The RUDs accurately estimated the emergence of the beet armyworm in the 25°

TABLE 15.—Egg and larval-pupal development of beet armyworm at various constant and programed temperatures

Temperature (° C.)	Constant temperatures					Programed temperatures			
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >14° C.‡	Insects	Σ RUD	Σ degree-2 hour >14° C.‡
				Units	Summation †				
EGG STAGE									
20	336	Days	Number	Number	Number	Number	Number	Number	Number
25	332	-----	67.0	0.0149	0.999	281	0.599	398	187
30	223	-----	35.1	.0290	1.017	323	1.124	735	387
33	173	-----	23.9	.0404	.966	339	.987	1,517	359
		-----	22.0	.0464	1.022	378	1.154	315	433
MALE LARVAL-PUPAL STAGE									
20	48	30.1	361	0.0026	0.939	2,130	0.831	45	2,088
25	58	20.9	251	.0043	1.079	2,736	1.162	47	3,231
30	54	14.9	179	.0057	1.020	2,846	1.016	45	2,974
33	35	12.7	152	.0064	.973	2,873	1.114	21	3,405

See footnotes at end of table.

Table 15.—Egg and larval-pupal development of beet armyworm at various constant and programed temperatures—Con.

Temperature (° C.)	Constant temperatures					Programed temperatures			
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >14° C.²	Insects	Σ RUD	Σ degree-2 hour >14° C.²
				Units	Summation 1				
20	46	29.0	348	0.0028	0.970	2,158	54	0.804	2,020
25	39	20.1	241	.0044	1.066	2,699	41	1.145	3,185
30	29	14.8	178	.0058	1.026	2,884	38	.988	2,892
33	24	12.7	152	.0065	.982	2,918	17	1.114	3,405

FEMALE LARVAL-PUPAL STAGE

1 Based on estimates from regression equations:

Eggs: $\hat{y} = -0.1736 + 0.1449 (\log t)$

Males: $\hat{y} = -0.0200 + 0.0174 (\log t)$

Females: $\hat{y} = -0.0192 + 0.0169 (\log t)$

where

\hat{y} = estimate of RUD

t = mean substrate temperature (° C.) for each 2-hour period

2 Calculated thresholds (° C.):

Eggs----- 15.8

Males----- 14.1

Females----- 13.8

Males + females----- 14.0

TABLE 16.—Development periods of beet armyworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1959

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar		
	Larvae	Period	Larvae	Period	Larvae	Period	Larvae	Period	
<i>Constant</i>	20:								
	♂	Number	48	Number	48	Number	48	Number	48
	♀	Days	3.6±0.5	Days	2.9±0.5	Days	2.8±0.8	Days	3.2±0.5
	♂	Days	3.6±.5	Days	2.9±.5	Days	2.7±.5	Days	3.3±.6
	25:	♂	62	62	62	62	62	62	62
	♀	Days	3.3±.5	Days	1.9±.4	Days	1.6±.5	Days	2.0±.7
	♂	Days	3.1±.4	Days	1.9±.6	Days	1.7±.5	Days	2.1±.7
	30:	♂	58	58	58	58	58	58	58
	♀	Days	2.7±.5	Days	1.4±.6	Days	1.2±.5	Days	1.5±.6
	♂	Days	2.4±.5	Days	1.6±.5	Days	1.1±.3	Days	1.5±.5
	33:	♂	44	44	44	44	44	44	44
	♀	Days	2.0±0	Days	1.1±.5	Days	1.1±.2	Days	1.2±.5
♂	Days	2.0±0	Days	1.2±.5	Days	1.2±.4	Days	1.3±.5	
<i>Programed</i>	20:	♂	45	45	45	45	45	45	
	♀	Days	3.1±.3	Days	2.9±.3	Days	2.0±.4	Days	2.4±.5
	♂	Days	3.2±.4	Days	2.8±.4	Days	2.4±.4	Days	2.5±.5
	25:	♂	47	47	47	47	47	47	
	♀	Days	3.0±0	Days	2.0±0	Days	1.7±.4	Days	1.4±.5
	♂	Days	3.0±0	Days	2.0±0	Days	1.6±.4	Days	1.5±.5

TABLE 16.—Development periods of beet armyworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar	
	Larvae	Period	Larvae	Period	Larvae	Period	Larvae	Period
30: <i>Programed—Continued</i>	Number	Days	Number	Days	Number	Days	Number	Days
	50	2.9 ± .2	50	1.1 ± .3	50	1.1 ± .3	50	1.4 ± .8
	44	2.8 ± .3	44	1.3 ± .5	44	1.1 ± .3	44	1.6 ± .8
	43	2.1 ± .3	43	2.0 ± .6	43	1.1 ± .3	43	1.3 ± .6
33: -----	33	2.1 ± .2	33	2.1 ± .6	33	1.0 ± .2	33	1.2 ± .6
	-----	-----	-----	-----	-----	-----	-----	-----
20: <i>Constant</i>	Number	Days	Number	Days	Number	Days	Number	Days
	48	6.0 ± 0.6	0	-----	48	11.2 ± 0.6	48	30.1 ± 0.9
	46	6.1 ± 1.2	3	6.0 ± 1.0	46	9.6 ± 1.8	46	29.0 ± 1.1
	62	3.9 ± .8	0	-----	58	8.2 ± 1.6	58	20.9 ± 3.0
25: -----	44	4.2 ± .9	0	-----	39	7.2 ± 1.4	39	20.1 ± 3.0
	-----	-----	-----	-----	-----	-----	-----	-----
	5th instar		6th instar		Pupal stage		Total	
	Larvae	Period	Larvae	Period	Pupae	Period	Adults	Period
	Number	Days	Number	Days	Number	Days	Number	Days
	48	6.0 ± 0.6	0	-----	48	11.2 ± 0.6	48	30.1 ± 0.9
	46	6.1 ± 1.2	3	6.0 ± 1.0	46	9.6 ± 1.8	46	29.0 ± 1.1
	62	3.9 ± .8	0	-----	58	8.2 ± 1.6	58	20.9 ± 3.0
	44	4.2 ± .9	0	-----	39	7.2 ± 1.4	39	20.1 ± 3.0

30:	♂	58	2.9 ± .7	0	-----	54	5.4 ± .6	54	14.9 ± .7
	♀	32	3.2 ± .6	1	2.0 ± 0	29	4.8 ± .5	29	14.8 ± .5
33:	♂	41	2.4 ± .6	1	2.0 ± 0	35	5.1 ± .5	35	12.7 ± .7
	♀	39	2.6 ± .6	0	-----	24	5.0 ± .7	24	12.7 ± .9
<i>Programed</i>									
20:	♂	45	5.0 ± .5	0	-----	45	9.3 ± .5	45	24.8 ± .8
	♀	54	5.1 ± .8	1	7.0 ± 0	54	8.2 ± .5	54	24.0 ± .8
25:	♂	47	4.1 ± .3	0	-----	47	8.5 ± .6	47	20.9 ± .8
	♀	41	4.6 ± .4	0	-----	41	7.5 ± .5	41	20.6 ± 1.1
30:	♂	46	2.9 ± .5	0	-----	45	5.1 ± .3	45	14.5 ± .5
	♀	37	3.0 ± .6	1	2.0 ± 0	38	4.6 ± .6	38	14.1 ± .4
33:	♂	41	2.4 ± .8	2	2.0 ± 0	21	5.7 ± .6	21	14.6 ± .6
	♀	27	2.7 ± .5	1	4.0 ± 0	17	5.5 ± .5	17	14.5 ± .8

constant regime; however, in the programed regime the error was about 20 percent or 3 to 4 days. The 30° regimes were both accurately predicted by the RUDs. The emergence at a constant 33° was accurately estimated, but at a programed 33° emergence came later than predicted, indicating that sustained high temperatures in the regime may have caused a physiological slowdown.

At lower temperatures 86 to 100 percent of the adults emerged, but mortality was appreciable at 33° C. Mortality was 20 percent of the males and 48 percent of the females at a constant 33° and about 50 percent of both sexes at a programed 33°, indicating that the higher temperature had deleterious effects on the developing insects. The most efficient rearing was at a constant 30°, where development was rapid and survival was about 90 percent.

The data in table 17 indicate that the preoviposition period for the beet armyworm was from 1 to 11 days, but with few exceptions all females were ovipositing before the fifth to sixth day. Thus the higher temperatures had little effect on the initiation of oviposition.

The data in table 18 indicate a declining longevity as the temperature was increased. In all except the 33° C. regime males were significantly longer lived. The greatest fecundity occurred at 20°. At 30° and 33° it was drastically curtailed.

In all programed regimes 50 percent of the eggs were laid by the fourth or fifth day and 90 percent by the seventh or eighth day after emergence (table 19). At 25°, 30°, and 33° C. the females completed oviposition by the 13th to 15th day; however, at 20° one female did

TABLE 17.—*Accumulated beet armyworms ovipositing at 4 programed temperatures*

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2	0	14.3	2.9	5.6
3	48.6	80.0	40.0	61.1
4	97.3	94.3	80.0	83.3
5	100.0	97.1	100.0	91.7
6		97.1		100.0
7		97.1		
8		97.1		
9		97.1		
10		97.1		
11		97.1		
12		100.0		

not complete oviposition until the 20th day. The data in table 20 indicate that the females lived from 1 to 10 days after oviposition was completed and that the males were slightly longer lived than the females.

Butler (3) reviewed the literature on the development of the armyworm and included additional data on an Arizona strain that are similar to the results in table 16. Guerra and Ouye (8) reported on

TABLE 18.—*Longevity and fecundity of beet armyworm at 4 programed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	37	15.3 ± 6.4	37	12.9 ± 4.2	1,521.9 ± 426.2
25.....	35	14.4 ± 4.4	35	8.7 ± 2.1	874.8 ± 360.3
30.....	35	14.9 ± 3.6	35	10.2 ± 2.1	636.6 ± 236.6
33.....	36	10.1 ± 5.3	36	10.2 ± 4.8	714.0 ± 543.1

TABLE 19.—*Accumulated eggs laid by beet armyworm at 4 programed temperatures*

Days after emergence	Eggs laid at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2.....	0	2.9	1.4	2.4
3.....	19.5	29.6	8.4	26.8
4.....	53.4	59.1	27.3	49.6
5.....	68.8	78.8	52.1	69.1
6.....	80.1	89.8	69.1	80.2
7.....	87.2	95.5	83.5	88.0
8.....	92.2	97.2	93.0	95.3
9.....	95.2	98.4	96.4	97.6
10.....	96.9	99.0	98.6	99.1
11.....	98.1	99.3	99.3	99.5
12.....	99.1	99.7	99.8	99.6
13.....	99.5	100.0	100.0	99.6
14.....	99.7			99.9
15.....	99.8			100.0
16.....	99.9			
17.....	99.9			
18.....	99.9			
19.....	99.9			
20.....	100.0			

the winter to be 37.6 days and Campbell and Duran (4) reported development periods for the larvae of 76 days during a winter in California. Though our study did not include low temperature regimes, the RUDs indicate that such would be the case in the Arizona strain.

CABBAGE LOOPER

The development data for the egg and larval-pupal stages of the cabbage looper are summarized in table 21. The data indicate that at constant temperatures of 20° to 33° C. the development of the cabbage looper can be accurately estimated with RUDs calculated with the regression equations. However, in the programmed regimes the development of the eggs was underestimated at 20° and the egg and larval-pupal developments were overestimated at 30° and 33°. However, the estimates were better than those utilizing the degree 2-hour $>12.1^\circ$ threshold concept. Again there was a better physiological efficiency at 20°, and adverse effects of temperatures above the upper threshold were apparent at 33°. Removal of temperatures greater than 36° brought the estimate of the total development closer to unity and indicated that the upper functional threshold of the cabbage looper is approximately 36°.

The development periods of the immature cabbage loopers are given in table 22. Most of the larvae had five instars with the fifth instar the longest. A few larvae required six instars for total development. The pupal period ranged from about 5.5 days at a constant 33° C. to a little more than 11 days at 20°. Overall the larval-pupal development ranged from 14.7 days for the females at a constant 33° to 29.8 days for the males at a constant 20°.

The emergence data indicated that a constant 30° C. was the most efficient for rearing the cabbage looper because the development was rapid and the mortality was less than 10 percent. At a constant 33° the development was more rapid, but mortality was about 40 percent. The higher mortality at constant 33° and at programmed 30° and 33° reflects the adverse effects of the high temperatures on the development and survival of the cabbage looper.

The data on the percentage of cabbage loopers ovipositing in table 23 indicate that some loopers have a preoviposition period as short as 1 to 2 days but a few have relatively long preoviposition periods of 7 to 10 days. Generally 85 to 100 percent of the moths oviposited by the fifth day.

The longevity and fecundity data on the cabbage looper are summarized in table 24. The longevity in the programmed regime for the

TABLE 21.—Egg and larval-pupal development of cabbage looper at various constant and programed temperatures

Temperature (° C.)	Constant temperatures						Programed temperatures				
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >12.1° C.†	Insects	Σ RUD	Σ degree-2 hour >12.1° C.†	Insects	
				Units	Summation †					Number	Number
EGG STAGE											
20	95	Days	Number	Number	Number	Number	Number	Number	Number	Number	Number
25	112	---	60.4	1.011	356	50	0.573	220	477	1.026	440
30	134	---	35.8	.982	390	478	1.095	498	478	1.095	498
33	82	---	27.8	1.006	442	71	1.290	613	442	1.095	498
		---	27.4	1.116	518				71	1.290	613
MALE LARVAL-PUPAL STAGE											
20	29	29.7	356.4	1.003	2,780	46	0.921	2,795	68	1.054	3,548
25	45	20.6	247.2	1.007	3,164	59	1.105	3,088	26	1.216	4,560
30	53	16.4	196.8	1.004	3,503						
33	38	14.9	178.8	1.008	3,719						

FEMALE LARVAL-PUPAL STAGE

20	60	28.5	342.0	0.0028	0.938	2,702	51	0.887	2,691
25	55	20.5	246.0	.0041	1.009	3,173	113	1.019	3,429
30	63	15.8	189.6	.0052	.986	3,393	45	1.086	3,034
33	15	14.7	176.4	.0057	1.005	3,687	27	1.147	4,302

¹ Based on estimates from regression equations:

Eggs: $\hat{y} = -0.1269 + 0.1104 (\log t)$

Males: $\hat{y} = -0.0141 + 0.0130 (\log t)$

Females: $\hat{y} = -0.0143 + 0.0132 (\log t)$

where

\hat{y} = estimate of RUD

t = mean substrate temperature (° C.) for each 2-hour period

² Calculated thresholds (° C.):

Eggs ----- 14.1

Males ----- 12.2

Females ----- 12.1

TABLE 22.—*Development periods of cabbage looper at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969*

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar	
	Larvae	Period	Larvae	Period	Larvae	Period	Larvae	Period
20: Constant	♂	3.2±0.4	30	2.9±0.3	30	2.2±0.4	30	3.3±0.4
	♀	3.2±.4	61	2.8±.4	61	2.2±.4	61	3.2±.4
	♂	3.0±.3	46	2.4±.8	46	2.3±1.5	46	2.4±.8
	♀	3.1±.4	55	2.5±.8	55	2.2±1.4	55	2.8±1.5
30: Constant	♂	2.1±.4	58	1.7±.5	58	1.4±.5	58	1.7±.5
	♀	2.1±.2	65	1.8±.4	65	1.3±.4	65	1.7±.5
	♂	2.1±.3	59	1.2±.4	59	1.5±.5	59	1.4±.6
	♀	2.1±.3	34	1.2±.4	34	1.4±.5	34	1.4±.5
20: Programed	♂	3.1±.3	47	2.6±.5	47	2.2±.4	47	2.7±.6
	♀	3.1±.3	51	2.7±.5	51	2.1±.4	51	2.7±.5
	♂	3.0±.3	68	1.2±.4	68	4.0±.5	68	3.8±.8
	♀	2.9±.3	113	1.3±.5	113	4.0±.7	113	3.8±.7

	5th instar		6th instar		Pupal stage		Total	
	Larvae	Period	Larvae	Period	Pupae	Period	Adults	Period
	Number	Days	Number	Days	Number	Days	Number	Days
30: ♂	70	2.7 ± .4	70	1.3 ± .5	70	1.3 ± .5	70	1.8 ± .3
♀	52	2.6 ± .5	52	1.4 ± .5	52	1.1 ± .4	52	1.9 ± .2
33: ♂	47	2.7 ± .6	47	1.3 ± .5	47	1.2 ± .4	47	1.8 ± .4
♀	37	2.7 ± .5	37	1.4 ± .5	37	1.1 ± .3	37	1.8 ± .5
<i>Constant</i>								
20: ♂	30	7.1 ± 0.4	0	-----	29	11.1 ± 0.6	29	29.8 ± 1.0
♀	61	6.9 ± .8	1	6.0 ± 0	60	10.3 ± .5	60	28.5 ± .8
25: ♂	40	3.2 ± 1.2	1	4.0 ± 0	45	7.6 ± 1.0	45	20.7 ± 2.2
♀	42	3.6 ± 1.2	0	-----	55	7.2 ± 1.2	55	20.5 ± 2.0
30: ♂	58	3.0 ± .7	0	-----	53	6.6 ± .6	53	16.4 ± .6
♀	65	2.9 ± .6	0	-----	63	6.1 ± .5	63	15.8 ± .8
33: ♂	58	3.0 ± .6	1	2.0 ± 0	38	5.5 ± .5	38	14.9 ± .7
♀	34	2.9 ± .6	2	1.5 ± .7	15	5.5 ± .5	15	14.7 ± .9

TABLE 22.—*Development periods of cabbage looper at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued*

Temperature (° C.) and sex	5th instar		6th instar		Pupal stage		Total		
	Larvae	Period	Larvae	Period	Pupae	Period	Adults	Period	
	Number	Days	Number	Days	Number	Days	Number	Days	
20:	♂	47	5.5 ± .7	1	6.0 ± 0	46	10.6 ± .6	46	26.7 ± 1.0
	♀	51	5.3 ± .6	0	-----	51	9.9 ± .5	51	25.7 ± .4
25:	♂	16	2.1 ± 1.9	1	5.0 ± 0	68	7.3 ± 1.0	68	20.0 ± 2.1
	♀	19	3.1 ± 2.1	0	-----	113	6.7 ± .9	113	19.3 ± 2.2
30:	♂	70	3.7 ± .5	0	-----	70	6.3 ± .5	59	17.4 ± .6
	♀	52	3.5 ± .7	0	-----	52	6.2 ± .7	45	17.1 ± .6
33:	♂	47	3.9 ± .4	0	-----	26	6.7 ± .5	26	17.7 ± 1.1
	♀	37	3.7 ± .6	1	4.0 ± 0	27	6.1 ± .7	27	16.7 ± 1.1

Programed

males ranged from 5.6 days at 33° C. to 23.9 days at 20°. The fecundity in the programed regime ranged from a mean of 72 eggs per female at 33° to 1,202 at 20°. The fecundity was reduced at 25° and drastically reduced at 30° and 33°. The small numbers of eggs at 30° and 33° were all laid within 2 weeks (table 25). However, at 20° and 25° the larger numbers of eggs were laid over a period of 4 to 5 weeks, though 85 to 90 percent were laid within 15 days.

The mortality data in table 26 indicate that a few moths survived after the major oviposition occurred and were responsible for the extended egg-laying period. In all but the 33° C. programed regime a few of the moths survived for a short period after oviposition ceased.

Shorey et al. (22) reared cabbage looper larvae on lima bean leaves

TABLE 23.—*Accumulated cabbage loopers ovipositing at 4 programed temperatures*

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2.....	0	19. 4	12. 1	6. 1
3.....	73. 0	64. 5	36. 4	53. 1
4.....	97. 3	80. 6	63. 6	77. 6
5.....	100. 0	87. 1	84. 8	93. 9
6.....		93. 5	93. 9	100. 0
7.....		96. 8	97. 0	
8.....		96. 8	100. 0	
9.....		96. 8		
10.....		96. 8		
11.....		100. 0		

TABLE 24.—*Longevity and fecundity of cabbage looper at 4 programed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	37	23. 9±5. 9	37	20. 1±6. 5	1, 202. 2±457. 8
25.....	31	16. 9±4. 5	31	18. 9±5. 6	806. 8±574. 5
30.....	33	14. 6±4. 3	33	12. 3±4. 7	129. 2±197. 9
33.....	49	5. 6±3. 6	49	7. 9±3. 2	72. 5±132. 3

and found the larval period to be about 18 days at 23° C. and about 15 days at 32° as compared to about 13 days at 25° and 10 days at 30° in the current study (table 22). This may indicate that the nutrition of the insect affects the development of the larvae. Shorey et al. also found the pupal period of the insects reared on lima bean leaves to be 7.5 to 8.5 days at 23° and 5.5 to 6 days at 32° as compared to 7.5 and 6.5 days at a constant 25° and 30° in this bulletin. Therefore it is

TABLE 25.—*Accumulated eggs laid by cabbage looper at 4 programmed temperatures*

Days after emergence	Eggs laid at indicated mean temperature (° C.)			
	20	25	30	33
2	0	0.2	0.7	0.3
3	.7	6.7	3.0	5.9
4	10.4	17.5	12.6	15.5
5	22.7	32.6	33.5	30.1
6	34.9	45.7	54.8	43.4
7	44.9	56.5	68.5	62.0
8	55.3	64.3	80.7	70.6
9	62.9	70.7	92.6	80.4
10	67.6	76.1	98.4	87.0
11	72.0	80.5	99.7	93.1
12	76.5	83.7	100.0	96.6
13	80.4	86.1	-----	99.9
14	84.0	88.3	-----	100.0
15	86.9	90.5	-----	-----
16	89.6	92.1	-----	-----
17	91.5	93.8	-----	-----
18	93.3	95.1	-----	-----
19	94.6	96.0	-----	-----
20	95.5	96.9	-----	-----
21	96.4	97.8	-----	-----
22	97.0	98.4	-----	-----
23	97.5	98.8	-----	-----
24	97.9	99.2	-----	-----
25	98.1	99.5	-----	-----
26	98.5	99.7	-----	-----
27	98.8	99.8	-----	-----
28	99.1	99.9	-----	-----
29	99.4	100.0	-----	-----
30	99.6	-----	-----	-----
31	99.7	-----	-----	-----
32	99.8	-----	-----	-----
33	99.9	-----	-----	-----
34	100.0	-----	-----	-----

loopers fed on cabbage leaves and those fed on bean leaves. Their studies indicated that if fully responsive models are to be developed, nutrition must be taken into account. This view is substantiated by Jackson et al. (12), who reared the cabbage looper on the pinto bean diet developed by Shorey and Hale (23) and found the development period for the larval-pupal stage to be 35.8, 23.0, 17.6, and 16.9 days at a constant 20°, 25°, 30°, and 32° C., respectively. Likewise Ignoffo (11) found a mean development period of 16 to 17 days using a diet with a wheat germ base. These periods are slightly longer than those determined in the current study, where a similar diet with lima beans was employed as the rearing medium. Shorey et al. (22) found the looper larvae had five to seven instars as compared to the five and six instars noted in this study.

Shorey et al. reported that most authors, including themselves, believed that the cabbage looper was a warm weather insect, and the current studies indicate the same, though the looper is apparently not a "hot" weather insect.

Shorey (20) found the fecundity of the cabbage looper at 27° C. ranged from 61 eggs per female for those reared on cabbage leaves and without males to 604 eggs per female for those reared on cabbage leaves with males present in the oviposition cage. Likewise Henneberry and Kishaba (10) found a mean fecundity of 408 to 606 eggs for cabbage loopers held at 15.6 to 32.2°. These data compare favorably with the 806 eggs per adult for the females reared at 25° in this study; however, these results do not approach the 1,202 eggs deposited at 20°.

Shorey (20) found the females had a mean longevity of 11.9 days or about 7 days less than the females in the 25° C. regime in this study. The longevity of mated females without viable eggs reported by Shorey at 19.3 days is closer to the 19-day longevity of the females in the 25° regime of this study. The preoviposition period of about 1.5 days reported by Shorey is comparable to the preoviposition period in all regimes in this study.

SALTMARSH CATERPILLAR

The development data for the saltmarsh caterpillar are summarized in table 27. In all constant temperature regimes the egg and larval-pupal developments were accurately estimated by the RUDs. More variation in the development estimate resulted when utilizing the degree-2-hour periods. However, in the programed regimes the development estimates utilizing either the RUDs or the degree-2-hour summations resulted in poor estimates of the development of the saltmarsh caterpillar. The data indicated that this insect is vulnerable to high temperatures in the egg, larval, and pupal stages. In fact, the

egg survival at the programmed 33° C. was very poor and the estimate was based on very few eggs. Although egg survival at the programmed 30° was slightly better, the number of hatched eggs was relatively small. Thus the eggs are apparently very vulnerable to high temperatures. This result was also indicated by Fye and Surber (7).

The development periods for the various stages are given in table 28. Most of the saltmarsh caterpillars required six instars, but a large number required seven. Three larvae completed development in eight instars and a single larva passed through nine. Generally the sixth and subsequent instars were the longest. The saltmarsh caterpillar required from 25.5 to 48.4 days in the larval-pupal stages.

The RUDs accurately estimated the development of the larvae and pupae at a constant 20° C.; however, a few individuals emerged late. In the programmed regime with a mean of 20° the RUDs underestimated their development. The development at a constant 25° was accurately estimated; however, at the programmed 25° it was overestimated. This indicated that some of the temperatures included in the 25° programmed regime probably approached the upper threshold of the saltmarsh caterpillar larvae.

The development at the constant 30° C. was slightly overestimated and poorly estimated at the programmed 30°. This indicated that the physiological systems, which are depressed when the upper threshold temperature is reached, began to slow down at about 30°, and when temperatures in excess of 30°, including several in the programmed regime, were included, the development was adversely affected.

Further evidence of the physiological slowdown as the upper threshold temperature was reached was apparent at the constant 33° C., and the development was very poorly estimated at the programmed 33°, which was above the apparent physiological threshold.

Although some development lag was caused by temperatures above 30° C., the most effective rearing temperature was still in the 30° to 33° range. Though the development was not as rapid as would have been calculated from the RUDs, the constant 30° and 33° were still the most effective in regard to time and low mortality.

The data in table 29 indicate that the saltmarsh caterpillar had a minimum preoviposition period of 1 to 2 days and that all moths were ovipositing by the fifth to the seventh day. The temperatures apparently had little effect on preoviposition.

In the programmed regimes the longevity of the saltmarsh caterpillar males ranged from 4.6 days at 33° C. to 11.2 days at 20°. The longevity of the females was similar at 20°, 25°, and 30° and slightly shorter at 33° (table 30). The highest fecundity occurred at 20°. The fecundity was effectively reduced at 25° and 30° and drastically so at 33°. These

TABLE 27.—Egg and larval-pupal development of saltmarsh caterpillar at various constant and programed temperatures

Temperature (° C.)	Constant temperatures						Programed temperatures			
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour $>10.7^{\circ}$ C. ²	Insects	Σ RUD	Σ degree-2 hour $>10.7^{\circ}$ C. ²	
				Number	Units					Summation †
EGG STAGE										
20	252	Days	Number	Number	Number	Number	Number	Number	Number	Number
	91.6	---	0.0113	1.035	568	497	0.703	535		
25	290	---	.0181	.988	612	486	1.214	714		
30	285	---	.0236	1.005	690	68	1.286	737		
33	34	---	.0265	1.203	872	8	1.423	897		
MALE LARVAL-PUPAL STAGE										
20	45	48.4	580.8	0.0018	1.032	5,401	45	0.909	5,008	
25	56	31.4	376.8	.0024	.921	5,388	103	1.088	6,642	
30	48	29.0	348.0	.0030	1.041	6,716	46	1.228	8,075	
33	41	25.5	306.0	.0033	1.003	6,824	43	1.188	8,150	

FEMALE LARVAL-PUPAL STAGE

20.-----	45	48. 2	578. 4	0. 0018	1. 050	5, 379	49	0. 907	4, 996
25.-----	60	32. 0	384. 0	. 0025	. 947	5, 491	85	1. 119	6, 836
30.-----	48	28. 8	345. 6	. 0030	1. 035	6, 670	38	1. 220	8, 026
33.-----	47	26. 0	312. 0	. 0033	1. 021	6, 958	48	1. 220	8, 369

¹ Based on estimates from regression equations:

Eggs: $\hat{y} = -0.0799 + 0.0701 (\log t)$

Males: $\hat{y} = -0.0072 + 0.0069 (\log t)$

Females: $\hat{y} = -0.0069 + 0.0067 (\log t)$

where

\hat{y} = estimate of RUD

t = mean substrate temperature (° C.) for each 2-hour period

² Calculated thresholds (° C.):

Eggs-----	13. 8
Males-----	11. 1
Females-----	10. 7

TABLE 28.—*Development periods of saltmarsh caterpillar at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued*

Temperature (° C.) and sex	7th instar		8th instar		9th instar		Pupal stage		Total	
	Larvae	Period	Larvae	Period	Larvae	Period	Pupae	Period	Adults	Period
20: ♂	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	5	10.0±0	0	---	0	---	45	13.0±.8	45	41.7±2.0
25: ♀	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	12	9.3±.6	0	---	0	---	49	12.5±1.1	49	41.6±2.5
30: ♂	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	13	7.2±1.1	1	5.0±0	1	8.0±0	103	11.5±.7	103	34.2±3.0
33: ♀	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	22	7.6±.6	3	6.0±1.7	0	---	85	11.1±.9	85	35.2±3.1
33: ♂	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	13	6.7±1.4	0	---	0	---	46	10.3±.7	46	33.0±2.4
33: ♀	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	14	7.2±1.3	0	---	0	---	38	9.8±.6	38	32.8±2.0
33: ♂	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	0	---	0	---	0	---	43	10.1±.5	43	29.7±.8
33: ♀	Number	Days	Number	Days	Number	Days	Number	Days	Number	Days
	0	---	0	---	0	---	48	10.1±.6	48	31.0±1.1

data clearly indicate why the saltmarsh caterpillar is a relatively rare insect in cottonfields in Arizona during the hot early part of the summer.

The oviposition period of the saltmarsh caterpillar is relatively short compared to that of the previously discussed species (table 31). At 20° C. it was 14 days; however, about 95 percent of the eggs had been laid by the end of the ninth day after emergence. At the other temperatures nearly all the eggs had been laid between the seventh and ninth days.

The data in table 32 indicate that the males lived slightly longer than the females and the females lived for a day or two after oviposition was completed (table 31).

As compared with the previous species, the saltmarsh caterpillar adults were short lived. With rare exception they emerged, had a brief preoviposition period, oviposited rapidly, and died shortly thereafter.

TABLE 29.—*Accumulated saltmarsh caterpillars ovipositing at 4 programed temperatures*

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2.....	0	25. 7	0	13. 8
3.....	37. 8	80. 0	17. 2	48. 3
4.....	81. 1	97. 1	51. 7	72. 4
5.....	100. 0	97. 1	82. 8	93. 1
6.....	-----	100. 0	93. 1	100. 0
7.....	-----	-----	100. 0	-----

TABLE 30.—*Longevity and fecundity of saltmarsh caterpillar at 4 programed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	37	11. 2±2. 7	37	9. 5±2. 2	1, 577. 2±500. 4
25.....	35	8. 2±1. 7	35	8. 1±1. 8	862. 2±363. 7
30.....	29	14. 9±3. 6	29	10. 2±2. 1	636. 6±236. 6
33.....	29	4. 6±. 9	29	5. 7±1. 4	80. 0± 99. 1

The results in table 28 are generally similar to data given by Malik,² although the duration of the various instars was variable in both studies. In these studies the later instars were longer than the earlier ones. The pupal period in the current study was shorter than that found by Malik at 20° C. However, it was longer at 25° and 30° than that reported by Malik. Generally the overall development time for the larval-pupal stages was similar at a constant 20°, 25°, and 30°.

Likewise the preoviposition periods noted by Malik at 20°, 25°, and 30° C. were similar to those in the current study. The oviposition period was similar although the moths in the current study oviposited slightly longer than those studied by Malik. The longevity of the moths in the current study was also longer and the fecundity was appreciably greater. However, the results may not be directly comparable because Malik's material was held at constant temperatures and the longevity and fecundity data in the present study were determined in programmed regimes with similar mean temperatures.

The results suggest that since the insects in both studies were drawn from the same culture approximately 2 years apart, the rearing procedures at the Biological Control Investigations Laboratory in Tucson, as reported by Patana (18), may inadvertently be selecting insects of a specific genetic makeup.

PINK BOLLWORM

The temperatures for the study of the pink bollworm are given in table 33 with their associated RUDs and the degree-2-hour period input. The regression lines for the development of the larval and pupal stages are shown in figure 2 and the regression equations are given in table 34.

The lines offer a convenient way to estimate the RUDs without doing the computations associated with the asymptotic regression equations. The development regression equations for the previous species have been linear through the temperature range considered. The data derived for the pink bollworm indicate that the asymptotic form is more appropriate, since the metabolic rate apparently levels off at a lower temperature. Although the underlying factors resulting in the asymptotic form at the lower temperatures were not determined, the points suggest that some physiological system begins to slow down near 23° C. and reaches a relatively consistent velocity at about 25°

² MALIK, M. Y. INFLUENCE OF VARIOUS CONSTANT TEMPERATURES ON THE RATE OF DEVELOPMENT, FECUNDITY AND LONGEVITY OF *ESTIGMENE ACREA* (DRURY) (LEPIDOPTERA: ARCTIIDAE). 1967. [Unpublished master's thesis. Copy on file Univ. of Ariz., Tucson.]

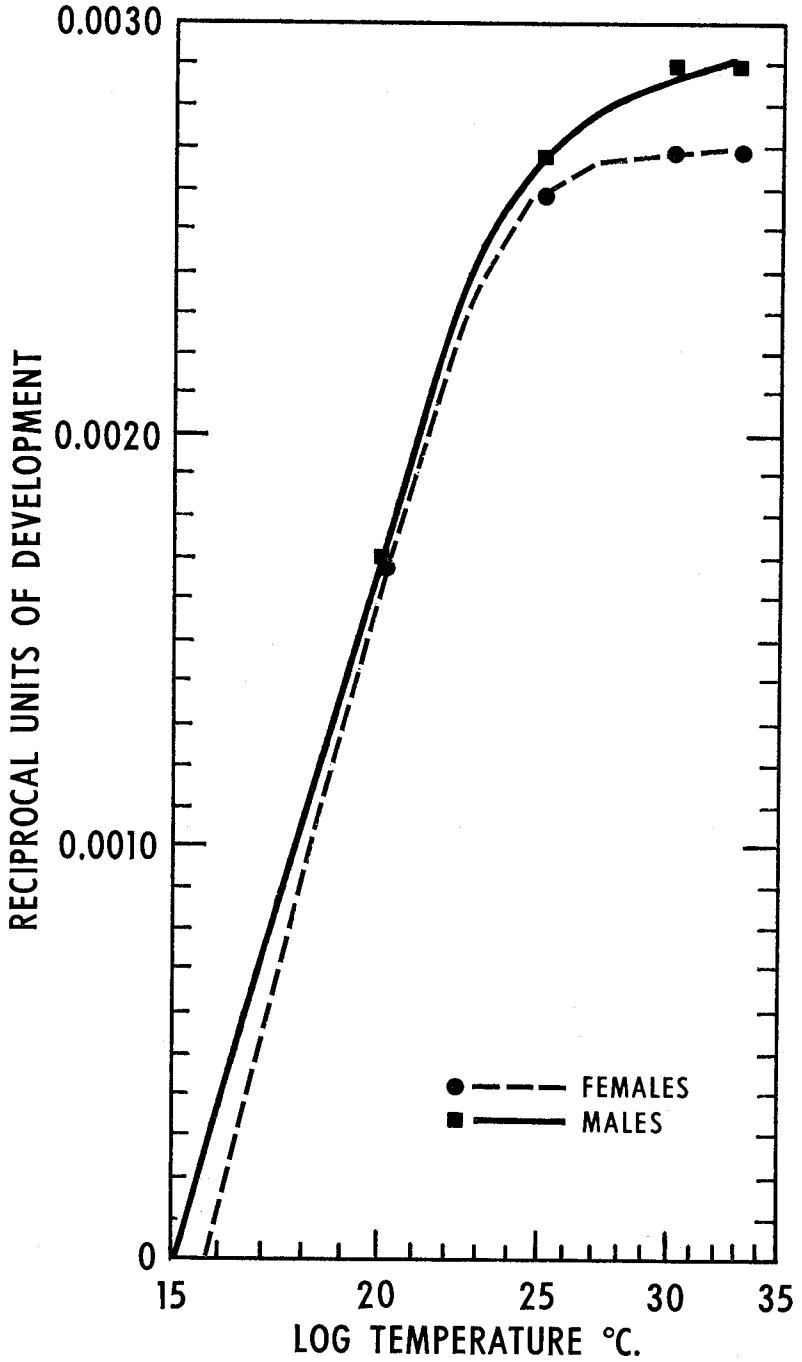


FIGURE 2.—Regression lines for reciprocal units of development of larvae and pupae of the pink bollworm on the logarithm of temperature (° C.).

TABLE 33.—Temperatures for study of pink bollworm development

Period	20° C.			25° C.			30° C.			33° C.		
	Mean tem- perature	RUD ¹	Degree- 2 hour >15.4° C. ²	Mean tem- perature	RUD	Degree- 2 hour >15.4° C.	Mean tem- perature	RUD	Degree- 2 hour >15.4° C.	Mean tem- perature	RUD	Degree- 2 hour >15.4° C.
<i>Constant</i>												
Each 2 hours.....	° C.	Number	Number	° C.	Number	Number	° C.	Number	Number	° C.	Number	Number
Daily.....	20.0	0.0017	4.6	25.0	0.0027	9.6	30.0	0.0029	14.6	33.0	0.0029	17.6
	20.0	.0204	55.2	25.0	.0324	115.2	30.0	.0348	175.2	33.0	.0348	211.2
<i>Programed</i>												
0001-0200.....	17.8	.0009	2.4	22.8	.0025	7.4	27.2	.0028	11.8	30.9	.0029	15.5
0201-0400.....	14.4	0	0	21.7	.0022	6.3	27.2	.0028	11.8	27.2	.0028	11.8
0401-0600.....	10.6	0	0	18.9	.0014	3.5	24.4	.0025	9.0	23.3	.0025	7.9
0601-0800.....	13.6	0	0	18.9	.0014	3.5	25.6	.0027	10.2	28.3	.0028	12.9
0801-1000.....	20.3	.0018	4.9	25.0	.0027	9.6	29.4	.0029	14.0	33.6	.0029	18.2
1001-1200.....	23.6	.0026	8.2	30.3	.0029	14.9	32.8	.0029	17.4	35.9	.0029	20.5
1201-1400.....	25.9	.0027	10.5	33.1	.0029	17.7	35.6	.0029	20.2	37.8	.0029	22.4
1401-1600.....	27.2	.0028	11.8	34.7	.0029	19.3	36.7	.0029	21.3	39.4	.0029	24.0
1601-1800.....	28.0	.0028	12.6	34.4	.0029	19.0	37.0	.0029	21.6	40.6	.0029	25.2
1801-2000.....	26.1	.0027	10.7	32.0	.0029	16.6	37.2	.0029	21.8	38.9	.0029	23.5
2001-2200.....	21.7	.0022	6.3	27.2	.0028	11.8	32.8	.0029	17.4	34.7	.0029	19.3
2201-2400.....	19.2	.0015	3.8	23.6	.0026	8.2	27.2	.0028	11.8	32.2	.0029	16.8
Total.....	-----	.0200	71.2	-----	.0301	137.8	-----	.0339	188.3	-----	.0342	218.0

¹ RUD=reciprocal units of development for 2-hour periods. ² Threshold temperature from the regression line (fig. 2).

even though the rearing temperatures for the insects are raised to higher levels.

The data in table 34 show that the linear regression equation for the development of the eggs provides a good estimate. Likewise the asymptotic regression equations give an accurate estimate of the larval-pupal development at a constant 20°, 25°, 30°, and 33° C. However, the regression equations fail to give good estimates of the development of the larvae and pupae in the programmed regimes.

The larval development period was divided into several instars (table 35). The most common number of instars was four; however, in the hotter regimes five instars were common and six and seven instars occurred occasionally. One larva in the 30° C. programmed regime required nine instars for full development and it was exceedingly large. Generally the final instar and, in the case of the several extra instars, the later instars were the longest. However, the first instar also was frequently long. Generally the pupal period was equivalent to the length of the later instars. At all temperatures the development varied appreciably as evidenced by the broad standard deviations.

A prolonged development period occurred at the constant 20° C., and the emergence of half the adults was accurately estimated by the RUDs. However, an extra temperature input, which would ordinarily equal that needed for one-half of a generation, was required before the entire group of adults emerged. About 28 percent entered diapause. When they were placed at a constant 25° for 10 to 34 days, and generally for only 10 to 20 days, they pupated and emerged in from 7 to 9 days.

At the programmed 20° C. the RUDs underestimated the development of the pink bollworm. An additional temperature input equivalent to a full one-third of a generation was required before all individuals had emerged. About 52 percent reared at the programmed 20° entered diapause. When they were returned to a constant 25°, they pupated in from 8 to 37 days and adults emerged 5 to 12 days later. Thus the programmed regime at 20° induced a relatively high level of diapause with a day length of 12 hours.

At the constant 25° C. about 30 percent emerged when the summation of the RUDs reached 1. However, a few individuals required as much as 2.5 times the normal summation of the RUDs before they emerged. At the programmed 25° the emergence commenced when the summation of the RUDs equaled 1, and emergence was completed when an additional 70 percent of the RUDs were added.

At the constant 30° C. the emergence of 50 percent was accurately estimated. However, a few individuals and one in particular required

TABLE 34.—Egg and larval-pupal development of pink bollworm at various constant and programed temperatures

Temperature (° C.)	Constant temperatures					Programed temperatures			
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour >19.4° C. ²	Insects	Σ RUD	Σ degree-2 hour >15.4° C. ²
				Units	Summation †				
EGG STAGE									
20	380	Days	Number	Number	Number	Number	Number	Number	Number
25	248	-----	122.7	0.0082	1.008	626	0.794	478	-----
30	152	-----	66.3	.0145	.964	670	1.059	797	-----
33	526	-----	51.6	.0197	1.017	779	1.144	907	-----
		-----	44.3	.0224	.992	802	1.235	1,025	-----
MALE LARVAL-PUPAL STAGE									
20	51	50.1	601.2	0.0017	1.022	2,766	0.889	3,163	-----
25	24	31.4	376.8	.0027	1.017	3,617	1.305	5,981	-----
30	69	28.6	343.2	.0029	.985	5,011	1.159	6,440	-----
33	53	28.9	346.8	.0029	1.005	6,104	1.204	7,674	-----

See footnotes at end of table.

Table 34.—Egg and larval-pupal development of pink bollworm at various constant and programed temperatures—Con.

Temperature (° C.)	Constant temperatures						Programed temperatures					
	Insects	Period	2-hour periods	Reciprocal unit of development for 2-hour periods (RUD)		Σ degree-2 hour > 15.4° C. ²	Insects	Σ RUD	Σ degree-2 hour > 15.4° C. ²			
				Units	Summation 1							
	Number	Days	Number	Number	Number	Number	Number	Number	Number			
20	58	50.2	602.4	0.0017	1.024	2,771	25	0.900	3,204			
25	23	31.7	380.4	.0026	.989	3,652	50	1.345	6,160			
30	75	31.1	373.2	.0027	1.008	5,449	32	1.363	7,570			
33	61	30.5	366.0	.0027	.988	6,442	27	1.194	7,630			

FEMALE LARVAL-PUPAL STAGE

¹ Based on estimates from regression equations:

$$\text{Eggs: } \hat{y} = -0.0766 + 0.0652 (\log \text{ temperature in } ^\circ \text{C.})$$

$$\text{Males: } \hat{y} = \frac{1}{340 + (248 \times 0.2323^*)}$$

$$\text{Females: } \hat{y} = \frac{1}{369 + (219 \times 0.1628^*)}$$

where

$$\hat{y} = \text{estimate of RUD}$$

$$x = a \text{ transformed value} = \frac{\log \text{ temperature} - 1.30103}{0.7250}$$

² Calculated or estimated thresholds (° C.):

$$\text{Eggs} \text{-----} 14.9$$

$$\text{Males} \text{-----} 15.0$$

$$\text{Females} \text{-----} 15.7$$

a summation of 2.2 before they emerged. At the programed 30° about 25 percent of the emergence was accurately predicted. However, several individuals required a prolonged period for development, and the temperature input normally needed for 2.3 generations was required before all had emerged.

At the constant 33° C. the emergence of 50 percent was accurately predicted. However, the temperature input normally required for 1.7 generations was needed before the last individual emerged. At the programed 33° the emergence commenced at about the time half the generation would have been expected to emerge, and an extra temperature input equivalent to 0.9 generation was required before the final individual emerged. Therefore at several of the higher programed temperatures the RUDs, as estimated by the asymptotic regression equations, tended to overestimate the development. This would be expected because if the hypothesized slowdown of some physiological system is responsible for the asymptotic nature of the curves, we would expect an unpredictable physiological complexity as the temperatures within the programed regimes were increased.

Keister and Buck (13) reported that the autotoxication mechanism in warm regimes is extremely complex and physiologists and biochemists have had difficulty characterizing other physiological systems. Therefore it is not surprising that the relatively simple regression approach, which considers only the central tendency of the response of the total physiological systems, fails to accurately estimate the development of the pink bollworm.

Emergence data for the pink bollworm indicated that a constant 33° C. was the most efficient in this study. Some mortality occurred at all temperatures and establishment of the newly hatched larvae in the medium in all the temperature regimes was similar; therefore the constant 30° or 33° would be desirable if a relatively efficient rearing regime was desired.

The preoviposition period of the pink bollworm was 1 to 22 days (table 36). At the programed 20° and 25° C. 90 percent were ovipositing on the ninth to the 11th day. However, at the 30° and 33° regimes 14 and 17 days, respectively, were required before 90 percent were ovipositing. These data indicate that the high temperatures effectively increased the preoviposition period.

Interference by high temperatures is also apparent in the reduced longevity and fecundity shown in table 37. The fecundity at 33° C. was actually only 10 percent of that at 20°. The oviposition period at 20° was relatively long; however, the data in table 38 indicate similar periods at 30° and 33°.

TABLE 35.—Development periods of pink bollworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969

Temperature (° C.) and sex	1st instar		2d instar		3d instar		4th instar		5th instar		6th instar	
	Larvae	Period Days	Larvae	Period Days	Larvae	Period Days	Larvae	Period Days	Larvae	Period Days	Larvae	Period Days
<i>Constant</i>												
20:												
♂	52	9.3 ± 1.5	52	4.4 ± 1.0	52	5.4 ± 1.4	52	15.6 ± 3.8	0	---	0	---
♀	59	9.7 ± 2.0	59	4.3 ± 1.3	59	5.5 ± 1.9	59	15.9 ± 4.1	0	---	0	---
25:												
♂	28	4.3 ± .7	28	4.4 ± 1.3	28	4.3 ± 1.2	28	9.8 ± 2.9	0	---	0	---
♀	25	4.4 ± .7	25	4.6 ± 1.8	25	4.8 ± 1.6	25	9.2 ± 2.4	0	---	0	---
30:												
♂	77	4.8 ± .8	76	2.2 ± .7	79	3.7 ± 1.1	80	9.1 ± 2.8	11	8.2 ± 3.4	0	---
♀	86	4.9 ± .8	86	2.3 ± .7	91	3.9 ± 1.1	91	9.4 ± 3.2	22	10.7 ± 4.7	3	8.7 ± 8.7
33:												
♂	54	5.0 ± 1.0	54	2.4 ± .6	54	4.3 ± 1.7	54	5.6 ± 2.2	36	6.3 ± 2.2	5	5.0 ± 2.8
♀	70	5.5 ± 1.3	70	2.5 ± 1.0	70	4.0 ± 1.4	70	5.6 ± 3.2	54	6.4 ± 2.1	13	6.7 ± 2.9
<i>Programed</i>												
20:												
♂	31	8.9 ± 1.4	31	3.5 ± .7	31	5.4 ± 1.7	31	13.9 ± 4.0	0	---	0	---
♀	30	9.2 ± 1.1	30	3.7 ± .7	30	5.1 ± 1.2	29	14.8 ± 4.1	0	---	0	---
25:												
♂	83	7.0 ± 1.5	83	4.8 ± 2.3	83	9.0 ± 4.2	81	9.2 ± 4.5	34	7.7 ± 1.7	0	---
♀	60	7.4 ± 1.5	60	5.0 ± 2.2	60	9.5 ± 3.6	60	9.9 ± 4.5	22	9.2 ± 3.8	1	1.0 ± 0

	7th instar		8th instar		9th instar		Pupal stage			Total			
	Larvae	Period	Larvae	Period	Larvae	Period	Pupae	Period	Adults	Period			
30: ♂	64	5.0 ± .9	64	2.3 ± 1.0	64	4.2 ± 1.9	61	9.0 ± 3.5	27	11.0 ± 3.4	5	16.6 ± 13.8	
♀	50	5.1 ± .9	50	2.3 ± 1.1	50	4.2 ± 2.0	46	9.2 ± 4.3	25	12.0 ± 6.2	10	9.6 ± 5.2	
33: ♂	39	6.1 ± 1.3	39	3.4 ± 1.1	40	3.6 ± 1.3	40	4.9 ± 2.6	35	7.6 ± 2.5	7	8.1 ± 2.1	
♀	44	6.2 ± 1.2	44	3.5 ± 1.1	49	3.9 ± 1.3	49	4.5 ± 1.8	44	7.3 ± 2.7	13	6.9 ± 3.3	
<i>Constant</i>													
20: ♂	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
♀	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
25: ♂	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
♀	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
30: ♂	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
♀	2	9.0 ± 1.4	0	-----	0	-----	0	-----	-----	-----	-----	-----	
33: ♂	1	4.0 ± 0	0	-----	0	-----	0	-----	-----	-----	-----	-----	
♀	0	-----	0	-----	0	-----	0	-----	-----	-----	-----	-----	
								Number	Days	Number	Days	Number	Days
								51	15.5 ± 1.7	51	50.1 ± 4.8	58	50.2 ± 6.0
								24	9.2 ± .6	24	31.4 ± 2.8	23	31.7 ± 4.0
								23	8.5 ± .7	23	28.6 ± 3.4	69	31.1 ± 6.6
								69	8.1 ± 1.0	69	28.9 ± 2.3	75	30.5 ± 3.4
								75	7.7 ± .7	75	31.1 ± 6.6	53	28.9 ± 2.3
								50	7.0 ± .6	50	28.9 ± 2.3	61	30.5 ± 3.4
								57	6.9 ± .6	57	30.5 ± 3.4		

TABLE 35.—Development periods of pink bollworm at various constant and programed temperatures in laboratory, Tucson, Ariz., 1969—Continued

Temperature (° C.) and sex	7th instar		8th instar		9th instar		Pupal stage		Total	
	Larvae	Period Days	Larvae	Period Days	Larvae	Period Days	Pupae	Period Days	Adults	Period Days
20: <i>Programed</i>	♂	0	0	0	0	0	30	12.5±1.0	30	44.4±6.2
	♀	0	0	0	0	0	24	12.0±1.1	25	45.0±4.7
25:	♂	0	0	0	0	0	72	10.0±1.0	72	43.4±4.8
	♀	0	0	0	0	0	50	10.0±1.8	50	44.7±4.5
30:	♂	0	0	0	0	0	42	8.3±1.1	42	34.2±7.2
	♀	5	6.6±5.0	2	6.5±2.1	1	32	8.4±2.1	32	40.2±13.3
33:	♂	1	10.0±0	0	0	0	31	8.5±.6	31	35.2±5.6
	♀	3	7.7±2.1	0	0	0	27	8.1±1.4	27	34.9±5.1

TABLE 36.—*Accumulated pink bollworms ovipositing at 4 programed temperatures*

Days after emergence	Oviposition at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2.....	0	0	0	4.8
3.....	12.5	10.3	0	11.9
4.....	20.0	33.3	6.1	16.7
5.....	32.5	53.8	16.3	16.7
6.....	47.5	64.1	26.5	19.0
7.....	52.5	76.9	42.9	23.8
8.....	65.0	89.7	57.1	28.6
9.....	77.5	89.7	67.3	33.3
10.....	82.5	94.9	77.6	40.5
11.....	90.0	94.9	83.7	52.4
12.....	92.5	94.9	87.8	61.9
13.....	95.0	94.9	87.8	66.7
14.....	100.0	97.4	89.8	73.8
15.....		100.0	91.8	76.2
16.....			91.8	83.3
17.....			93.9	90.5
18.....			98.0	92.9
19.....			98.0	97.6
20.....			98.0	97.6
21.....			98.0	100.0
22.....			98.0	
23.....			100.0	

TABLE 37.—*Longevity and fecundity of pink bollworm at 4 programed temperatures*

Daily mean temperature (° C.)	Males		Females		
	Adults	Longevity	Adults	Longevity	Fecundity
	<i>Number</i>	<i>Days</i>	<i>Number</i>	<i>Days</i>	<i>Eggs</i>
20.....	40	22.1 ± 7.4	40	27.8 ± 5.9	169.0 ± 135.0
25.....	39	10.3 ± 5.5	39	11.7 ± 6.9	61.0 ± 61.6
30.....	49	18.4 ± 5.8	49	19.9 ± 6.3	55.5 ± 60.8
33.....	42	13.9 ± 5.6	42	18.7 ± 6.5	16.3 ± 23.8

The mortality data in table 39 indicate that the pink bollworm was fairly long lived regardless of the temperatures to which it was subjected. As in the development and oviposition data certain individuals had exceedingly short or long lives, and the genetic plasticity of their population is evident.

TABLE 38.—*Accumulated eggs laid by pink bollworm at 4 programed temperatures*

Days after emergence	Eggs laid at indicated mean temperature (° C.)			
	20	25	30	33
	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
2.....	0	0	0	0.3
3.....	.9	5.6	0	.7
4.....	4.0	18.5	3.8	1.0
5.....	8.7	29.5	11.0	1.0
6.....	15.6	37.9	24.4	1.6
7.....	19.9	50.8	36.1	4.0
8.....	27.0	65.8	46.6	11.4
9.....	35.9	72.3	53.8	18.2
10.....	44.4	79.9	63.2	23.9
11.....	52.7	86.4	72.6	33.7
12.....	61.8	90.1	78.2	47.1
13.....	68.4	93.4	84.5	52.4
14.....	76.0	95.0	88.4	57.7
15.....	81.2	97.2	92.5	61.9
16.....	85.5	97.5	95.7	70.3
17.....	89.1	98.1	97.3	74.5
18.....	92.3	99.3	98.7	82.7
19.....	93.4	99.9	99.2	86.1
20.....	94.7	100.0	99.6	91.5
21.....	96.4	-----	99.6	95.5
22.....	97.4	-----	99.6	97.2
23.....	98.5	-----	99.8	98.5
24.....	99.0	-----	99.8	99.0
25.....	99.4	-----	99.9	99.0
26.....	99.7	-----	100.0	99.1
27.....	99.8	-----	-----	99.1
28.....	99.8	-----	-----	99.3
29.....	99.9	-----	-----	99.3
30.....	100.0	-----	-----	99.3
31.....	-----	-----	-----	99.3
32.....	-----	-----	-----	99.9
33.....	-----	-----	-----	100.0

TABLE 39.—*Accumulated mortality of pink bollworm at 4 programmed temperatures*

Days after emergence	Mortality at indicated mean temperature (° C.)							
	20		25		30		33	
	♂	♀	♂	♀	♂	♀	♂	♀
	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
1.-----	0	0	0	0	0	0	1.4	0
2.-----	0	0	0	0	0	0	5.5	0
3.-----	0	0	2.0	3.5	0	0	9.6	0
4.-----	0	0	2.0	8.8	1.1	2.0	11.0	1.3
5.-----	0	0	5.9	14.0	2.2	2.0	13.7	1.3
6.-----	0	0	11.8	21.1	2.2	3.1	13.7	2.7
7.-----	0	0	31.4	33.3	2.2	3.1	13.7	4.0
8.-----	0	0	43.1	50.9	3.3	4.1	13.7	5.3
9.-----	0	0	52.9	54.4	4.4	5.1	16.4	9.3
10.-----	0	0	64.7	56.1	9.9	6.1	20.5	9.3
11.-----	0	0	72.5	61.4	12.1	8.2	26.0	12.0
12.-----	2.9	0	80.4	64.9	18.7	9.2	32.9	18.7
13.-----	2.9	0	88.2	68.4	22.0	12.2	39.7	22.7
14.-----	2.9	0	88.2	71.9	24.2	16.3	52.1	28.0
15.-----	11.8	0	90.2	77.2	28.6	18.4	60.3	29.3
16.-----	14.7	2.9	92.2	77.2	31.9	25.5	64.4	38.7
17.-----	26.5	5.9	92.2	78.9	45.1	35.7	75.3	46.7
18.-----	26.5	5.9	96.1	80.7	49.5	42.9	86.3	50.7
19.-----	26.5	5.9	96.1	82.5	59.3	46.9	89.0	53.3
20.-----	32.4	5.9	96.1	82.5	65.9	57.1	93.1	60.0
21.-----	41.2	11.8	96.1	82.5	72.5	65.3	94.5	68.0
22.-----	50.0	11.8	96.1	87.7	76.9	71.4	95.9	70.7
23.-----	55.9	17.6	98.1	89.5	81.3	76.5	95.9	74.7
24.-----	64.7	17.6	98.1	93.0	86.8	79.6	97.3	81.3
25.-----	70.6	32.4	98.1	94.7	90.1	84.7	98.6	88.0
26.-----	73.5	32.4	98.1	96.5	93.4	86.7	100.0	90.7
27.-----	79.4	41.2	98.1	100.0	93.4	88.8	-----	92.0
28.-----	79.4	50.0	98.1	-----	94.5	88.8	-----	93.3
29.-----	79.4	64.7	98.1	-----	97.8	89.8	-----	93.3
30.-----	79.4	73.5	98.1	-----	100.0	92.9	-----	96.0
31.-----	82.4	76.5	98.1	-----	-----	94.9	-----	97.3
32.-----	85.3	79.4	98.1	-----	-----	96.9	-----	97.3
33.-----	88.2	85.3	98.1	-----	-----	98.0	-----	97.3
34.-----	97.0	85.3	98.1	-----	-----	99.0	-----	98.7
35.-----	97.0	94.1	98.1	-----	-----	99.0	-----	100.0
36.-----	97.0	97.0	98.1	-----	-----	99.0	-----	-----
37.-----	100.0	97.0	98.1	-----	-----	100.0	-----	-----
38.-----	-----	97.0	98.1	-----	-----	-----	-----	-----
39.-----	-----	97.0	100.0	-----	-----	-----	-----	-----
40.-----	-----	100.0	-----	-----	-----	-----	-----	-----

Guerra and Ouye (8) reported 15.7, 8.9, and 23.5 days for larval development, pupal development, and longevity, respectively, at 26.7° C. for a Texas strain of the pink bollworm. Shaver and Lukefahr (19) reported 16.2 and 9.2 days for the larval and pupal stages, respectively. Thus the larval development was slightly shorter than that of the insects reared at 25° in this study. However, the pupal period was similar. The longevity reported by Guerra and Ouye was nearly double that found for the pink bollworm in this study.

Noble (17) reported a longevity of 10 days to 2 weeks for a Texas strain of the moths in midsummer and this is comparable because the moths in our study were held in programmed regimes similar to the temperature in cottonfields. He noted a fecundity of 100 to 200 eggs per female, and in our study the moths held at the programmed 20° C. averaged 169 eggs. Noble gave an incubation period of 4 to 5 days in the summer and this is comparable to the data in table 34. He stated that the pink bollworm has four larval instars. Though this was the most common number of instars in our study, a considerable percentage had five or more instars. The added instars were particularly prevalent in the programmed regimes, which included relatively high temperatures. Thus in our study, with the exception of the extended larval period, the development, longevity, and fecundity data are comparable with those of the Texas strain of the pink bollworm.

DISCUSSION

A study such as described here frequently makes the scientist more aware of the difficulties confronting him as he develops 'predictive capability' for the population dynamics of insects.

The results of this study should make the researcher aware of the broadness of the gene pool in the development of individuals in an insect population. The pink bollworm data are a strong case in point. The genetic plasticity of this insect was apparent in its extended emergence period, its entering diapause at lower temperatures, and the broad variance of its fecundity. Though the other species also showed some variance among these characters, it was not so broad as that of the pink bollworm. However, these species had been in culture for several generations before this study was made and some selection probably occurred that narrowed the gene array in the gene pool. One must conclude that if an accurate 'predictive capability' is to be developed, the populations under study will necessarily be divided into proportions that reflect a similar genetic make-up in regard to the various facets of the insect's physiology.

Throughout this study we have been confronted with appreciable

variation in the development, fecundity, and longevity of the various species. However, if we consider that these variations are the results of a multifaceted system of biochemical and physiological reactions, a partial explanation is apparent. The data suggest that (1) the physiological systems associated with development may be more efficient at the lower temperatures and that (2) as the temperatures were increased the complexity of the systems entering into the total physiological reaction resulted in a reduced development rate.

The statement of Keister and Buck (13) on gas exchange is pertinent: “. . . in a system in which overall gas exchange almost certainly involves a complex of sequential and parallel oxygen-requiring and carbon dioxide-producing reactions differing in intrinsic temperature coefficients, temperature thresholds, denaturation temperatures and rates. It is illusory to apply analysis based on assumed single rate-limiting or ‘master reactions’.”

They have succinctly stated the quandary in which the insect physiologist finds himself in respect to unraveling the systems associated with respiration and thus all physiological activity. The physiologist, with his highly refined laboratory techniques in which the variables affecting a physiological system can be controlled to the maximum, should be envied by the insect ecologist attempting to project such physiological reactions to insect populations in the field. However, if the physiologist with his refined techniques is unable to effectively predict the end result of a multivariate physiological system, it is evident that the ecologist, with a much broader range of considerations, must accept considerable variability in his results.

In our study only the effect of temperature on insect development, longevity, and fecundity has been considered. The assumption was made that other factors were adequate. They would include, among many, nutrition, moisture, and light. In several of the species some differences associated with nutrition have been noted when comparisons were made with the results of other authors. Moisture was partially considered in the study of egg viability (Fye and Surber 7), and inducement of lowered fecundity and partial sterility by high temperatures was discussed (Fye and Poole 6). However, additional considerations in experimental work must be devoted to these matters if suitable predictive models are to be constructed.

Thus the insect ecologist projecting development data into field conditions will be confronted with many problems associated with the multitude of variables. However, until such time as the effects of these variables are studied and their interactions developed into quantitative predictive models, the entomologist will be severely handicapped in his efforts to predict and assess the potential of insect populations and damage.

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