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Abstract
Effects of temperature on development, survival, and fecundity of boll weevil, *Anthonomus grandis grandis* Boheman, were assessed at 10, 11, 12, 15,20,25,30,35,45, and 46 °C; 65% relative humidity; and a photoperiod of 13:11 (L: D) h. The mortality of boll weevil immature stages was 100% at 12°C and decreased to 36.4% as the temperature increased to 25°C. When the temperature increased from 30 °C to 45 °C, the mortality of weevils also increased from 50.1% to 100%. From 15°C to 35°C, the bollweevilpreimaginal development rate was linearly related to temperature. The average development time of total boll weevil immature lifestages decreased 3.6-fold and the preovipositional period decreased 3.3-fold when the temperature was increased from 15°C to 30°C. The lower threshold for development was estimated at 10.9, 6.6, 7.0, and 9.0 °C for eggs, larval, pupal, and total immature stages, respectively, with total thermal time requirement to complete immature stages of 281.8 DD (degree day) (15°C) and 247.8 DD (35 °C). At 1LC and 46°C, weevil females did not oviposit. Longevity of adult females decreased 4.6-fold with increasing temperatures from 15°C to 35°C. Fecundity increased with increasing temperatures up to 30°C and significantly decreased thereafter. These findings will be useful in creating a temperature-based degree-day model for predicting the occurrence of key life stages in the field. An accurate predictor of a pest's development can be very important in determining sampling protocols, timing insecticide applications, or implementing an integrated pest management control strategy targeting susceptible life stages.

Keywords
Anthonomus grandis grandis, boll weevil, temperature, development, mortality, fecundity

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Temperature-dependent development and reproduction of the boll weevil (Coleoptera: Curculionidae)

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Abstract Effects of temperature on development, survival, and fecundity of boll weevil, *Anthonomus grandis grandis* Boheman, were assessed at 10, 11, 12, 15, 20, 25, 30, 35, 45, and 46℃; 65% relative humidity; and a photoperiod of 13:11 (L: D) h. The mortality of boll weevil immature stages was 100% at 12℃ and decreased to 36.4% as the temperature increased to 25℃. When the temperature increased from 30℃ to 45℃, the mortality of weevils also increased from 50.1% to 100%. From 15℃ to 35℃, the boll weevil preimaginal development rate was linearly related to temperature. The average development time of total boll weevil immature lifestages decreased 3.6-fold and the preovipositional period decreased 3.3-fold when the temperature was increased from 15℃ to 30℃. The lower threshold for development was estimated at 10.9, 6.6, 7.0, and 9.0℃ for eggs, larval, pupal, and total immature stages, respectively, with total thermal time requirement to complete immature stages of 281.8 DD (degree day) (15℃) and 247.8 DD (35℃). At 11℃ and 46℃, weevil females did not oviposit. Longevity of adult females decreased 4.6-fold with increasing temperatures from15℃ to 35℃. Fecundity increased with increasing temperatures up to 30℃ and significantly decreased thereafter. These findings will be useful in creating a temperature-based degree-day model for predicting the occurrence of key life stages in the field. An accurate predictor of a pest's development can be very important in determining sampling protocols, timing insecticide applications, or implementing an integrated pest management control strategy targeting susceptible life stages.

Key words *Anthonomus grandis grandis*, boll weevil, temperature, development, mortality, fecundity
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Introduction

Identifying and understanding the factors that affect the development, survival, and oviposition behavior of boll weevil, *Anthonomus grandis grandis* Boheman, in cotton, *Gossypium hirsutum* L., is important in designing and implementing successful control strategies. Temperature plays a critical role in determining the rate of development and survival of insect species (Hunter & Pierce, 1912; Isley, 1932; Cole & Adkisson, 1982). Models of temperature-dependent development are useful in predicting insect activity and population dynamics in the field. Effects of temperature alone and in relation to other abiotic and biotic factors are well documented for predicting boll weevil overwintering survival and spring emergence (Parajulee *et al*., 1996,1997; Westbrook *et al*., 2003), diapause induction and control (Brazzel & Newsom 1959; Earle & Newsom 1964; Lloyd *et al*., 1967; Wagner & Villavaso, 1996;

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Spurgeon & Raulston, 1998; Rummel *et al*., 1999), and on boll weevil mortality in fallen infested cotton fruit on the soil surface (Fye & Bonham, 1970; Greenberg *et al*., 2003, 2004). However, publications about the effects of temperature on boll weevil development, reproduction, and survival during the cotton growing season are limited. The studies of Parrott *et al*. (1970) and Roach (1973) were conducted at one temperature, while Bacheler & Bradley (1975) evaluated the effects of temperature on development and mortality only of boll weevil eggs. The objectives of this study were to determine development and survival of immature boll weevils, and the low and high temperature developmental thresholds, which could be used to construct a degree-day model.

Materials and methods

Boll weevil culture and cotton squares

To help avoid potentially confounding effects of developmental history, we reared all experimental insects in the laboratory. Adult boll weevils were reared from larval-infested squares (flower buds) collected from cotton fields in the Lower Rio Grande Valley of Texas during summer 2002. Infested squares were held in screen cages (20 cm × 20 cm × 20 cm) in an environmental chamber at 27 ± 1℃, 65% RH, and a photoperiod of 13: 11 (L: D) h. Temperature and humidity were monitored by a Fisherbrand Traceable Relative Humidity Meter with temperature readout (Fisher Cat. No.11-661-12, Control Company, Friendswood, TX). When ≈ 60% of boll weevil larvae had pupated, the pupae were harvested and placed in Petri dishes (150 mm × 20 mm, 15−20 pupae in each) containing a shallow layer of moistened vermiculite, and subsequently returned to the environmental chamber until adult eclosion. Newly eclosed adults were collected, weighed, and sexed by the method of Sappington and Spurgeon (2000). Males were marked with a red paint pen on the right elytron. Only adults weighing between 10−15 mg on the day of the eclosion were used in this study. During a 5-day conditioning period to allow mating, 10 males and 10 females were held in 150 mm × 20 mm Petri dishes with a 40 mm diameter circular screened hole in the lid under the same conditions as for larval rearing. Each Petri dish was supplied with a cotton wick saturated with distilled water, and weevils were provided with uninfested, greenhouse-grown squares, 7−10 mm in diameter at the widest part, and with intact bracteoles for feeding, at a rate of five squares per weevil per day. We assumed all females were mated by the end of the conditioning period.

Experimental design

Boll weevil development, survival, and reproduction were examined at 10.0, 11.0, 12.0,15.0, 20.0, 25.0, 30.0, 35.0, 40.0, 45.0, and 46.0℃ in environmental chambers (Percival Scientific, Boone, IA).

Immature mortality

Life tables were constructed (Harcourt, 1969) for boll weevil at different temperatures, using the methodology of Sterling *et al*. (1990) for mortality assessment. Cohorts of 168, 363, 660, 388, and 604 infested squares, each containing a single egg puncture, were held at 15, 20, 25, 30 and 35℃, respectively. The number of eggs hatching, number of larvae developing to the pupal stage, and the number of pupae developing to pre-emergent adults (i.e. adults still within the square) were recorded for each of the five temperatures. All recorded or calculated parameters were arranged as follows: x−stage (eggs, 1st, 2nd, and 3rd instars, pupae, pre-emergent adults) at which the sample was taken; l_x−the number living at the beginning of the stage noted in the x column; d_x−the number dying within an age interval stated in the x column; %−percent of individuals starting the stage; and q_x−mortality rate (d_x/l_x). A second-order polynomial model was fitted by regression to describe the relation between mortality and temperature for each life stage (SAS Institute, 1999).

Development

Infested squares containing a single egg puncture were used to evaluate developmental time. The time of egg deposit until egg hatch was recorded as the development time for eggs. Development time of different instars was determined to the nearest day by checking daily for moulted exoskeletons and measuring head capsule width (Parrott *et al*., 1970). Pupal duration was calculated as the number of days from pupal formed to an adult emerging inside the cotton fruit. Pre-emergent adult duration was the number of days required by adults to successfully emerge from the fruit after moulting from the pupal stage. Squares with single egg punctures were periodically collected and assigned to developmental time treatments until a total of 25, 50, 100, 100, and 50 were collected for assignment to the 15℃, 20℃, 25℃, 30℃, 35℃ treatments, respectively. Lower developmental threshold temperatures (T_o) for preimaginal development were estimated by weighted linear regression on mean developmental rates (reciprocal of mean developmental times, weighted by the number of individuals) against temperature, i.e., $y = a + bT_o$, where y is development rate, the a and b are constants, and $T_o = a/$

b. In the figures, T_o is the *x*-intercept. The number of degree-days (*DD*) needed for development was calculated as $DD = (T - T_o)D$, where *T* is the temperature tested (℃), and *D* is the mean development time in days at temperature *T* (Tshernyshev, 1996).

Adult life span and fecundity

After the 5-day conditioning period, five groups of 20, 20, 20, 25, and 22 randomly selected boll weevil females were individually placed in Petri dishes (150mm × 20 mm) with a ventilation window as described above, and were held at 15, 20, 25, 30 and 35℃, respectively. Each female was provided with a daily supply of five uninfested greenhouse-grown squares, 7−9 mm in diameter, with intact bracteoles. Squares were replaced daily until the weevil died. Squares were examined each day for feeding and oviposition punctures. Unsealed punctures were considered feeding punctures, while oviposition (sealed) punctures were distinguished by a frass plug and/or a waxy substance closing either the puncture or its periphery (Everett & Ray, 1962). The total number of punctures (feeding and oviposition) in each square constituted boll weevil puncturing activity (Everett & Earle, 1964). The egg-puncture ratio (ratio of sealed to total punctures) constituted oviposition activity (Everett & Earle, 1964). Sex ratio was estimated (Sappington & Spurgeon, 2000) from five cohorts of periodically collected squares containing a total of 53, 52, 51, 51, and 53 eggs maintained at 15, 20, 25, 30 and 35℃, respectively. To prevent cannibalism by siblings, only squares containing a single egg puncture were selected.

Life table parameters

An estimate of boll weevil population growth rate was obtained for females at each temperature by calculating life table statistics. For each treatment, the jackknife program of Hulting *et al*. (1990) was used to calculate net reproductive rate (R_o), the intrinsic rate of natural increase (r_m), the finite capacity of increase (λ, defined as the number of times a population multiplies itself per unit of time), mean generation time (*T*), doubling time (*DT*) of the population, and the total progeny produced per female.

Statistical analyses

Data for preovipositional period, life-time fecundity, adult longevity, total development time, and the percentage of female progeny were subjected to one-way analyses of variance (ANOVA) using PROC GLM (SAS Institute 1999) to determine the significance of temperature effects. Whenever significant *F*-values were obtained, means were separated using the Tukey-Kramer test via the LS Means statement in SAS (SAS Institute, 1999). Percentage and proportion data were arcsine-square root transformed before statistical analysis (Sokal & Rohlf, 1995). Results are presented as untransformed means. The respective relationships between the temperature and the number of egg punctures, feeding punctures, egg puncture ratio, and the proportion of squares attacked (punctured) by each female were assessed by linear regression using PROC GLM. The number of sealed punctures per day for each weevil was subjected to a repeated measures analysis, with time, temperature, and their interaction as factors, using PROC MIXED of SAS (Littell *et al*., 1997). Homogeneity of female boll weevil survival curves among different temperatures was tested with the LIFETEST procedure of SAS (SAS Institute, 1999). Subsequently, the closed testing procedure was used to discriminate among survival curves of different treatments (Hommel, 1988). The population growth index (*GI*) was calculated by dividing the percentage survival of immatures by developmental time (Sétamou *et al*., 1999).

Results

Immature mortality

Overall, the mortality of boll weevil immature stages was 100% at 12 ℃ and decreased to 36.4% as the temperature increased to 25 ℃. Then as temperatures increased from 25 ℃ to 45 ℃, mortality gradually increased to 100% (Table 1). The egg stage was more vulnerable to low and high temperatures, and mortality was less in later stages. At 12 ℃, 40 ℃, and 45 ℃, boll weevil females oviposited, but the eggs did not hatch, while at 11 ℃ and 46 ℃ they failed to oviposit. The effect of temperature on mortality at each immature life stage was described by a second-order polynomial function (Fig.1A−H). Temperature significantly affected mortality of egg ($P = 0.013$), total larva instars ($P = 0.005$), pupal ($P = 0.027$), and total immature ($P = 0.049$) stages, but not preemergent adults ($P = 0.613$). Temperature also affected boll weevil death rate (q_x) [$q_x = d_x$ (mortality) / l_x (survival)]. The polynomial model, $y = 0.01x^2 \times 0.495x + 6.3$, described a significant relationship for temperature and death rate ($F = 62.3$; df = 2, 2; $P = 0.016$).

Development

Temperature also affected immature development (Table 2; egg, $F = 478.7$; df = 4, 320; $P = 0.001$; total larva instars, $F = 356.3$; df = 4, 320; $P = 0.001$; pupal, $F = 99.3$; df = 4,

Table 1 Age-specific mortality (%) of boll weevils reared at different constant temperatures.

Age intervals†	Temperature (℃)									
	11	12	15	20	25	30	35	40	45	46
n‡	0	27	168	363	660	388	604	52	16	0
EGG		100.0	35.1	21.5	15.0	12.1	22.2	96.2	100.0	
L1			7.7	2.2	1.8	4.9	8.9			
L2			11.2	10.2	10.0	14.0	25.0			
L3			12.0	8.8	7.0	10.0	18.0			
PUP			6.0	4.0	2.0	7.0	15.0			
PEA			0.0	0.6	0.6	2.1	0.0			
Immature stage	0	100.0	72.0	47.3	36.4	50.1	89.1	96.2	100.0	0

†Age intervals are: egg (EGG), larval first instar (L1), second instar (L2), third instar (L3), pupal (PUP), and pre-emergent adult (PEA), ‡Initial numbers of tested individuals (eggs).

320; $P = 0.001$; total immature stages, $F = 2404.4$; df = 4, 320; $P = 0.001$). Boll weevils achieved complete development from egg to adult emergence at temperatures that ranged from 15℃ to 35℃. Mean development time of immature stages was longest at 15℃, and shortest at 35℃. Developmental time of each life stage significantly decreased as temperature increased. Males developed significantly faster than females at 3.6 days (15℃) and at 1.9 days (35℃) (Table 3). Between 15℃ and 35℃, the preimaginal development rate (1/development time) was linearly related to temperature. Based on a linear regression analysis, lower developmental thresholds were estimated as 10.9℃, 6.6℃, 7.0℃, and 9.0℃ for egg, larval, pupal, and total immature stages, respectively (egg, $F = 21.9$; df = 1, 3; $P = 0.018$; larval, $F = 16.2$, df = 1, 3; $P = 0.028$; pupal, $F = 174.7$; df = 1, 3; $P = 0.001$, total immature stage, $F = 89.9$; df = 1, 3; $P = 0.002$) (Fig. 2A −D). Total thermal times to complete immature stages required 281.8 DD (15℃) and 247.8 DD (35℃). Degree-days estimates for eggs, larvae, pupae are described in Table 4.

Sex ratio, longevity, and oviposition

The number of eggs oviposited per female per day significantly increased with temperature ($F = 3.9$; df = 1, 105; $P = 0.05$), except at 35 ℃ when oviposition was not significantly different from that at 15 ℃ (Table 5). The fewest eggs per day were oviposited at 15 ℃ (0.347 ± 0.028) and 35 ℃ (0.351 ± 0.087) while the highest number of eggs per female per day was recorded at 30 ℃ (7.931 ± 0.734). We observed that at 11 ℃ and 46 ℃ weevil females ceased oviposition. The temperature significantly and positively affected the average numbers of feeding punctures ($F = 35.8$; df = 1, 105; $P = 0.001$), and the proportion of squares attacked per female per day ($F = 16.5$; df = 1, 105; $P = 0.001$). On average, 16.4% ± 0.8% of squares were punctured at 15℃, while 58.2% ± 5.5%, 77.0% ± 4.1%, 77.1% ± 2.7%, and 44.4% ± 4.0% of squares were punctured at 20, 25, 30 and 35℃, respectively. The temperature did not significantly affect the ratio of egg punctures to total punctures (egg plus feeding punctures) ($F = 1.1$; df = 1, 105; $P = 0.307$) (Table 5).

Temperatures did not significantly influence offspring sex ratio ($F = 1.1$; df = 4, 20; $P = 0.384$) (Table 6). The preovipositional period significantly decreased from 11.7 ± 0.4 to 2.7 ± 0.2 days when the temperature increased from 15 to 35℃ ($F = 206.6$; df = 4, 70; $P = 0.001$). Adult female longevity tended also to increase with temperature. Females held at 15℃ lived significantly longer than those held at 20℃ or higher ($F = 12.8$; df = 4, 102; $P = 0.001$) (Table 6). Lifetime oviposition also increased with temperature, with the highest (185.6 ± 20.1 egg punctures) at 25℃ ($F = 38.6$; df = 4, 102; $P = 0.01$) (Table 6). The percentage of days on which females oviposited during their lifetime increased with increasing temperature to 30℃, then decreased at 35℃ ($F = 37.8$, df = 4, 66; $P = 0.001$). On average, females which were held at 15℃ oviposited on 19.2% ± 2.6 % of their lifetime days. Females which were held at 20℃, 25℃, 30℃, and 35℃ laid eggs on 70.2% ± 8.7%, 85.1% ± 2.3%, 83.4% ± 1.9%, and 21.3% ± 3.2% of their lifetime days, respectively. Approximately 90.0, 87.5, and 81.8% of females at 20℃, 30℃, and 35℃ oviposited at least once. All females at 15℃ and 25℃ oviposited at least once. Both time (day) ($F = 8.6$; df = 63, 1521; $P < 0.001$) and temperature ($F = 4.6$; df = 4, 63; $P < 0.001$) significantly affected the number of eggs oviposited. In addition, the time by temperature interaction was significant ($F = 2.7$; df = 190, 1521; $P < 0.001$), indicating that the temporal pattern of oviposition activity differed among temperatures. The oviposition activity curves at the different temperatures were characterized by a pattern of plateauing, peaking, and declining, but with differences in the timing and duration of those phases (Fig. 3).

Survivorship of female weevils (percentage of weevils remaining alive each day) varied significantly among temperatures ($\chi^2 = 34.3$; df = 4; $P < 0.001$), with that of

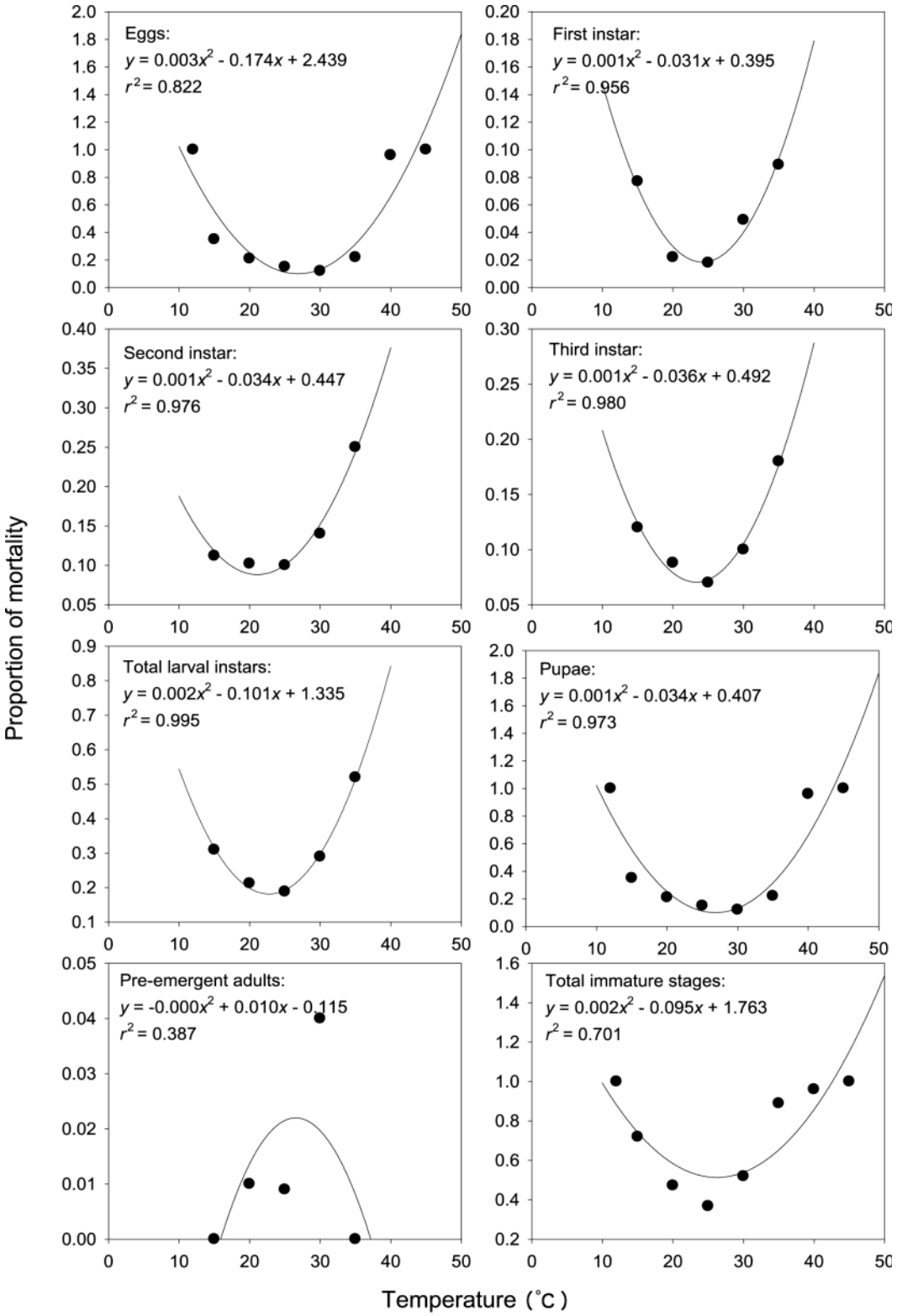

Fig. 1 Age-specific mortality (%) of boll weevil stages at different temperatures: A, egg; B, 1st instar; C, 2nd instar; D, 3rd instar; E, total larval stage; F, pupa; G, pre-emergent adult; H, total immature stages.

Table 2 Mean (± SE) developmental time (days) of boll weevil life stages at different temperatures.

℃	EGG	L1	L2	L3	L1−3	PUP	PEA	Immatures
15	12.1 ± 0.5 a (25)	8.0 ± 0.5 a (25)	6.4 ± 0.4 a (25)	8.1 ± 0.4 a (25)	22.5 a	5.4 ± 0.4 a (25)	7.2 ± 0.5 (25)	47.2 ± 0.5 a (25)
20	4.3 ± 0.1 b (50)	3.1 ± 0.2 b (50)	2.8 ± 0.2 b (50)	7.3 ± 0.3 a (50)	13.2 b	3.4 ± 0.3 b (50)	6.7 ± 0.3 (50)	27.6 ± 0.3 b (50)
25	2.1 ± 0.1 c (100)	1.8 ± 0.1 c (100)	1.9 ± 0.1 c (100)	4.0 ± 0.3 b (100)	7.7 c	2.0 ± 0.2 c (100)	4.2 ± 0.2 (100)	16.0 ± 0.2 c (100)
30	1.9 ± 0.1 c (100)	1.4 ± 0.1 c (100)	1.8 ± 0.1 c (100)	3.2 ± 0.2 c (100)	6.4 d	1.4 ± 0.2 d (100)	3.4 ± 0.1 (100)	13.1 ± 0.1 d (100)
35	1.7 ± 0.1 c (50)	1.6 ± 0.1 c (50)	1.7 ± 0.1 c (50)	2.8 ± 0.1 c (50)	6.1 d	1.2 ± 0.1 d (50)	2.9 ± 0.2 (50)	11.9 ± 0.2 e (50)

Numbers in parentheses are total of replications to each stage at studied temperatures. Mean (±SE) within a column followed by different letters are significantly different (Tukey honestly significant difference, $P < 0.05$).

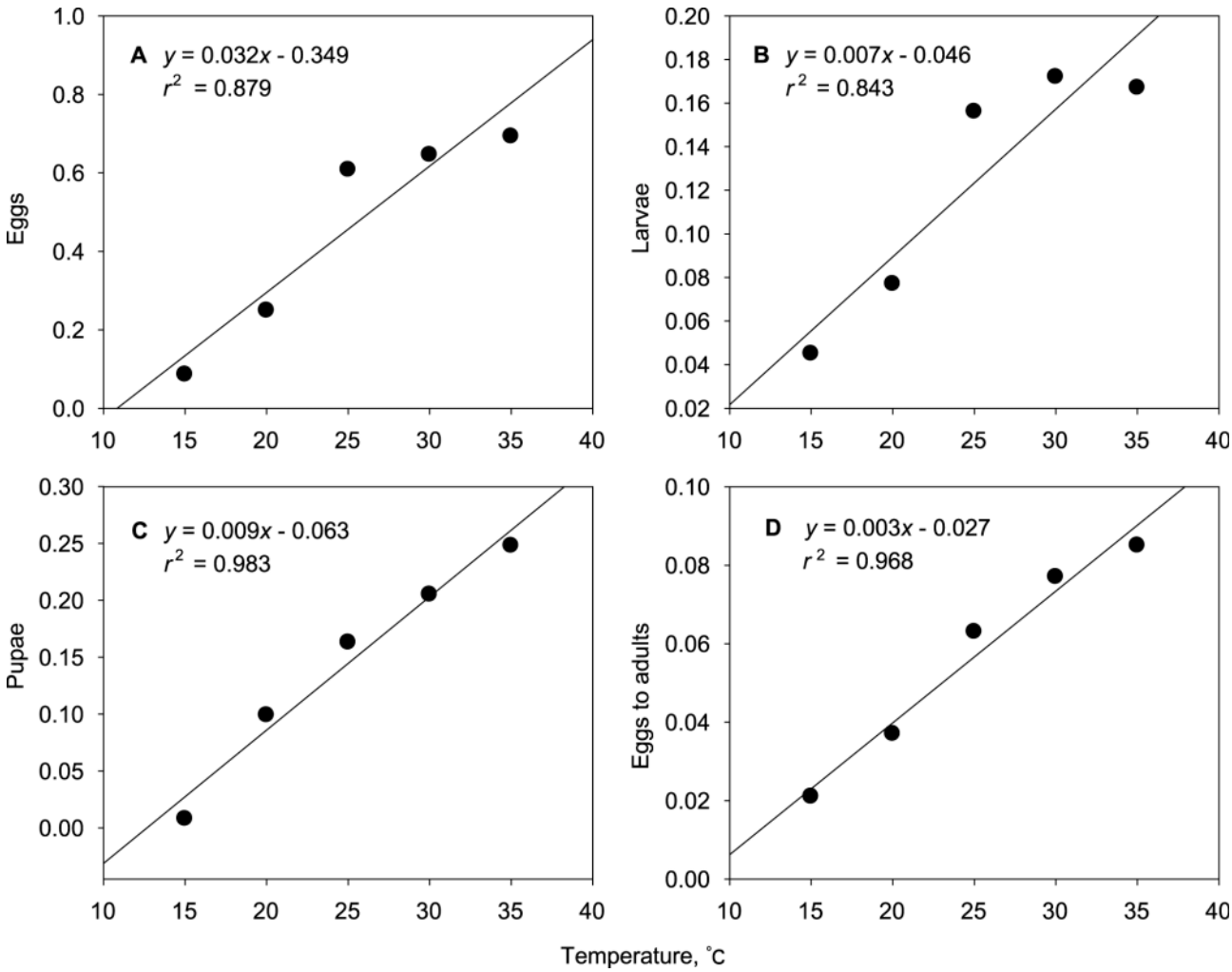

Fig. 2 Temperature-dependent developmental rate of boll weevil life stages: A, egg; B, total larval stage; C, pupa; D, egg to adult.

Table 3 Effects of different temperatures on development time (Mean ± SE) of boll weevil females and males.

Temperature ℃	Development time (days)		
	Females	Males	*t* -test
15	48.0 ± 2.7	44.4 ± 2.2	$t = 3.2$; df = 18; $P = 0.004$
20	29.7 ± 2.1	26.2 ± 2.5	$t = 5.3$; df = 48; $P = 0.001$
25	17.1 ± 1.4	14.9 ± 1.3	$t = 5.6$; df = 48; $P = 0.001$
30	14.2 ± 1.2	11.1 ± 1.0	$t = 9.6$; df = 48; $P = 0.002$
35	13.1 ± 1.3	11.2 ± 0.7	$t = 6.8$; df = 58; $P = 0.001$

Table 4 Degree-days required for boll weevil stages to complete development in the laboratory under different constant temperatures.

Temperature (℃)	Egg	Larval	Pupal	Total immature stages
15	49.6	189.0	43.2	281.8
20	39.1	176.9	44.2	260.2
25	29.6	141.7	36.0	207.3
30	36.3	149.8	32.2	218.3
35	41.0	173.2	33.6	247.8

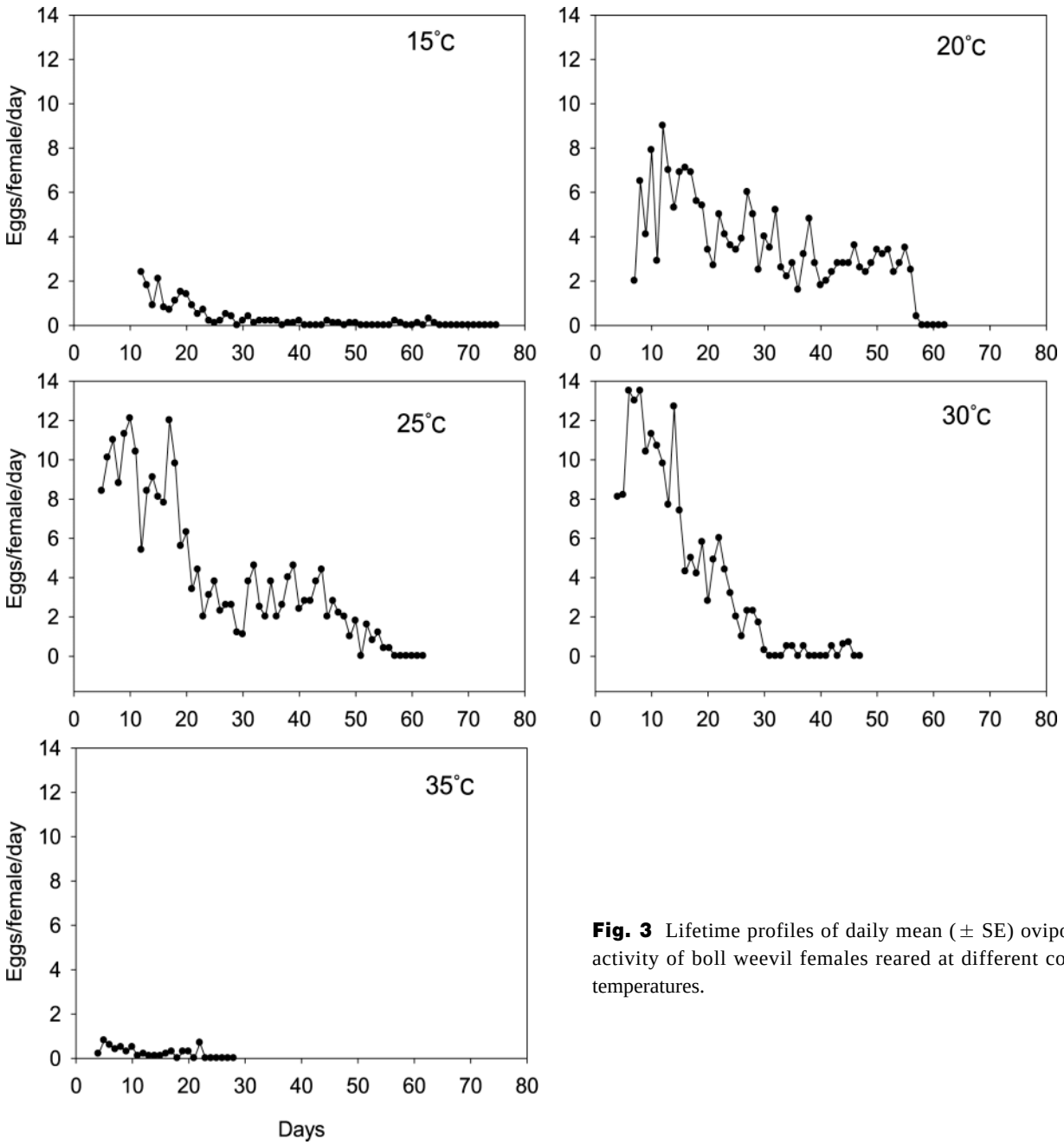

Fig. 3 Lifetime profiles of daily mean (± SE) oviposition activity of boll weevil females reared at different constant temperatures.

Table 5 Regression parameters relating temperature (T) to egg punctures (EP), feeding punctures (FP), ratio of egg punctures to total punctures (R), and squares attacked (SA) per boll weevil female per day.

Relation	*n*	Slope (SE)	P_{slope}	Intercept (SE)	$P_{intercept}$	R^2
T-EP	107	0.099 (0.050)	0.050	0.889 (1.321)	0.503	0.036
T-FP	107	0.197 (0.033)	0.001	−0.130 (0.869)	0.881	0.254
T-R	107	− 0.003 (0.003)	0.307	0.384 (0.067)	0.001	0.010
T-SA	107	1.469 (0.361)	0.001	18.156 (9.529)	0.059	0.136

Table 6 Effects of temperature on boll weevil sex ratio, preoviposition period, lifetime oviposition, and longevity.

Temperature, (℃)	Percentage female	Preoviposion period (d)	Oviposition (egg punctures)	Longevity (D)
15	45.2 ± 3.0 a	11.7 ± 0.4 a	19.4 ± 1.6 c	57.1 ± 1.0 a
20	50.0 ± 3.5 a	6.3 ± 0.2 b	120.6 ± 17.1 b	37.8 ± 3.4 b
25	52.9 ± 3.7 a	4.4 ± 0.2 c	185.6 ± 20.1 a	36.0 ± 3.4 b
30	50.9 ± 0.9 a	3.5 ± 0.2 cd	154.8 ± 13.4 ab	28.3 ± 7.6 b
35	49.1 ± 1.0 a	2.7 ± 0.1 d	3.5 ± 0.7 c	12.3 ± 1.3 c

Means (± SE) within a column followed by different letters are significantly different (Tukey honestly significant difference, $P < 0.05$).

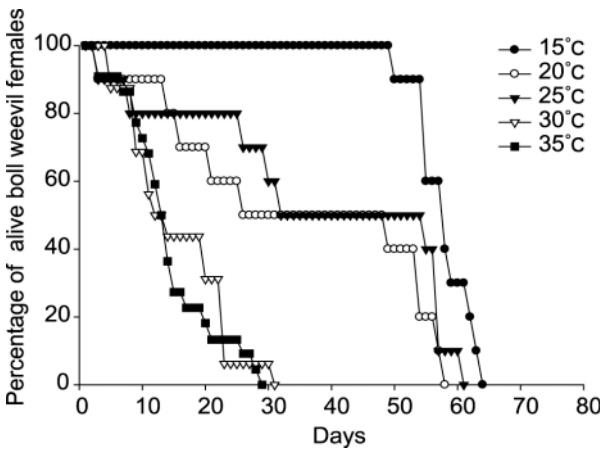

Fig. 4 Survivorship (percentage of live weevils per day from total used in the test) profiles of boll weevil females reared at different constant temperatures.

females held at 15℃ being the highest (Fig. 4). The percentage of boll weevil females remaining alive at 15℃ was significantly higher than that at 25℃ ($\chi^2 = 4.6$; df = 1; $P = 0.03$). Percent survival at 25℃ was not significantly different than that at 20℃ ($\chi^2 = 0.9$; df = 1; $P = 0.34$), but was significantly higher than that at 30℃ ($\chi^2 = 5.6$; df = 1; $P = 0.018$) and 35℃ ($\chi^2 = 8.9$; df = 1; $P = 0.003$). Survivorships of weevil females held at 30℃ and 35℃ were not significantly different ($\chi^2 = 1.9$; df = 1; $P = 0.2$).

The values of life table statistics calculated for boll weevil females varied with temperature (Table 7). The populations of boll weevils maintained at 25℃ and 30℃ were predicted to grow at significantly higher mean constant exponential rates (r_m) than those maintained at 15℃ and 20℃. Life table calculations indicated that boll weevil populations maintained at 25℃ or 30℃ would increase 39.3-fold or 25.2-fold, respectively, each generation (R_o), a rate

Table 7 Life table statistics of boll weevil females as affected by temperature (values in parentheses are 95% confidence intervals).

Temperature (℃)	R_o	r_m	λ	T	DT
15	1.7	0.009	1.01	58.0	67.8
	(1.08−2.27)	(0.003−0.015)	(1.00−1.02)	(56.7−59.2)	(7.9−127.6)
20	38.0	0.084	1.09	43.3	8.2
	(16.10−59.82)	(0.070−0.100)	(1.07−1.10)	(38.5−48.4)	(6.8−9.6)
25	66.8	0.146	1.16	28.9	4.8
	(32.90−100.65)	(0.120−0.170)	(1.13−1.19)	(24.3−33.7)	(3.9−5.6)
30	42.8	0.182	1.20	20.7	1.2
	(27.62−57.93)	(0.160−0.200)	(1.17−1.22)	(18.8−22.6)	(3.4−4.2)
35	0.5	−0.026	0.97	27.2	−26.9
	(0.28−0.71)	[−0.040−(−0.010)]	(0.96−0.98)	(23.6−30.8)	[−41.5−(−9.3)]

R_o, net reproductive rate; r_m, intrinsic rate of increase; λ, finite rate of increase; T, mean period over which progeny are produced (d); DT, doubling time of the population (d).

significantly higher than that at 15℃. The doubling time (DT) of weevils maintained at 35℃ could not be estimated because the population was not increasing (r_m is not different from zero).

When boll weevil females were held at 25 or 30℃, the population growth index (*GI*) was 6.0-fold higher than the *GI* of females held at 15℃, 4.2-fold higher than that at 35℃, and 2-fold higher than that at 20℃ (Fig. 5). A significant treatment effect on *GI* was indicated by a peak function with a gaussian model of 3 parameters:

$$y = a \cdot e^{\{-0.5 \cdot [\ln(x - x_o)/b]2\}},$$

where $a = 4.4$, $b = 5.1$, and $x_o = 26.7$ ($F = 41.7$; df = 2, 4; $P = 0.02$; $R^2 = 0.977$).

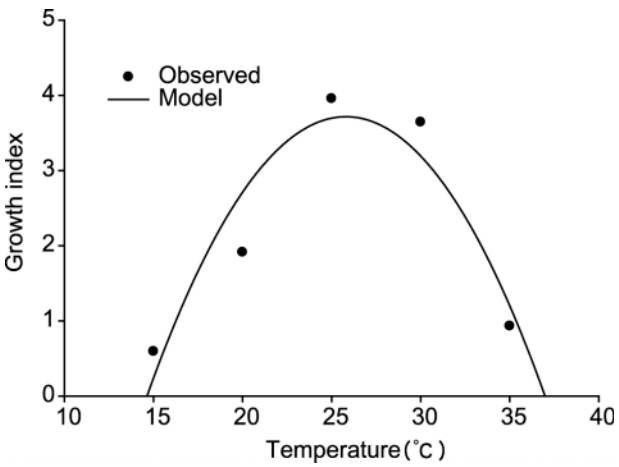

Fig. 5 Population growth indices of boll weevil females reared at different constant temperatures.

Discussion

Ecologically sound pest management should be based on pest ecology, which can be described and understood in part by life table statistics and phenology. Estimation of life table parameters under a given temperature regimen when taking into account the total life history, that is development rate, mortality, and fecundity, permits estimation of temperature-dependent growth potential of insects. Temperature-dependent development and reproduction have been described for numerous coleopteran species (Fan *et al*., 1992; Lapointe, 2000; Lan *et al*., 2004). Effects of temperature on development and mortality of boll weevil immature stages were conducted by Hunter and Pierce (1912), Grossman (1930), and Isley (1932) on wild weevil strains fed with cotton squares, but their results were highly variable and difficult to compare with each other and results of our study. These authors did not control certain factors that can influence responses during an experiment (geographic diversity among weevils obtained, fruit size, precise temperature control). In the early 1970s, researchers (Fye *et al*., 1969; Cole, 1970; Parrott *et al*., 1970; Roach, 1973) continued the studies of temperature effects with weevils reared on an artificial diet, which were genetically different from field populations.

The tendency of increased mortality and reduced development to adulthood with increasing temperature was overlooked in other studies. Cole and Adkisson (1982) reported that only 4.7% of a cohort reared at 15.6℃ reached the adult stage, but there was not significant difference among survival rates of weevils at temperatures ranging from 18.3℃ to 32.2℃ (the total survival to adult ranging from 35.8% to 48.3%). At a constant temperature of 35℃, only 43.6% of eggs hatched, and neonate larvae did not survive longer than 2−3 days (Cole & Adkisson, 1982). Bacheler *et al*. (1975) found that the optimum developmental (14.5 d) and survival (84.5%) temperature for a North Carolina boll weevil strain was 30℃, and the survival (76.7%) and developmental time (13.8 d) for immature stages at 34℃ were not significantly different. The authors did not calculate a developmental threshold, but they suggested that 34℃ approached the upper threshold for development. Mortality began to increase at that temperature and acceleration in rate of development slowed dramatically (Bacheler *et al*., 1975). Isley (1932) demonstrated that developmental time of boll weevils from eggs to adults declined from 35 to 12 days with an increase of temperature from 18℃ to 34℃. Fye and Bonham (1970) estimated that the lower temperature threshold for boll weevil development was 13℃ and the upper was 38℃. Fye *et al*. (1969) calculated from a regression model a hypothetical developmental threshold for boll weevil of 12.9℃. Development at 35℃ suggested a slowing of undetermined physiological reactions by excessive heat (Fye *et al*., 1969). The authors above noted that the highest survival was at 20℃, and as temperature increased, developmental time decreased and mortality increased.

Our study showed that boll weevil adult longevity and oviposition also were affected by temperature. Longevity of adult females decreased 4.6-fold with increasing temperatures from 15℃ to 35℃. Fecundity increased with increasing temperatures up to 30℃ and significantly decreased thereafter. Temperature has multiplicative effects, and their joint impacts on population growth can be substantial. For example, the number of female progeny produced per female, estimated by oviposition, proportion surviving and percent female progeny, was 328.4-fold higher at 25℃ than that at 35℃; 25-fold higher than that at 15℃; and 1.6-fold higher than those at 20℃ and 30℃. Spurgeon and Raulston (1998) indicated a marked tem-

perature dependence on reproductive development, with both low-and high-temperature inhibition at observed temperature extremes. Cole and Adkisson (1981) reported that the total number of eggs laid increased as temperature increased. The greatest mean number of eggs were produced by boll weevil females at 29.5℃ (253.5 eggs). No eggs were deposited at 15.6℃, and temperatures above 29.5℃ also suppressed egg-laying. In west Tennessee, insectary-reared boll weevils that emerged in July averaged 4.5 eggs/female (mean air temperature of 25℃), and only 0.5 eggs/female in September (21.6℃) (Cole & Adkisson, 1981).

The information presented forms the basis for developing a more complete understanding of boll weevil development. These data will be useful in creating a temperature-based degree-day model for predicting the occurrence of key life stages in the field. An accurate predictor of a pests' phenology can be very important in developing sampling protocols, timing insecticide applications, or implementing an integrated pest management control strategy targeting susceptible life stages.

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Notes

This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation by the USDA for its use.

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