Low Temperature Effects on Development, Mortality, Fecundity, and Viability of the Ectoparasitoid *Catolaccus grandis* (Hymenoptera: Pteromalidae)[1]

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ABSTRACT The low temperature threshold for development of *Catolaccus grandis* (Burks) was 12°C for eggs, 11.5°C for larvae, and 9.5°C for pupae. The developmental time for male or female parasitoids increased by 4.6 to 5.3 times and the preovipositional period of females increased from 2.2 to 9.3 days when the temperature was reduced from 30°C to 15°C. The number of degree-days to complete development was 225.6 for females and 197.2 for males. The mean duration of emergence for *C. grandis* ranged from 2.6 days at 27°C - 30°C to 5.7 days at 20°C. Reduction of the temperature from 25°C to 15°C increased the death rate of *C. grandis* 2.3 times and reduced emergence of parasitoid females by 77.8%. The percentage of emergence of females from pupae with the black thorax-yellow abdomen held at temperatures lower than 15°C for 20 days or more and pupae with yellow color held at 5°C for 10 or more days decreased significantly compared with females from pupae held at 25°C. Storage of pupae at 20°C or lower resulted in adult females with reduced fecundity. However, the sex ratio of the progeny was not significantly affected.

KEY WORDS *Catolaccus grandis*, low temperature threshold, biological parameters, degree-days, developmental time, storage

Catolaccus grandis (Burks) is a highly effective biological control agent against the boll weevil. *Anthonomus grandis grandis* (Boheman), on cotton (King et al. 1993). The known distribution of this tropical-ectoparasitoid ranges from El Salvador to northwestern Mexico (Cross and Mitchell 1969). The larvae of *C. grandis* develop externally on third-instar boll weevils (Johnson et al. 1973). The adult female may deposit 1 to 5 eggs within cavities of cotton squares and bolls containing boll weevil larvae. First-instar parasitoids are cannibalistic, and only one *C. grandis* develops per host (Morales-Ramos and Cate 1993).

[1] Mention of a proprietary product does not constitute an endorsement by the USDA. Received 19 November 1995; Accepted for publication 04 August 1996.

Augmentative releases of *C. grandis* females have controlled the boll weevil in small plots in the Lower Rio Grande Valley of Texas (Summy et al. 1992, 1993, 1994, 1995) and in commercial cotton fields (R. J. Coleman, personal communication). However, mass rearing of entomophagous insects has been identified as a main constraint to successful commercialization for augmentative releases of natural enemies (King 1993). *Catolaccus grandis* has been successfully reared in the laboratory on third-instar boll weevils (Cate 1987, Morales-Ramos et al. 1992, Roberson and Harsh 1993). The objective of a mass-rearing program is to produce the maximum quantity of quality-assured individuals by predetermined dates at a minimal cost. Current rearing procedures for *C. grandis* are expensive and only about one-third of the weevil larvae exposed produce female parasitoids. Efficient mass rearing of the parasitoid requires definition of the optimal conditions for its growth, development, and reproduction.

Studies on the developmental time, rate of increase, and fecundity of *C. grandis* at different temperatures have been published by Morales-Ramos and Cate (1992a, 1992b, 1993). However, the lowest temperature used by these authors was 18°C. No attempt was made by Morales-Ramos and Cate to determine the low temperature threshold for development.

The objectives of this study were to determine the effects of different temperatures, especially low temperatures, on *C. grandis* developmental time, preovipositional period, death rate, fecundity and the sex ratio of progeny; emergence rate and duration of emergence in days; low temperature threshold for development of the different preimaginal stages; and to apply the degree-day model in establishing the degree-days required to complete development.

Materials and Methods

Catolaccus grandis used in the study were derived from individuals imported from southern Mexico in 1987. The colony has been under continuous laboratory culture since that time (Summy et al. 1992). The parasitoids were maintained at 26 ± 1°C, 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h on third-instar boll weevils enclosed in Parafilm® capsules. The capsules were constructed by impressing the surface of Parafilm® sheets between 2 aluminum molds, one having 0.8-cm diam holes, and the other with 1.4-cm aluminum pegs, resulting in Parafilm® sheets, each containing 120 to 132 capsules. One host larva was placed inside each capsule, and then the sheet containing the host larvae was sealed with another flat sheet of Parafilm® (Cate 1987). The parasitoids were reared in transparent Plexiglas® cages measuring 40×40×26 cm (Morales-Ramos et al. 1992).

Temperature and photoperiod were controlled inside environmental chamber (Percival® 1-30BLL). Temperature was constantly monitored by Miller and Weber® thermometers. Humidity was controlled by saturated solution of sodium nitrate (100g of $NaNO_2$ were added to 100 ml of H_20, Winston and Bates 1960) thereby maintaining a relative humidity of 65.5% at 20°C, 64% RH at 25°C, and 63% at 30°C.

Developmental time. Third-instar boll weevils encapsulated in Parafilm® were exposed to *C. grandis* females (790 weevils with 400 10-d-old parasitoid females per cage) for 4 h. The parasitoids in Parafilm® capsules were allowed to

develop to adult stage inside a cylindrical paper carton (18 cm × 16 cm) modified with an exit hole on top connected to a large (15 cm diam) Petri dish. Groups of immature parasitoids were held at five different temperatures: 15, 20, 25, 27, 30 ± 1°C, 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h until they completed development (100 for each of the selected temperature). The developmental time of males or females from egg to adult were recorded for all temperatures.

Duration of emergence. Groups of immature parasitoids were held at conditions described above until they completed emergence (400 for each of the selected temperature, 4 replications with 100 individuals per each). The number of adults emerging daily was recorded. The median (Me) and mode (Mo) of emergence distribution were calculated as described by Schefler (1980) and Sokal and Rohlf (1981).

Preovipositional period. Five groups of 10 newly-emerged female *C. grandis* were individually placed in Petri dishes (15 cm × 1.5 cm) with a 5-cm diam screened (nylon) window on top. Each group was held at 1 of 5 different temperatures (15, 20, 25, 27, 30°C), 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h. Each female parasitoid was provided with a daily supply of 10 third-instar boll weevils. The weevils encapsulated in Parafilm® were inspected daily until the parasitoid started to oviposit.

Death rate. The parasitization of third instars was as described in the section on developmental time. The number of parasitized host and number of eggs in each cell with a boll weevil larva were recorded. They were then held at 4 different temperatures: 15, 20, 25 and 30 ± 1°C (250 parasitized encapsulated weevils per temperature), 65 ± 5% RH, and a photoperiod 12:12 (L:D) h. The number of eggs hatching, number of larvae developing to the pupal stage, and number of pupae emerging to adult were recorded for each of the four temperatures. The death rate (K) (Varley et al. 1974) was calculated using the formula:

$$K = (\text{In NE} - \text{In NL}) + (\text{In NL} - \text{In NP}) + (\text{In NP} - \text{In NA})$$

where In NE is the logarithm of the number of eggs, In NL is the logarithm of the number of larvae, In NP is the logarithm of the number of pupae, and In NA is the logarithm of the number of adults.

Lower temperature threshold of development. Eggs, larvae, and pupae (100 individuals per stage) of *C. grandis* were held at temperatures from 14°C to 8°C. A sample of each life stage (20 individuals) was visually inspected every 5 days for evidence of development. If no development was evident, they then were placed at 25°C to determine their ability to continue development whether the *C. grandis* were alive or dead. The conditions in which development stopped but the parasitoids remained alive were recorded. The number of degree days (Yakhontov 1964,Varley et al. 1974) needed for development of female or male *C. grandis* was calculated using the formula;

$$X = (T - c)^{*}t$$

where **T** is the temperature at which the parasitoid developed (°C), **c** is the low temperature threshold of development (°C), and **t** is developmental time (days) at temperature 'T'.

Fecundity and progeny sex ratio. Two different colors of pupae were used in this experiment, based on age-dependent color changes in pupae of *C. grandis* (Morales-Ramos and Cate 1992a): the dark yellow (younger pupae) and the black thorax-yellow abdomen (older pupae). The female pupae were obtained from single exposure (cohort) to a cage of 400 parasitoid females (10 d old). The pupae were exposed to 9 different storage conditions: 5, 10, and 15°C for 10, 20 and 30 days (per 30 pupae in each group). The environmental chambers were maintained in continuous darkness at 65 ± 5% RH. After these periods, the pupae were transferred to a chamber with a constant temperature of 25°C, 65% RH, and 12:12 (L:D) h photoperiod to complete development. A control group of pupae with dark yellow or black thorax-yellow abdomen were maintained at 25°C, 65 ± 5% RH, and photoperiod of 12:12 (L:D) h. Another control group of pupae from each color was allowed to develop at 20°C, 65 ± 5% RH, and photoperiod of 12:12 (L:D) h. The experiment was replicated 3 times. Percentage emergence of wasps from each group was determined.

Ten mated females from each treatment were selected and individually confined in Petri dishes to determine fecundity. These females were held at 25° C, 65 ± 5% Rh, and photoperiod 12:12 (L:D) h. Each female was provided daily with water, honey, and 15 encapsulated third-instar boll weevils. The number of eggs oviposited by each female was recorded daily during the first 10 days of oviposition. Sex ratio, number of fertile females, and number of females producing only male progeny were recorded. The number of females produced per female was calculated.

Statistical analyses were conducted using analysis of variance (ANOVA) and Tukey's studentized range test (SAS Institute 1988).

Results and Discussion

This paper is the first attempt to determine low temperature threshold of development for *C. grandis*. Eggs did not hatch at 12°C; larvae and pupae did not develop at 11.5°C and 9.5°C, respectively.

The mean developmental time from eggs to adults at different constant temperatures is presented in Tables 1 and 2. The developmental time of male or female *C. grandis* increased 4.6 to 5.3 times (from 9.8 to 52.3 days for males; from 12.1 to 55.2 days for females) when the temperature decreased from 30°C to 15°C.

The length of preovipositional period increased from 2.2 to 9.3 days when temperature decreased from 30°C to 15°C ($F = 113.3$; df = 4, 45; $P < 0.05$) (Table 2).

The estimated of degree-days required to complete development by *C. grandis* were 225.6 ± 11.6 for females and 197.2 ± 20.3 for males.

The accuracy of the estimated degree days required to complete development of *C. grandis* was tested against the experimental data reported by Morales-Ramos and Cate 1993 (Table 3). The results show no significant differences between experimental and estimated data (for females, $F = 0.151$; df = 1, 192, $P = 0.698$; for males, $F = 0.077$; df = 1, 108; $P = 0.782$).

Table 1. Mean developmental period of *C. grandis* males at different temperature regimes.

Temperatures, °C	Developmental time, days	Degree-days
30	9.8 ± 1.3 a	186.2 a
27	11.1 ± 1.1 a	177.6 a
25	13.3 ± 1.3 b	186.2 a
20	25.2 ± 2.5 c	226.8 a
15	52.3 ± 1.6 d	209.2 a

Means (± SD) in each column followed by different letters are significantly different at the 5% level, as determined by Tukey's studentized range test.

Table 2. Mean developmental and preovipositional period of *C. grandis* females at different temperature regimes.

Temperatures, °C	Developmental time, days	Degree-days	Preovipositional period, days
30	12.1 ± 1.0 a	229.9 a	2.2 ± 0.8 a
27	13.5 ± 1.1 a	216.0 a	3.1 ± 0.6 a
25	15.6 ± 1.1 b	218.0 a	4.2 ± 0.8 b
20	27.2 ± 1.7 c	244.0 a	7.0 ± 0.9 c
15	55.2 ± 1.6 d	220.0 a	9.3 ± 1.2 d

Means (± SD) in each column followed by different letters are significantly different at the 5% level, as determined by Tukey's studentized range test.

Table 3. Comparison of developmental time of *C. grandis* determined by Morales-Ramos and Cate 1993 and estimated by the degree-day model.

Temperatures, °C	Developmental time, days	
	experimental	estimated
	Males*	
18	32.3	28.2
24	15.3	15.2
27	13.0	12.3
30	11.9	10.4
	Females**	
18	38.2	32.3
21	22.5	22.6
24	18.8	17.4
27	15.0	14.1
30	13.3	11.9

* $F = 0.077$, df = 1,108, $P = 0.782$
** $F = 0.151$, df = 1,192, $P = 0.698$

The mean (± SD) duration of emergence of *C. grandis* ranged from 2.6 ± 0.5 days at 27°C - 30°C to 3.8 ± 0.4 and 5.7 ± 0.4 days at 25 and 20°C, respectively. Temperatures of 27°C or 30°C resulted in the shortest period of emergence. At temperatures of 20°C or 25°C, emergence was distributed over a significantly longer period of time ($F = 139.4$; df = 2, 37; $P < 0.05$). The medians were 43.5 and 46.0% (1st day emergence) at 27°C and 30°C, respectively, compared with medians of 6.0 and 16.0% (1st day emergence) at 20°C and 25°C, respectively. The modes were 42.5 and 45.5% (1st day emergence) at 30°C and 27°C, respectively, compared with 8.0 and 13.0% (1st day emergence) at 20°C and 25°C, respectively (Table 4).

Physical factors, especially temperature, can affect the efficiency of *C. grandis* rearing. We observed that reducing the temperature from 25°C to 15°C increased death rate of *C. grandis* by 2.3-fold and reduced the percentage of emergence of parasitoid females by 77.8% (Table 5).

There was no significant reduction in numbers of adults emerged from female pupae with black thorax-yellow abdomen held for 10 days at 5, 10 or 15°C, from female pupae of yellow color held for 10 to 20 days at 10°C or for 10, 20, 30 days at 15°C compared with emergence from female pupae held at 25°C (control group). Adult emergence was significantly lower in the other

Table 4. Period of emergence of *C. grandis* at different constant temperatures.

Temperatures °C	Distribution of emergence, % per day					
	1-st	2-nd	3-rd	4-th	5-th	6-th
			Median*			
30	46.0	52.0	0	–	–	–
27	43.5	50.5	5.5	–	–	–
25	16.0	41.5	32.5	10.0	–	–
20	6.0	18.5	25.5	28.5	16.5	4.5
			Mode**			
30	42.5	50.0	2.5	–	–	–
27	45.5	48.0	2.5	–	–	–
25	13.0	43.0	33.0	8.0	–	–
20	8.0	17.0	23.0	33.0	13.0	2.5

* Median: measurement which has 50% of the members of the distribution above it and 50% below it (Schefler 1980).

** Mode: value represented by the greatest number of individuals (Sokal and Rohlf 1981).

Table 5. Survival of *C. grandis* at different temperature regimes.

Temper., °C	Death rate (K)	Proportion of females from parasitized hosts	Survival from egg to adult,%
30	1.21 ± 0.4 a	0.43 ± 0.1 a	32.2 ± 12.7 a
25	1.02 ± 0.3 a	0.55 ± 0.2 b	38.2 ± 12.2 a
20	1.66 ± 0.5 b	0.25 ± 0.1 c	19.5 ± 10.1 b
15	2.34 ± 0.3 c	0.12 ± 0.09 d	8.5 ± 4.6 c

Means (±SD) in each column followed by different letters are significantly different at the 5% level, as determined by Tukey's studentized range test.

experimental groups of female pupae than in the control group (Table 6). We did not observe adult emergence when female pupae of both colors were held for 30 days at 5°C. The younger pupae (dark yellow color) were less affected by colder temperatures than the older pupae (black thorax - yellow abdomen). From 47.4 to 51.6% parasitoids emerged and died before the end of the term storage from female pupae of different ages held for 30 days at 10°C. We observed 11.1 to 46.2% females emerged from the dark yellow colored pupae before the end of the 20 or 30 days holding period at 15°C. The rate of emergence from black thorax-yellow abdomen pupae was 8.3 to 89.5% before end of the 10 to 30 days holding period at 10°C, and it was 79% when they were held for 20 days at 15°C. Morality was between 4.4 to 16.1 times higher in female pupae of the black thorax-yellow abdomen or yellow color held for 20 days at 5°C, 30 days at 10°C, and 20 or 30 days at 15°C, than in female pupae held at 25°C.

Storage of female *C. grandis* pupae at temperatures lower than 25°C significantly reduced their fecundity ($F = 10.8$, df = 7, 60; $P < 0.05$). The highest fecundity was observed in the control group held at 25°C (13.9 ± 5.7 eggs/female/day) compared with 8.3 ± 0.6 eggs/female/day for female parsitoids held at 20°C and 1.7 ± 1.7 to 9.4 ± 2.6 eggs/female/day by females from other experimental groups (Table 7). From 33.3 to 44.4% of the females held at temperatures below 15°C produced only male progeny.

The different conditions tested did not significantly affect the sex ratio of progeny. Female *C. grandis* in the control group held at 25°C produced 67.4 ± 7.4% female progeny. This percentage was not significantly different from that observed for females held at the other conditions ($F = 0.7$, df = 6, 33; $P = 0.625$) (Table 7). Only 50% of the females held at 15°C for 30 days during the pupal stage were fertile. Females held at 10°C for 15 and 20 days during the pupal stage showed 88.9 and 90.0% fertility, respectively.

Figure 1 graphically shows the additive effect of low temperature on the number of females produced per female per day. These showed that holding female pupae of *C. grandis* at temperatures below 20°C reduced the number of female progeny from 2.0 to 8.4 times compared with the control group (25°C).

Studies on high temperature threshold of development for *C. grandis* were described by Morales-Ramos and Cate (1992b, 1993). Temperature stress at 35°C manifested in the form of reduced fecundity, egg survival, longevity, progeny survival, and prolonged preovipositional period. At 40°C, *C. grandis* was unable to reproduce probably as a result of a heat-induced sterility.

Entomophagous insects are often more vulnerable to abiotic factors than are their insect hosts (Bodenheimer and Schiffer 1952). However, the boll weevil is no more tolerant than *C. grandis* to low or high temperatures. Fye et al. (1970) claimed overwintered adult weevils became active when the temperature reached the threshold for development of immature stages (13°C), although it is not clear whether they meant walking or flying activity. Jones and Sterling (1979) observed that temperature thresholds for flight and walking averaged 14.0°C and 2.6°C, respectively. Boll weevils fed on cotton squares (flower buds) began to experience developmental stress at 34°C (Bacheler et al. 1975, Sharpe and Hu 1980). In fact, developmental rates of the boll weevil resemble those of *C. grandis* at the same temperatures (Bacheler et al. 1975), showing that the

Table 6. Emergence of *C. grandis* at different temperature regimes.

Conditions		Percentage of emergence from pupae*	
Temp., °C	Term, days	yellow colored	black thorax
25**	–	97.5 a	
5	10	70.0 ± 15.8 b	92.5 ± 6.4 ab
	20	38.9 ± 5.6 bc	0.0 c
	30	0.0 d	0.0 c
10	10	81.3 ± 1.3 ab	96.0 ± 6.4 a
	20	85.0 ± 1.4 ab	76.0 ± 1.6 d
	30	61.1 ± 5.6 bc	79.2 ± 7.2 bd
15	10	90.0 ± 16.5 a	92.6 ± 6.4 ab
	20	91.7 ± 14.4 a	76.0 ± 1.6 d
	30	89.6 ± 0.6 a	–

* Each column followed by different letters are significantly different at the 5% level, as determined by Tukey's studentized range test.
** Term days – until development was complete.

Table 7. Influence of low temperature on the reproductive potential of *C. grandis*.*

Temperatures, °C	Term, days	Fecundity, eggs/female/day	Percentage female progeny
25**	–	13.9 ± 5.7 a	67.4 ± 7.4 a
20**	–	8.3 ± 0.6 b	60.6 ± 0.7 a
5†	10	9.4 ± 2.6 b	62.6 ± 4.2 a
	20	0	–
10†	10	8.0 ± 3.5 b	67.0 ± 2.9 a
	15	3.7 ± 2.7 c	62.3 ± 3.7 a
	20	3.6 ± 2.4 c	57.6 ± 19.8 a
	30	3.3 ± 3.9 c	–
15†	10	8.7 ± 2.1 b	69.9 ± 20.5 a
	20	7.1 ± 1.7 b	62.7 ± 8.0 a
	30	1.7 ± 1.7 c	–

* Means (± SD) in each column followed by different letters are significantly different at 5% level, as determined by Tukey's studentized range test.
** term days-until development was complete
† evaluation at 25°C

life cycle of this parasitoids and its host are remarkably synchronic. This suggests that both species have physiological adaptations to similar ranges of temperatures. However, when the boll weevil feeds on cotton bolls (fruits), its developmental times increase significantly (Sharpe and Hu 1980). Consequently, the boll weevil is, theoretically, more vulnerable to parasitism when it is developing on cotton bolls because of the longer potential time of exposure.

Bracon mellitor Say, the most commonly-occurring native parasite of boll weevil, starts experiencing developmental stress at temperatures approaching 38°C (Barfield et al. 1977). This parasitoid is more tolerant to high temperatures than *C. grandis*.

In summary, the low temperature threshold for development of *C. grandis* was 12°C for eggs, 11.5°C for larvae, and 9.5°C for pupae. The number of degree-days required to complete development of *C. grandis* were 225.6 for females and 197.2 for males.

The preovipositional period increased from 2.2 days at 30°C to 9.3 days at 15°C.

The distribution of emergence in time at 27° and 30°C was compact, while at low temperatures distribution of emergence in time was longer. At lower temperatures the death rate of *C. grandis* was higher.

Holding female pupae of *C. grandis* at temperatures below 20°C reduced the number female progeny from 2.0 to 8.4 times compared with the control group held at 25°C.

Understanding the relationships of temperature to development, mortality, fecundity, and viability of *C. grandis* is significant in improving systems for mass rearing. The results of this study are biotechnological substantiation for mass rearing of parasitoid and using them to increase quantity and quality of production.

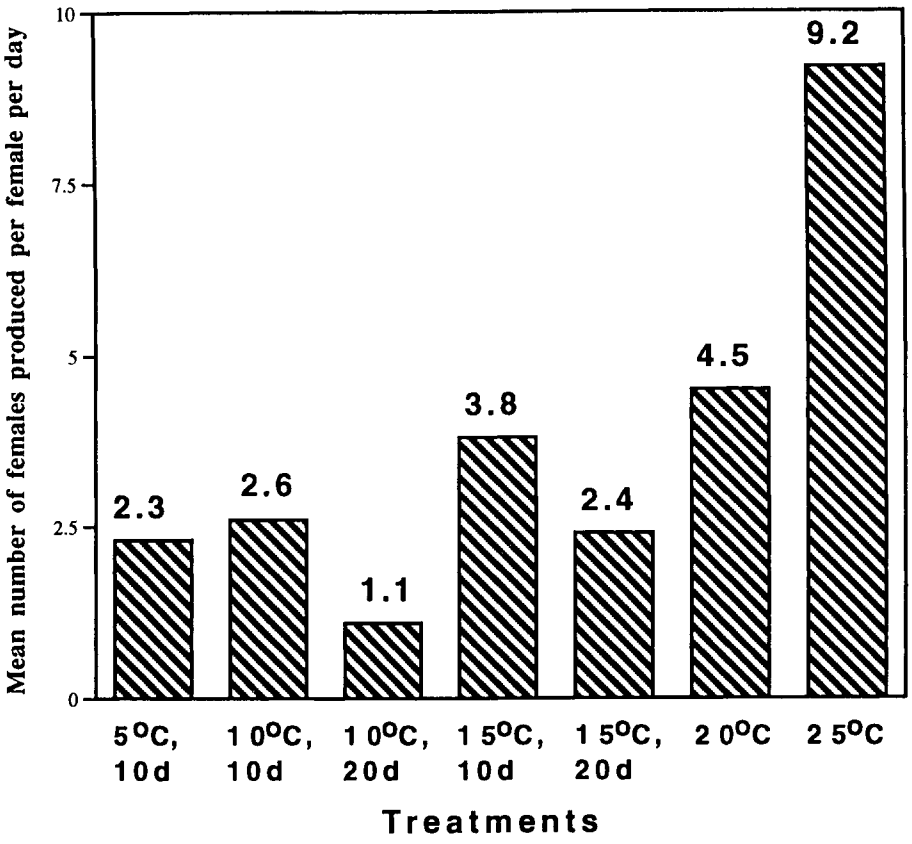

Fig. 1. The influence of different low temperatures and holding period for female pupae on number of *C. grandis* females produced per female.

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