Effect of Temperature on the Life History of the Mealybug *Paracoccus marginatus* (Hemiptera: Pseudococcidae)

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ABSTRACT Effect of temperature on the life history of the mealybug *Paracoccus marginatus* Williams & Granara de Willink (Hemiptera: Pseudococcidae) was investigated in the laboratory. *P. marginatus* was able to develop and complete its life cycle at 18, 20, 25, and 30 ± 1°C. At 15, 34, and 35°C, the eggs hatched after 27.5, 5.9, and 5.5 d of incubation, respectively, but further development of the first-instar nymphs was arrested. No eggs hatched at 37°C. The developmental time for egg to adult was the longest at 18°C for both males and females. Approximately 80–90% of the eggs survived between 20 and 30°C. The highest fecundity was at 25°C with each female producing an average of 300 eggs. Adult longevity, and preoviposition and oviposition periods increased with decreasing temperature up to 25°C. The proportion of females was ≈42% at 25°C and was between 70 and 80% at 18, 20, and 30°C. Adult males and females required 303.0 and 294.1 degree-days (DD), respectively, to complete their development. The estimated minimum temperature thresholds for the adult males and females were 14.5 and 13.9°C, respectively. For adult males, the estimated optimum and maximum temperature thresholds were 28.7 and 31.9°C; and for adult females, they were 28.4 and 32.1°C, respectively. The ability of *P. marginatus* to develop, survive, and reproduce successfully between 18 and 30°C suggests that it has the capability to develop and establish in areas within this temperature range.

KEY WORDS development, survival, reproduction, thermal constants, development thresholds

The mealybug *Paracoccus marginatus* Williams & Granara de Willink (Hemiptera: Pseudococcidae) is a significant pest of many tropical and subtropical fruits, vegetables, and ornamental plants (Miller and Miller 2002), and it has a wide host range, including *Carica papaya* L. (papaya), *Persea americana* P. Mill. (avocado), *Citrus* spp. (citrus), *Solanum melongena* L. (eggplant), *Hibiscus* spp. (hibiscus), *Plumeria* spp. (plumeria), and *Acalypha* spp. (acalypha) (Walker et al. 2006). First described by Williams and Granara de Willink (1992) and redescribed by Miller and Miller (2002), *P. marginatus* is thought to be native to Mexico and Central America (Miller et al. 1999). It is an important pest in the Caribbean and has recently been introduced into the United States (Miller and Miller 2002) and several Pacific islands, such as the Republic of Palau (Muniappan et al. 2006), Guam (Meyerdirk et al. 2004), and Hawaii (Heu et al. 2007). The first

discovery of *P. marginatus* in the United States was in Manatee, Palm Beach, and Broward counties of Florida in 1998 (Miller and Miller 2002). It potentially poses a threat to numerous agricultural products in Florida as well as similar crops grown in other states (Walker et al. 2006). Temperature is one of the important environmental factors that could influence the distribution and abundance of *P. marginatus* in the United States.

The ability of an insect to develop at different temperatures is an important adaptation to survive in various climatic conditions (tropical, subtropical, and temperate), which is important in predicting insect outbreaks (Mizell and Nebeker 1978). Temperature is one of the most important and critical of the abiotic factors that can affect insect development as well as influence the population dynamics of insect pests and their natural enemies (Huffaker et al. 1999). The rate of insect development is affected by the temperature to which the insects are exposed (Campbell et al. 1974). Insects require a certain amount of heat units (degree-days) to develop from one life stage to the next (Gordan 1999). Determining the effect of temperature on the development, survival, and reproduction of *P. marginatus* and estimating its thermal requirements will be useful in predicting its possible

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distribution and abundance in the United States. The purpose of this study is to investigate the effect of temperature on the life history of *P. marginatus* and to estimate its thermal requirements.

Materials and Methods

Insect Rearing. *P. marginatus* was initially collected from a papaya field in Homestead, FL. Mealybug colony was maintained using sprouted red potatoes in an environmental growth chamber (Percival I-36LL, Percival Scientific Inc., Perry, IA) set at 25° ± 1°C, 65 ± 2% RH, and a photoperiod of 14:10 (L:D) h. Before sprouting, potatoes (Ryan Potato Company, East Grand Forks, MN) were washed and air-dried. Each week, 35 sprouted potatoes were infested with *P. marginatus* ovisacs (each potato with three to five ovisacs) collected from the previously infested potatoes selected from the colony to maintain the mealybug population. Rearing methods were similar to methods used by Amarasekare et al. 2008.

Development and Survival. Development and survival of *P. marginatus* was assessed under eight temperatures: 15, 18, 20, 25, 30, 34, 35, and 37°C, all ± 1°C. Fully expanded hibiscus (*Hibiscus rosa-sinensis* L.) leaves were used as the host tissues. Leaves were excised from 1-yr-old container-grown plants (Garden Depot, Miami, FL) maintained outdoors under overhead irrigation and without any pesticide applications. The experimental arena consisted of a 9-cm-diameter petri dish. A 0.6-cm-diameter hole was created in the bottom of the petri dish by using a heated cork borer. A newly expanded hibiscus leaf (5–10 d old and ≈6 cm in length) selected from the upper leaf canopy (with a 4-cm-long stem) was placed in to each petri dish with the stem inserted through the hole in the bottom of the petri dish. A lid was placed on top to avoid mealybug escape. Each petri dish containing a hibiscus leaf was placed on a 162-ml plastic soufflé cup (Georgia Pacific Dixie, Atlanta, GA) so that the stem below the petiole was immersed in water. For each temperature, 35 gravid females (each from different infested potato and ≈ 30–35 d old) were collected from the colony to obtain eggs. Forty-eight hours before the experiment, gravid females (kept individually on hibiscus leaves prepared as described above) were transferred to environmental growth chambers (TCI model, Environmental Growth Chambers, Chagrin Falls, OH) at the test temperatures, 65 ± 2% RH, and a photoperiod of 14:10 (L:D) h to acclimatize them for experimental temperatures. Eggs were collected within 24 h of oviposition. Ten eggs (same age) were collected from a single female and placed into each experimental arena (hibiscus leaf arranged in a petri dish) by using a (no. 000) paintbrush (American Painter 4000, Loew-Cornell Inc., Englewood Cliffs, NJ). The experimental arenas were placed into each environmental chamber set at the specific temperature. For each temperature, there were 35 petri dishes (replicates) containing 10 eggs. Petri dishes were checked daily for egg hatch and shed exuviae to identify emergence of nymphal instars.

When eggs started to hatch, the lights were turned off for 72 h to encourage the first-instar nymphs (crawlers) to settle on the leaves. The number of days to each instar, percentage of survival, and number of adult males and females were recorded. The sex of each individual was determined during the latter part of the second instar when males change color from yellow to pink. At this point, developmental times and survival of males and females were recorded separately.

Reproduction and Adult Longevity. Newly emerged virgin females and males obtained from the first experiment at 18, 20, 25, and 30 ± 1°C were used to assess reproduction. These were the only experimental temperatures, at which *P. marginatus* was able to develop and complete its life cycle. Adult females <24 h old were placed individually in the experimental arenas. Each female was paired with two to three newly emerged adult males. There were 35 females (replicates) for each temperature. The number of days until preoviposition (number of days from adult emergence to oviposition) and oviposition (number of days from beginning to end of oviposition), number of eggs laid, and adult mortality were recorded. Sex ratio was calculated as a proportion (percentage) of females.

Developmental Thresholds and Thermal Constants. The linear degree-day model (thermal summation model) (Campbell et al. 1974) was used to estimate the linear relationship between temperature and the rate of development of *P. marginatus.* The linear relationship is $Y (=1/D) = a + bT$, where Y is the rate of development $(1/d)$, T is the ambient temperature (°C), and the regression parameters are the intercept (a) and slope (b). The thermal constant $K (=1/b)$ is the number of degree-days above the threshold summed over the development period. Lower development threshold T_{min} $(= -a/b)$ is the minimum temperature at which the rate of development is zero or no measurable development occurs (Campbell et al. 1974).

A nonlinear model (Logan 6 model) was used to estimate the upper development threshold (T_{max}) and the optimum temperature threshold (T_{opt}) (Logan et al. 1976). T_{max} is the maximum temperature at which the rate of development becomes zero. T_{opt} is the temperature at which the maximum rate of development occurs (Walgama and Zalucki 2006). The Logan model does not estimate T_{min}, because it is asymptotic to the left of the temperature axis. The relationship between development rate $(1/D)$ and T_{max} is described in the Logan 6 model as

$$1/D = \psi \left[\exp(\rho T) - \exp\left(\rho T_{max} - \frac{T_{max} - T}{\Delta T} \right) \right],$$

where ψ is a measurable rate of temperature-dependent physiological process at some base temperature, ρ is the biochemical reaction rate, and ΔT is the temperature range over which "thermal breakdown" becomes the overriding influence (Logan et al. 1976). To determine the optimum temperature (T_{opt}) for de-

Table 1. Mean number of days (± SEM) for each life-history stage of *P. marginatus* reared at different temperatures

| Temp (±1°C) | Egg | First | Second | | Third | | Fourth | Cumulative | |
			Male	Female	Male	Female	Male	Male	Female
15	27.5 ± 0.2a								
18	23.1 ± 0.2b	25.3 ± 0.5a	21.1 ± 1.6a	13.5 ± 1.3a	7.0 ± 1.8a	13.2 ± 0.9a	11.7 ± 1.8a	85.2 ± 1.8a	74.4 ± 1.4a
20	14.4 ± 0.2c	14.6 ± 0.5b	13.6 ± 0.8b	9.3 ± 0.7b	4.5 ± 0.7ab	8.9 ± 0.9b	8.9 ± 0.7a	53.4 ± 0.7b	45.9 ± 0.9b
25	8.7 ± 0.1d	6.5 ± 0.1c	6.6 ± 0.5c	5.5 ± 0.5c	2.4 ± 0.5b	5.2 ± 0.2c	4.1 ± 0.5b	28.5 ± 0.3c	25.9 ± 0.2c
30	7.3 ± 0.2e	6.1 ± 0.2c	6.3 ± 0.4c	5.7 ± 0.4c	2.6 ± 0.4b	4.4 ± 0.3c	3.6 ± 0.4b	24.9 ± 0.6c	23.2 ± 0.3d
34	5.9 ± 0.1f								
35	5.5 ± 0.1f								
37	0.0								
F	1922.10	400.59	57.41	17.09	5.35	15.31	15.66	725.42	521.23
df	6, 212	3, 132	3, 97	3, 101	3, 94	3, 95	3, 91	3, 84	3, 90
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0020	<0.0001	<0.0001	<0.0001	<0.0001

Means within a column followed by the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD test; $n = 35$).

velopment, the following equation (Logan et al. 1976) was used.

$$T_{opt} = T_{max}\left[1 + \varepsilon\left(\frac{\ln(\varepsilon b_o)}{1 - \varepsilon b_o}\right)\right]$$

Here, ε is $\Delta T/T_{max}$ and b_0 is ρT_{max}.

Developmental thresholds and thermal constants were estimated for eggs, male and female nymphs, and cumulative adult males and females.

Statistical Analysis. The experimental setup used for both experiments was completely randomized design. Before statistical analysis, the mean individuals in each petri dish/replicate was calculated and used in the analyses. A one-way analysis of variance (ANOVA) was conducted using PROC GLM for both experiments with temperature as the main effect (SAS Institute 1999). Means were compared at $P = 0.05$ significance level by using the Tukey's honestly significant difference (HSD) test. Proportion of females (sex ratio) and percentage of survival were arcine square-root transformed (Zar 1984) to adjust the variances before ANOVA.

Linear regression was performed using PROC REG to determine any linear relationships between developmental rate and temperature and to estimate the parameters a and b. Nonlinear regression using PROC NLIN was performed for the nonlinear section of the relationship between developmental rate and temperature to find the estimates for the parameters, ψ, ρ, T_{max}, and ΔT of the Logan 6 model.

Voucher Specimens. Voucher specimens (SEL identification lot 0708566, identified by Gregory A. Evans, Systematic Entomology Laboratory, USDA–ARS) of *P. marginatus* were deposited in the Entomology and Nematology Department insect collection, at the Tropical Research and Education Center, University of Florida, Homestead, FL.

Results

Development and Survival. Eggs hatched at all temperatures except 37°C (Tables 1 and 2). Eggs took 5 times longer to hatch at 15°C than 35°C. First-instar nymphs failed to complete development at 15, 34, and 35°C (Table 1). First-instar developmental time was 4 times longer at 18°C than at 30°C. Developmental times for male and female nymphs, and cumulative adult males were similar at 25 and 30°C. The cumulative development time for adult females was the shortest at 30°C (Table 1).

Percentage of egg survival (percentage of egg hatch) increased until 20°C and started to decrease at 35°C (Table 2). Percentage of survival of first-instar

Table 2. Mean (± SEM) percentage of survival (%) for each life-history stage of *P. marginatus* reared at different temperatures

| Temp (±1°C) | Egg | First | Second | Third | | Fourth male | Egg to adult |
				Male	Female		
15	60.9 ± 3.3cd						
18	80.0 ± 2.9b	54.1 ± 4.7d	80.1 ± 4.8b	96.4 ± 1.9ab	73.2 ± 7.7	98.4 ± 1.6a	30.5 ± 4.4c
20	90.1 ± 2.1a	77.2 ± 3.0c	94.1 ± 1.3a	98.1 ± 1.0a	83.5 ± 3.8	75.4 ± 5.7c	41.4 ± 3.5bc
25	83.3 ± 3.4ab	83.2 ± 4.3bc	97.5 ± 1.3a	89.2 ± 3.1b	79.9 ± 4.8	86.7 ± 2.9bc	51.4 ± 4.0b
30	85.9 ± 3.3ab	90.5 ± 2.5ab	91.0 ± 4.0ab	96.9 ± 1.5ab	92.6 ± 2.9	97.8 ± 1.6a	70.8 ± 4.9a
34	73.4 ± 5.1bc						
35	33.4 ± 6.9d						
37	0.0						
F	16.70	16.52	4.89	3.46	1.82	10.36	15.43
df	6, 205	3, 131	3, 122	3, 91	3, 90	3, 89	3, 121
P	<0.0001	<0.0001	<0.0030	<0.0196	<0.1494	<0.0001	<0.0001

Means within a column followed by the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD test; $n = 35$).

Table 3.   Mean (± SEM) proportion of females, adult longevity, fecundity, and preoviposition and oviposition periods of *P. marginatus* reared at four temperatures

Temp (±1°C)	Sex ratio (%) (proportion of females)	Adult longevity (d)		Fecundity (no.)	Preoviposition period (d)	Oviposition period (d)
		Male	Female			
18	69.4 ± 8.2a	5.5 ± 0.5a	40.2 ± 1.1a	160.6 ± 13.8cd	16.7 ± 0.7a	19.6 ± 1.0a
20	81.7 ± 3.6a	4.8 ± 0.3a	35.7 ± 1.0b	231.6 ± 12.8bc	13.5 ± 0.5b	21.4 ± 1.1a
25	42.6 ± 5.3b	2.9 ± 0.2b	21.1 ± 0.7c	300.2 ± 40.4ab	6.8 ± 0.4c	11.4 ± 0.8b
30	71.6 ± 4.2a	—[a]	19.2 ± 1.4c	82.0 ± 11.7d	7.6 ± 0.7c	11.6 ± 1.4b
F	10.38	14.91	93.25	15.13	70.33	24.99
df	3, 89	2, 73	3, 92	3, 92	3, 92	3, 92
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means within a column followed by the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD test; $n = 35$).
[a] Not assessed (males produced at 30°C died within 24 h and none was collected in time to assess longevity).

nymphs was the lowest at 18°C. Cumulative adult percentage of survival was the highest at 30°C (Table 2).

Reproduction and Adult Longevity. Preoviposition and oviposition periods were not different at 25 and 30°C (Table 3). Fecundity was the highest at 20 and 25°C but declined at 30°C (Table 3). There was no difference in female longevity at 25 and 30°C (Table 3). Adult male longevity was less at 25°C compared with other temperatures (Table 3). The proportion of females was the lowest at 25°C (Table 3).

Development Thresholds and Thermal Constant. Between 18 and 25°C, there was a linear relationship ($R^2 = 0.94$, $P < 0.0001$) between developmental rate and temperature in the linear degree-day (DD) model for egg, male and female nymphs, and cumulative adult males and females (Table 4). Thermal constants (K) for development rates associated with egg and male and female nymphs were 100.0, 204.8, and 175.4 DD, respectively. For cumulative development of adult males and females, the thermal constants were 303.0 and 294.1 DD, respectively. The estimated T_{min} thresholds for egg and male and female nymphs were 13.3, 14.8, and 14.3°C, respectively. For cumulative development of adult males and females, the estimated T_{min} thresholds were 14.5 and 13.9°C, respectively.

For the developmental rate versus temperature, the Logan 6 model assessed relationships (pseudo-R^2 = 0.97, $P < 0.0001$) for egg, male and female nymphs, and cumulative adult males and females (Table 5). The estimated T_{opt} threshold for egg and male and female nymphs was 34.8, 27.9, and 28.3°C, respectively. For adult males and females, the T_{opt} threshold was 28.7 and 28.4°C, respectively. The estimated T_{max} threshold for egg and male and female nymphs was 41.6, 30.5, and 31.7°C, respectively. The estimated T_{max} threshold for adult males and females was 31.9 and 32.1°C, respectively.

Discussion

For a majority of insects, their physiological systems (e.g., respiratory, digestive, circulatory, and reproductive) function optimally within a limited range of temperatures (Chapman 1998). Temperature had a significant effect on the development of *P. marginatus*. Overall, the linear degree-day model and the nonlinear Logan 6 model estimated minimum, optimum, and maximum temperature thresholds for *P. marginatus* that were analogous to the results obtained in the laboratory experiments.

At similar temperatures, there were differences and similarities in the development and estimated thermal constants and thresholds for other mealybug species. For example, *P. marginatus* failed to complete development at 15°C, which is in contrast to the Madeira mealybug, *Phenacoccus madeirensis* Green, which has been shown to complete development at 15°C (Chong et al. 2003). Although ≈61% of *P. marginatus* eggs

Table 4.   Summary statistics and the estimates (± SE) of the fitted parameters based on the linear thermal summation model, $Y = a + bT$

Statistics parameter	Life-history stage				
	Egg	Nymph		Adult	
		Female	Male	Female	Male
$a \pm$ SE	−0.133 ± 0.007	−0.082 ± 0.004	−0.073 ± 0.002	−0.047 ± 0.002	−0.048 ± 0.001
$b \pm$ SE	0.01 ± 0.001	0.0057 ± 0.001	0.0049 ± 0.001	0.0034 ± 0.001	0.0033 ± 0.001
K (=1/b) (DD)	100.0	175.4	204.1	294.1	303.0
T_{min} (= −a/b) (°C)	13.3	14.3	14.8	13.9	14.5
R^2	0.9356	0.9491	0.9764	0.9599	0.9812
F	1,640.79	1,286.51	2,606.13	1,653.01	3,493.67
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
df	1, 113	1, 69	1, 67	1, 69	1, 67

Y = rate of development (=1/D); D = days; T = ambient temperature (°C); a = intercept; b = slope; K = thermal constant (=1/b) (DD); T_{min} = minimum temperature threshold (= −a/b) (°C); R^2 = coefficient of determination.

Table 5. Summary statistics and the estimates (± SE) of the fitted parameters based on the nonlinear Logan 6 model and estimated optimum temp thresholds (T_{opt})

Statistics parameter	Life-history stage				
	Egg	Nymph		Adult	
		Female	Male	Female	Male
Logan 6 model: $1/D = \psi\left[\exp(\rho T) - \exp\left(\rho T_{max} - \dfrac{T_{max} - T}{\Delta T}\right)\right]$					
$\Psi \pm SE$	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
$\rho \pm SE$	0.11 ± 0.02	0.15 ± 0.04	0.21 ± 0.04	0.13 ± 0.03	0.15 ± 0.03
$T_{max} \pm SE$	41.6 ± 0.9	31.7 ± 1.3	30.5 ± 0.3	32.1 ± 1.2	31.9 ± 1.5
$\Delta T \pm SE$	5.24 ± 0.06	1.93 ± 0.46	1.62 ± 0.42	2.05 ± 0.36	1.88 ± 0.47
Pseudo-R^2	0.9796	0.9868	0.9864	0.9912	0.9929
F	22354.5	6092.2	5620.06	10500.7	10252.5
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
SS_R	0.00024	0.00003	0.00003	0.000009	0.000007
SS_{CT}	0.01177	0.00228	0.00221	0.00102	0.00099
$T_{opt} = T_{max}\left[1 + \varepsilon\left(\dfrac{\ln(\varepsilon b_o)}{1 - \varepsilon b_o}\right)\right]$					
T_{opt} (°C)	34.8	28.3	27.9	28.4	28.7

$1/D$ = rate of development (Y); D = days; ψ = rate of temperature-dependent physiological process at some base temperature; ρ = biochemical reaction rate; T = ambient temperature (°C); T_{max} = upper developmental threshold; ΔT = temperature range over which "thermal breakdown" becomes the overriding influence; pseudo-$R^2 = 1$-SS_R/SS_{CT}; SS_R = residual sums of squares; SS_{CT} = corrected total sums of squares; T_{opt} = optimum temperature threshold; $\epsilon = \Delta T/T_{max}$; $b_0 = \rho T_{max}$.

hatched at 15°C, none of the pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green), eggs was able to hatch (Chong et al. 2008).

Tropical insect species have higher minimum temperature thresholds than temperate species (Trudgill et al. 2005). Thermal constants decrease with the increase of minimum temperature thresholds (Trudgill et al. 2005). The eggs of *M. hirsutus* (Chong et al. 2008) and *P. marginatus* (this study) had similar estimated minimum temperature thresholds (14.5 and 13.3°C, respectively), whereas it was 10.9°C for *Planococcus citri* (Risso) eggs (Laflin and Parrella 2004). The estimated thermal constants for adult female *P. marginatus* and *M. hirsutus* were 294 and 347 DD, respectively (Chong et al. 2008), whereas at fluctuating temperatures averaging 20.3°C, it was 365 DD for adult female *P. citri* (Laflin and Parrella 2004). Both *M. hirsutus* and *P. citri* have wider distributions in the United States than *P. marginatus* (Ben-Dov 1994). The estimated high minimum temperature threshold and low thermal constant of *P. marginatus* demonstrate characteristics of tropical insects and thus are expected to have a smaller distribution of *P. marginatus* in the United States than *M. hirsutus* or *P. citri.*

Although at 30°C, *P. marginatus* females took less time to develop and had higher survival rates than at the other temperatures, fecundity at 30°C was lower than at 20 and 25°C. The drastic drop in fecundity at 30°C suggests that even though the developmental time was shorter and survival was higher at 30°C than at 25°C, *P. marginatus* may have reached its optimal temperature for development and reproduction at a temperature below 30°C. The optimal temperature for development estimated using the Logan 6 model for female nymphs and the cumulative adult females was 28.3 and 28.4°C, respectively, supporting the results obtained. Other mealybug species such as *P. madeirensis* and *M. hirsutus* showed differences in fecundity

at similar temperatures. In contrast to the fecundity of *P. marginatus,* at 20 and 25°C, the fecundity of *P. madeirensis* at 20°C (491) was higher than the fecundity at 25°C (288 eggs) (Chong et al. 2003). Similar to *P. marginatus,* the fecundity at 30°C (103 eggs) was significantly lower for *M. hirsutus* compared with its fecundity at 25°C (300 eggs) (Chong et al. 2008).

The developmental threshold and thermal constant of an insect are potential indicators of its distribution and abundance (Messenger 1959, Campbell et al. 1974). The estimated development thresholds and thermal constants obtained in this study may be useful in predicting the distribution and establishment of *P. marginatus* in the United States. This information is also useful in comparing development thresholds and thermal constants of *P. marginatus* under fluctuating temperatures, which were not investigated in this study. According to the comparative climatic data from the National Climatic Data Center (NCDC 2005), southern California, southern Texas, Hawaii, and Florida have daily average temperatures that are suitable for the development of *P. marginatus.* A large number of economically important fruits, vegetables, and ornamental plants are grown in southern California including citrus, avocado, beans, hibiscus, and plumeria. Southern Texas has the third largest citrus production in the United States (CNAS 2007), and citrus is one of the host plants of *P. marginatus* (Walker et al. 2006). *P. marginatus* is already established on Hawaii and the islands of Maui, Oahu, and Kauai (Heu et al. 2007). Papaya, which is a very susceptible host plant, is the second most important fruit crop after pineapple, and Hawaii currently has ≈864 ha of papaya in production (USDA–NASS 2007). In Florida, where ≈100 ha of papaya are grown (Mossler and Nesheim 2002), *P. marginatus* has been found in most of the counties of central and south Florida (Walker et al. 2006). Distribution and establishment of *P. mar-*

ginatus throughout the southern portions of the United States may be influenced by other factors such as crops grown and interstate movement of plant materials and commodities.

Although nearly constant temperatures were used in these experiments, in nature temperature may fluctuate during the day and night. The living system of plants and animals may be better adapted to temperature fluctuations than to an artificial constant state (Gordan 1999). In the natural environment, *P. marginatus* may be able to develop and survive at a higher temperature than observed in this study.

In addition to temperature, plant type is another important abiotic factor that may influence the distribution and abundance of *P. marginatus* in other areas in the United States. *P. marginatus* was able to develop, survive, and reproduce successfully on ornamental plants such as *H. rosa-sinensis, Acalypha wilkesiana* (Muell.-Arg.), and *Plumeria rubra* L., and weed species such as *Parthenium hysterophorus* L. (Amarasekare et al. 2008). The ability of *P. marginatus* to develop on these plant species demonstrates the possibility of movement, distribution, and establishment of *P. marginatus* into new areas in the United States. Other abiotic and biotic factors such as moisture and fertility levels of growing medium and plant size can influence the development of *P. marginatus*, although none of these factors was investigated in this study.

This information may also be helpful in managing the susceptible stages of *P. marginatus* at different environmental temperatures. Extended development time of eggs and the immature stages of *P. marginatus* at low temperatures may increase their exposure to natural enemies and insecticides. Early-instar mealybugs are easier to control than late instars (Townsend et al. 2000). However, at high temperatures (25 and 30°C) *P. marginatus* nymphs develop rapidly and become adults 2–3 times sooner than at low temperatures (18 and 20°C), which may reduce exposure time to natural enemies and insecticides.

Life history of *P. marginatus* is affected by temperature. However, it has the ability to develop, survive, and reproduce at temperatures 18, 20, 25, and 30°C. The information gathered from this study will be important in the management of *P. marginatus*, by providing a better understanding of its life history and ability to survive in different temperatures. This information is needed in predicting distribution and abundance of this pest in the United States.

Acknowledgments

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