DEVELOPMENTAL AND REPRODUCTIVE BIOLOGY OF PLANOCOCCUS MINOR (HEMIPTERA: PSEUDOCOCCIDAE) UNDER CONSTANT **TEMPERATURES**

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ABSTRACT

Effect of temperature on the developmental and reproductive biology of the passionvine mealybug, Planococcus minor (Maskell) (Hemiptera: Pseudococcidae), was investigated on sprouted potatoes. P. minor was able to develop and complete its life cycle at 20, 25, and 29 °C. No eggs eclosed at 15 and 35 °C. The developmental time from egg to adult female was approximately 49 d at 20 $^{\circ}$ C, 31 d at 25 $^{\circ}$ C, and 27 d at 29 $^{\circ}$ C. Between 20 and 29 $^{\circ}$ C, 58-71% of eggs survived to adulthood. Female mealybugs made up 60-73% of the adult populations in the 3 temperature treatments. Preoviposition and oviposition times decreased as the temperature increased. Females reproduced sexually and produced the highest number of eggs (270 eggs/female) at 20 °C. Adult female longevity declined from 34 d at 20 °C to 19-22 d at the 2 higher temperatures. Adult males were short-lived and their longevity declined with increasing temperature. At 25 $^{\circ}\text{C}$, the gross reproductive rate (GRR) and net reproductive rate (R_c) were estimated at 445.7 \Im and 325.4 \Im , respectively, the generation time (T_c) was 39.5 d, the intrinsic rate of increase (r_m) was 0.147 (9/9/d), the finite rate of increase (λ) was 1.158 ($\mathcal{P}/\mathcal{P}/d$), and the doubling time (DT) was 4.7 d. The ability of *P. minor* to develop, survive, and reproduce successfully from 20 to 29 °C suggests that the mealybug has the potential to develop and establish in climatic zones that fall within this temperature range.

Key Words: passionvine mealybug, development, survivorship, reproduction, life table parameters

RESUMEN

El efecto de la temperatura sobre el desarrollo y la reproducción de Planococcus minor (Maskell) (Hemiptera: Pseudococcidae) fue investigado en papas germinadas. Planococcus minor pudo completar su ciclo de vida a 20, 25 y 29 °C. Los huevos no eclosionaron a 15 y 35 °C. El tiempo de desarrollo de huevo a adulto hembra fue de aproximadamente 49 dias a 20 °C, 31 d a 25 °C, y 27 d a 29 °C. Entre 20 y 29 °C el 58-71% de los huevos sobrevivieron y alcanzaron la adultez. El porcentaje de hembras fue de 60 al 73% en las tres temperaturas. Los períodos de preoviposición y oviposición, y la longevidad de los adultos, aumentaron con la disminución de la temperatura. Las hembras se reproducen sexualmente. La fecundidad más alta fue a los 20 °C cuando cada hembra produjo un promedio de 270 huevos. La longevidad de las hembras se redujo de 34 d a 20 °C a 19 -22 días a las dos temperaturas más altas. Los machos viven poco tiempo y su longevidad se reduce con incrementos en la temperatura. A los 25 °C, la tasa neta de reproducción (R) fue 325.4 \$\text{\$\gamma\$}\$, el tiempo de generación (T_o) 39.5 días, la tasa intrínseca de crecimiento (r_m) 0.147 (2/2/d), la tasa finita de incremento (λ) 1.158, y el tiempo de duplicación (TD) fue de 4.7 días. La capacidad de P. minor para completar su desarrollo, sobrevivir y reproducirse con éxito de los 20 a los 29 °C sugiere que esta cochinilla tiene potencial para establecerse en zonas climáticas con este mismo rango de temperatura.

Palabras	clave:	cochinilla,	desarrollo,	sobrevivencia,	reproducción,	parámetros	de tabla	de
vida								

The passionvine mealybug, *Planococcus minor* (Maskell) (Hemiptera: Pseudococcidae), is a pest

with a reported host list of more than 250 plants (Venette & Davis 2004). It was probably intro-

duced to the Neotropics through trade (Cox 1989) and is currently reported in at least 21 countries (Williams & Granara de Willink 1992), including the island of Trinidad (Francis et al. 2012) where the study was undertaken. *P. minor* is morphologically very difficult to separate from *Plano*coccus citri (Risso) (Cox 1983), and these cryptic species share similarities such as host plants and geographical distribution (Cox 1989; Williams & Granara de Willink 1992). Therefore, estimating economic damage caused by P. minor alone is difficult (Venette & Davis 2004). However, given the reported polyphagous nature of this mealybug, its accidental introduction can potentially cause serious economic damage in newly infested areas. P. minor is considered a significant threat to noninfested countries in the Caribbean basin and the continental United States, where it was recently identified for the first time on Mussaenda sp. (Gentianales: Rubiaceae) in south Florida (Stocks & Roda 2011).

Despite the potential threat P. minor poses, there is limited life history information available on the pest. Information on its developmental and reproductive biology was provided by Martinez & Suris (1998) whose study was conducted at a single temperature, by Maity et al. (1998) and Biswas & Ghosh (2000) at fluctuating temperatures, and by Sahoo et al. (1999) under field conditions with seasonal changes. The host plants used varied from a single (Martinez & Suris 1998) to multiple species (Maity et al. 1998; Biswas & Ghosh 2000). Thus, comprehensive knowledge on the influence of environmental conditions such as temperature on developmental and reproductive biology is limited. Knowledge on whether or not parthenogenesis occurs in the species is also lacking. The data from the study will provide relevant information for use in predictive models that determine potential spread and distribution and improve risk assessments for pests.

Against this background, the goal was to provide a better understanding of the life history of *P. minor*. The specific objectives were: 1) to determine the effect of temperature on the development, survival, reproduction and adult longevity of the mealybug and 2) to determine key life table parameters.

Materials and Methods

Maintenance of Host Material and Mealybug Colony

This study was carried out at CABI Caribbean and Latin America Regional Center, Curepe, Trinidad. A colony of *P. minor* was established on factitious hosts (potato, *Solanum tuberosum* L.; Solanales: Solanaceae) under laboratory conditions in June 2008. The insects used to establish the colony were obtained from infested co-

coa (Theobroma cacao L.; Malvales: Malvaceae) pods at a plant propagation station, LaReunion, Trinidad and were identified by Douglass Miller at the USDA ARS Systematic Entomology Laboratory, Beltsville, Maryland (Lot # 0607069). Unsprouted potatoes were washed and rinsed with clean water and left to dry. The potatoes were placed on plastic trays in a room at 25 ± 2 °C, 60 ± 10% RH, and complete darkness to encourage sprouting. Sprouting took 2-4 wk, and potatoes were ready for use in the experiments when the blanched sprouts were 2.0-2.5 cm long. Each wk, 20-25 sprouted potatoes were individually infested with 4-6 adult female P. minor with ovisacs transferred from the colony using a small camel hair brush. The infested potatoes were kept on plastic trays for mealybug development. This procedure was done in a separate room on a weekly basis to maintain a continuous supply of different mealybug stages. Methods used were modified from those described by Meyerdirk et al. (1998).

Development and Survival

Development, survival, and sex ratio were assessed at 5 temperatures (15, 20, 25, 29, and 35 °C) in 2 environmental growth chambers (TC1 model, Chagrin Falls, Ohio and Precision model, Thermo Scientific, Dubuque, Iowa). Chambers were maintained at $60 \pm 10\%$ RH and a photoperiod of 0:24 h L:D. Mealybugs used in the experiment were reared on blanched, tender potato sprouts in total darkness in order to encourage their settlement and growth on the sprouts. Fluctuations across the range of temperatures never exceeded \pm 1.0 °C, and relative humidity was maintained within the range of \pm 10% by placing plastic trays with water at the bottom of the chambers. Temperature and relative humidity inside the chambers were verified with HOBO® data loggers (Onset Computer Co., Bourne, Massachusetts) at 30 min intervals. Treatment temperatures were replicated twice, once in each environmental growth chamber model.

Twenty potato tubers were used in this experiment. All sprouts on individual potato tubers were removed except for 2 to facilitate observations during daily scoring of mealybug development. Twenty large gravid adult females were collected from the mealybug colony and maintained on the sprouted potatoes until oviposition at each treatment temperature. Five eggs were carefully collected from the ovisac of each female with a camel hair brush within 24 h of oviposition at each treatment temperature. They were transferred onto the sprouts of each of the 20 potatoes and placed in polyethylene containers (12 cm diam × 8 cm high) with muslin cloth secured at the top of the containers with rubber bands. Each potato tuber represented a cohort, and 20 cohorts were prepared for each treatment temperature.

The cohorts were examined every 24 h under a dissecting microscope for egg eclosion and molting of immature stages. Successful development from one instar to the next was indicated by the presence of cast skins or exuviae (inclusive of third- and fourth-instar males in puparia).

Survival rate for each stadium was assessed as the proportion of individuals that successfully developed to the next stadium. The sex of individual mealybugs could not be determined at the egg and first-instar stages. The gender of each individual was determined by careful observation during the latter part of the second-instar when the males changed their color from vellow to pink. At this point, the developmental times of males and females were recorded separately. The cumulative survival rate from egg to adult (females and males) was determined by dividing the total number of adults by the number of eggs used to establish each cohort. The sex ratio was determined by dividing the number of adult females successfully molted by the total number of surviving adults in each cohort.

Reproduction and Adult Longevity

Reproductive periods, fecundity, and adult longevity were evaluated at 3 treatment temperatures (20, 25, and 29 °C). Twenty females were collected from the cohorts produced at each treatment temperature immediately after adult molt. Each female was paired with 3 newly emerged adult males on individual sprouted potatoes, prepared as previously outlined, in polyethylene containers at each treatment temperature. There were 20 cohorts per treatment temperature and treatment temperatures were replicated twice as previously described. The pre-oviposition period (duration between adult female molt and first day of egg production) and oviposition period (duration between start and end of egg production) were determined. Females were examined every 24 h during the oviposition period and eggs produced by individual females were removed and placed in 70% alcohol to dissolve away the ovisacs. The eggs were then counted under a dissecting microscope. Adult female and male mealybugs from the mating experiment were kept at the assigned temperatures and they were inspected every 24 h to determine if they were still alive. Longevity was recorded as the duration between adult molt and death.

The possibility of asexual reproduction was evaluated at 25 °C in a non-mating experiment. Twenty virgin females were collected from the cohorts immediately after adult molt at the treatment temperature of 25 °C. Cocoons (tests) indicated the presence of immature males in a cohort where virgin females were collected. These tests were first inspected to ensure that adult males had not emerged and possibly mated with the fe-

males. Each female was isolated without males on a sprouted potato in a polyethylene container as previously described. The adult females were kept at this temperature until death. Twenty replicates were prepared for this experiment.

Life Table Analysis

The effect of temperature (20, 25, and 29 °C) on the population growth and age structure of $P.\ minor$ was assessed based on 6 life table parameters. Data on survivorship and reproduction were used to construct a life table of l_x (age-specific survival rate) and m_x (age-specific fecundity). Age-specific fecundity at a given temperature was obtained by multiplying the mean daily fecundity with the proportion of females that was calculated from the developmental experiment at that temperature. The formulae for calculating the life table parameters (Carey 1993) of female $P.\ minor$ at each temperature were:

gross reproductive rate, GRR = $\sum m_x$; net reproductive rate, $R_o = \sum (l_x m_x)$; mean generation time, $T_G = \sum (x l_x m_x)/\sum (l_x m_x)$; intrinsic rate of increase, $r_m = (lnR_o)/T_G$; finite rate of increase, $\lambda = \exp(r_m)$; and doubling time, $DT = ln2/r_m$.

Data Analysis

One-way analysis of variance (ANOVA) was used to determine the effect of temperature on the stage-specific and cumulative developmental times, survival rate and sex ratio, pre-oviposition and oviposition periods, fecundity, and adult longevity of *P. minor* using PROC GLM (SAS Institute 2002). The survival rate and sex ratio were arcsine square-root transformed (Zar 1984), and tests for normality and homogeneity of variances of the dependent variables were performed using PROC UNIVARIATE prior to the analysis. Tukey's honestly significant difference (HSD) test was used to separate the means when the statistical model indicated significant treatment effects on the dependent variables.

RESULTS

Development and Survival

Results from the 2 chambers were similar; therefore, data were combined in the final statistical analyses. No eggs eclosed at 15 and 35 °C. At 20 °C, eggs of P. minor eclosed in less than 13 d, which was longer than those held at 25 and 29 °C (< 7 d) (Table 1). The developmental times of female and male nymphs decreased as the temperature increased. The mean total duration of nymphal development of females was 36 d at 20 °C, 23 d at 25 °C, and 21 d at 29 °C (Table 1). Males required a longer duration (0.8 to 3.4 d) for

Table 1. Mean number of days $(\pm SEM)$ for each developmental stadium of PLANOCOCCUS minor reared on sprouted potatoes at 5 constant temperatures

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

nymphal development than females within the same temperature range. The mean total duration of development of females was reduced from 48.8 ± 0.3 at $20\,^{\circ}\mathrm{C}$ to 26.9 ± 0.5 d at $29\,^{\circ}\mathrm{C}$ (Table 1). Adult males emerged 0.6 to 2.7 d after the adult molt of females, depending on the temperature.

The highest (35 °C) and lowest (15 °C) temperatures adversely affected the survival of *P. mi*nor (Table 2). Eggs turned brown and appeared desiccated after incubating for 45 and 15 d at 15 and 35 °C, respectively. More than 90% of eggs survived at 20 and 25 °C, but only 84% survived at 29 °C (Table 2). Survival rates were high for the first 2 instars (Table 2). From 20 to 29 °C. 83-88% of first-instar nymphs survived. At 20 °C, 98% of second-instar nymphs survived, and 80-87% survived at 25 and 29 °C. Survival rates of third-instar females averaged 89-100% from 20 to 29 °C (Table 2). Survival rates were very high for third- and fourth-instar males from 20 to 29 °C (Table 2). Amongst third-instar males, 96-98% survived to the fourth-instar, and 97-100% of these individuals successfully reached adulthood. Overall, 68, 71, and 58% of the eggs incubated at 20, 25, and 29 °C, respectively, developed to adulthood (Table 2).

Reproduction and Adult Longevity

Results from the 2 chambers were similar and data were likewise combined in the statistical analyses. Isolated virgin females did not produce any eggs and some females lived up to 2 mo at 25 °C. Sex ratio expressed as percent females, reproductive periods, and fecundity of mated females differed among the temperature treatments. Females comprised 64.6 ± 2.5 , 73.4 ± 4.3 , and 60.1 ± 4.3 8.5% of the total adult populations at 20, 25, and 29 °C, respectively (Table 3). The pre-oviposition period decreased with increasing temperature and was nearly twice as long at 20 °C (<15 d) than at 29 °C (>8 d) (Table 3). The oviposition period was longest at 20 °C (<14 d), compared with 6-9 d at 25 and 29 °C (Table 3). Female mealybugs maintained at 25 and 29 °C produced significantly lower numbers of eggs (205.6 \pm 7.0 and 187.9 \pm 22.5) compared with those at 20 °C (269.8 \pm 17.8 eggs) (Table 3).

Adult longevity decreased as temperature increased. Females lived for approximately 34 d at 20 °C, and those maintained at 25 and 29 °C lived for 19-22 d (Table 3). Adult males were shortlived. Males lived more than twice as long (>4 d) at 20 °C compared with those maintained at 25 and 29 °C (<2 d) (Table 3).

Life Table Analysis

The lowest values for the gross and net reproductive rates (GRR and R_{\circ}) were at 20 °C and increased to their highest values at 25 °C, followed

Table 2. Mean (\pm SEM) survival rate (%) for each developmental stadium of *Planococcus minor* reared on sprouted potatoes at 5 constant temperatures.

			Develo	opmental stage				
				Third		Fourth		
T. (°C)	Egg	First	Second	Female	Male	Male	Egg to adult	
15 20 25 29 35	$0 c$ $91 \pm 1 ab$ $93 \pm 5 a$ $84 \pm 5 b$ $0 c$	88 ± 6 a 87 ± 1 a 83 ± 5 a	98 ± 1 a 87 ± 5 b 80 ± 1 b	100 a 97 ± 3 ab 89 ± 1 b	98 ± 2 a 96 ± 2 a 97 ± 1 a	97 ± 2 a 98 ± 2 a 100 a	$0 c$ $68 \pm 1 b$ $71 \pm 2 a$ $58 \pm 1 a$ $0 c$	
			ANC	VA statistics				
$_{\substack{\text{df}\\P}}$	3.43 2, 540 0.0357	0.78 $2,538$ 0.4618	8.00 $2,317$ 0.0006	3.49 $2, 267$ 0.0337	0.37 $2,219$ 0.6916	0.62 $2, 214$ 0.5386	2.82 2, 487 0.0639	

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

by a decrease at 29 °C (Table 4). As temperature increased, the mean generation time (T_G) of 63.5 d at 20 °C decreased to less than 40 d at 25 and 29 °C (Table 4). The intrinsic rate of increase (r_m) was lower at 20 °C (0.077) than at 25 and 29 °C (\geq 0.139) (Table 4). The finite rate of increase (λ) followed the same trend as r_m , with higher estimated values at 25 and 29 °C. A population of P_G minor required approximately 5 d to double its numbers at 25 and 29 °C, but the doubling time (DT) was increased to approximately 9 d at 20 °C.

DISCUSSION

Temperature had pronounced effects on the developmental and reproductive biology of $P.\ minor$. Egg to adult female developmental time was 49 d at 20 °C, 31 d at 25 °C, and 27 d at 29 °C. When reared on different hosts from 19.7 to 28.9 °C, Biswas & Ghosh (2000) reported that $P.\ minor$ females completed their development in 16-22 d. Although Biswas & Ghosh (2000) did not report the duration to egg eclosion, the developmental time for females minus egg eclosion in our study was similar for that of females at the high end of

their temperature range. Temperature effects on development were also reported for similar species. At 20, 25 and 30 °C, the developmental time of *P. citri* from egg to adult female reared on coleus (*Solenostemon scutellarioides* L.; Lamiales: Lamiaceae) was 46, 19, and 24 d (Goldasteh et al. 2009). The developmental time of *Planococcus ficus* (Signoret) from egg to adult female reared on grapevine was 41, 25, and 23 d at 20, 25 and 30 °C (Walton & Pringle 2005).

Unlike *P. minor*, *P. citri* was able to complete its development at 15 °C and achieved some development to early third instars at 35 °C (Goldasteh et al. 2009). However, high survival rates of *P. minor* from 20 to 29 °C compared favorably with *P. citri* at similar temperatures. Reports on other mealybug species showed that both development and survival differed or were similar to results presented in this study. Some eggs of *Paracoccus marginatus* (Williams & Granara de Willink) eclosed at 15 and 35 °C, but the mealybug was unable to complete its development at either temperature (Amarasekare et al. 2008). No eggs of *Maconellicoccus hirsutus* (Green) eclosed at 15 °C, but there was some eclosion at 35 °C

Table 3. Mean (±SEM) percent females, pre-oviposition and oviposition periods, fecundity, and adult longevity of Planococcus minor reared on sprouted potatoes at 3 constant temperatures.

		Pre-oviposition Period (d)	Oviposition Period (d)		Adult longevity (d)	
T. (°C)	Percent females			Fecundity (no.)	Female	Male
20 25 29	$64.6 \pm 2.5 \text{ ab}$ $73.4 \pm 4.3 \text{ a}$ $60.1 \pm 8.5 \text{ b}$	14.8 ± 0.1 a 10.2 ± 0.4 b 8.4 ± 0.3 c	13.9 ± 0.4 a 9.2 ± 0.9 b 6.9 ± 0.3 c	269.8 ± 17.8 a 205.6 ± 7.0 b 187.9 ± 22.5 b	$33.8 \pm 1.5 \text{ a}$ $22.2 \pm 1.8 \text{ b}$ $19.5 \pm 0.5 \text{ c}$	4.3 ± 0.4 a 1.7 ± 0.7 b 1.3 ± 0.3 c
		A	NOVA statistics			
$_{\mathrm{df}}^{F}$	3.38 2, 117 0.0373	218.34 2, 117 <0.0001	190.05 2, 117 <0.0001	55.90 2, 117 <0.0001	334.56 2, 117 <0.0001	216.89 2, 269 <0.0001

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

4.9

Doubling time, DT (d)

		Temp. (°C)	
Life table parameters	20	25	29
Gross reproductive rate, GRR (♀/♀)	194.8	445.7	332.4
Net reproductive rate, $R_{o}(9/9)$	135.6	325.4	190.1
Mean generation time, T_C^0 (d)	63.5	39.5	37.7
Intrinsic rate of increase, $r_m (9/9/d)$	0.077	0.147	0.139
Finite rate of increase, $\lambda (\sqrt[]{\varphi}/Q)$	1.080	1.158	1.149

8.9

Table 4. Life table parameters of Planococcus minor reared on sprouted potatoes at three constant temperatures.

with no subsequent development (Chong et al. 2008). These two studies suggest that some development and survival of *P. minor* would therefore be possible at temperatures intermediate between 15 and 20 °C and 29 and 35 °C.

In the absence of adult males, virgin female $P.\ minor$ did not produce eggs. The female-biased sex ratios were similar to $P.\ citri$, but more males comprised the populations at 32 °C (Goldasteh et al. 2009). Female-biased sex ratios were also reported from 20 to 27 °C and male-biased sex ratios at 18 and 30 °C for $P.\ ficus$ (Walton & Pringle 2005). The phenomenon of male-biased sex ratios at extreme temperatures is known to occur in some insects and is thought to increase the probability of survival of these populations (Margolies & Wrensch 1996).

Mated P. minor females produced up to 270 eggs and their reproductive potential was similar to findings from other studies. Martinez & Suris (1998) reported a fecundity of 219 eggs per female *P. minor* when reared on potato sprouts at 26 °C. Maity et al. (1998) reported a range of 266-466 eggs when females were reared on several hosts from 14.5 to 31 °C. Fecundity also varied greatly (66-139 eggs) from 19.7 and 28.9 °C on different hosts (Biswas & Ghosh 2000). These differences were likely due to the utilization of different host plants and experimental conditions and were also reported for other species. P. citri laid fewer than 100 eggs above 30 °C, but had the potential to lay more than 400 eggs at 18 °C (Copland et al. 1985). For P. ficus, fecundity averaged 300 or more eggs from 20 to 25 °C, but egg production decreased significantly at 18, 27 and 30 °C (Walton & Pringle 2005). Decreased fecundity was reported for *P. marginatus* at 30 °C (82 eggs per female) compared with 231 and 300 eggs at 20 and 25 °C (Amarasekare et al. 2008). Likewise, fecundity of M. hirsutus at 30 °C (103 eggs) was lower at 20 and 25 °C (260 and 300 eggs, respectively) (Chong et al. 2008).

Life table parameters indicated that *P. minor* can increase its population within a short period of time from 20 to 29 °C. The highest values of $r_{\rm m}$ and λ and lowest values of DT and $T_{\rm G}$ occurred primarily at 25 °C, suggesting that it is the optimal temperature for development, survival, and

reproduction. Similar trends were reported for *P. citri* (Goldasteh et al. 2009) and *P. ficus* (Walton & Pringle 2005) at the same temperature.

4.7

P. minor had rapid development, high survival rates, and high fecundity from 20 to 29 °C. The developmental and reproductive data will provide a more realistic prediction of its potential distribution and help to refine the output of predictive models. By providing a better understanding of its life history, the data will also aid in predicting abundance of the mealybug in the U. S. Given the likelihood that *P. minor* will inevitably spread into new areas, such information could also be important for the development and implementation of mitigation measures against this pest.

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