

# Temperature Effects on the Development, Survival, and Reproduction of the Madeira Mealybug, *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae), on Chrysanthemum

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**ABSTRACT** The Madeira mealybug, *Phenacoccus madeirensis* Green (Hemiptera: Pseudococcidae), has become an increasingly damaging pest in greenhouse ornamental production. Current management tactics of *P. madeirensis* require a regular chemical application schedule targeting the immature stages. Knowledge of the life cycle of *P. madeirensis* is important to the success of its management program. We investigated the effects of constant temperature (15, 20, 25, 30, 35, and 40°C) on the development, survival, and reproduction of *P. madeirensis* on chrysanthemum (*Dendranthema x grandiflora* Kitam.). We failed to establish colonies at 30–40°C. Between 15 and 25°C, the duration of development of all developmental stages were shortened at higher temperatures. The total duration of development of female mealybugs was  $\approx 30$  d at 25°C, 46 d at 20°C, and 66 d at 15°C. Developmental time of males was 3–9 d longer than females. Survival rates of individual instars ranged between 88 and 100% and were not influenced by temperature. Overall, >75% of eggs completed development to adulthood. Female mealybugs made up 50% of the adult populations in all temperature treatments. Adult longevity at 25°C was  $\approx 3$  and 20 d for males and ovipositing females, respectively. Females at 20°C produced the highest number of eggs ( $491 \pm 38$  eggs/female).

**KEY WORDS** Pseudococcidae, *Phenacoccus madeirensis*, development, survival, reproduction

SCALE INSECTS AND MEALYBUGS are the most damaging insect pests in ornamental production and maintenance in Georgia. In 1996, the estimated losses and cost of control of scale insects and mealybugs in Georgia amounted to \$98,658,000 (Hudson et al. 1997). Conventional chemical control of mealybugs, especially the Madeira mealybug, *Phenacoccus madeirensis* Green, seems to be insufficient in many commercial greenhouses. *P. madeirensis* has a worldwide distribution and a wide host range (Williams and Granara de Willink 1992, Ben-Dov 1994). *P. madeirensis* infestation of greenhouse ornamentals in the southeastern United States has become a major problem since the early 1990s (Townsend et al. 2000). Successful control has required repeated insecticide applications directed against immature stages of *P. madeirensis* (Townsend et al. 2000). Understanding the development of this pest is important in predicting the population level of the mealybug and determining the timing of insecticide applications to achieve effective control.

The life cycle of a female *P. madeirensis* consists of an egg stage, three nymphal instars, and an adult stage.

A male goes through an additional nymphal instar. The first-instar nymph is called a crawler. The sex of the first two nymphal instars is indistinguishable. Female and male third-instar nymphs have different appearances and behaviors. Male second-instar nymphs secrete waxy filamentous tests just before molting and develop into the third- (prepupal) and fourth-instars (pupal) inside the tests. Adult males emerge from the tests as nonfeeding, winged individuals. Females are wingless. Third-instar females do not secrete tests and are similar in external morphology to adult females.

Little is known about the effect of temperature on the development of *P. madeirensis*. In this study, the development, survival, and fecundity of *P. madeirensis* on chrysanthemum (*Dendranthema x grandiflora* Kitam.) were studied at various constant temperatures.

## Materials and Methods

**Experimental Conditions.** Experiments were conducted in controlled environment chambers (model I-35VL; Percival Manufacturing Co., Boone, IA) maintained at six constant temperatures (15, 20, 25, 30, 35, and 40°C) and a light and dark period of 14:10 (L:D) h. The air temperature and relative hu-

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midity inside the growth chambers were recorded with StowAway temperature and humidity loggers (Onset Computer Corporation, Pocasset, MA) at 15-min intervals.

**Preparation of the Host Plants.** Chrysanthemums (*Dendranthema x grandiflora* Kitam, cultivar "Pomona") were used as host plants in this study. Cuttings were obtained from Yoder Brothers (Barberton, OH). The chrysanthemums were grown under natural light in greenhouses at the UGA/CAES, Griffin campus, Griffin, GA. Throughout the growing period, the chrysanthemums were continuously fertilized with 200 mg/liter N of Peters Peat-lite Special 20-10-20 water-soluble fertilizer (Scotts-Sierra Horticultural Products Co., Marysville, OH).

A hole was burnt with a heated cork borer (5 mm in diameter) in the bottom of a 100 by 20 mm petri dish. The petri dish was then rested on top of a 112-ml specimen cup filled with water. The third fully expanded leaf from the shoot apex of a chrysanthemum was chosen to standardize the quality of the host plant and was excised at the base of petiole. The petiole of the excised leaf was put through the hole of the petri dish and was immersed in the water. The leaves used in 15, 20, and 25°C treatments were rooted in their respective environment chambers before mealybug infestation. The leaves used in 30, 35, and 40°C treatments were rooted at 25°C before they were moved into their respective chambers. The detached leaves rooted in  $\approx 2$  wk at 25°C.

**Mealybug Development.** Adult *P. madeirensis* females were collected from a colony maintained on coleus (*Coleus blumei* Benth., cultivar "Volcano") at the UGA/CAES, Griffin campus, Griffin, GA. Twenty preovipositing adult females were randomly assigned to each temperature treatment for egg collection. After the females start laying eggs, 5–10 eggs were collected daily from the ovisac of a female within 24 h and transferred onto a rooted chrysanthemum leaf. All the mealybugs on an individual leaf constituted a cohort. The mealybugs were left to develop on the rooted leaves in the environment chambers. The mealybug cohorts on each leaf were observed daily under a dissecting microscope at 10 $\times$  magnification.

Developmental time for each instar was recorded by checking for exuvia. The duration of development of third- and fourth-instar males was determined by checking for exuvia pushed to the end of the tubular tests. Dissection of the tests was not necessary because the exuvia were visible through the loose waxy filaments. Means for duration of development of individual cohorts were calculated for each instar. Survival rate of each instar was recorded by counting the number of individuals that had successfully molted to the next instar. Because the sex of the eggs could not be determined, the overall survival rate from egg to adult female or male in each temperature treatment was determined by the number of adult females (or males) divided by the total number of eggs.

The proportion of females was used as a measure of secondary sex ratio and was determined at the end of experiments by dividing the number of adult females

successfully emerged by the total number of surviving adults in each cohort. Adult males were isolated in the original petri dishes with the host leaf in the respective environment chambers. Because adult males are non-feeding, food provision was not of concern in this study. Male mealybugs were active during the dark period so their reproductive behaviors were not observed. The life span of adult males was simply measured as the duration between adult emergence and death. Individual female longevity was calculated as the sum of the preoviposition time and the duration of reproduction, which were determined in the mealybug reproduction studies.

**Mealybug Reproduction.** The possibility of asexual reproduction and the reproductive potential of *P. madeirensis* were tested in fecundity experiments. In each temperature treatment, 40 females were collected from the cohorts immediately after adult molt to ensure their virginity. Twenty of the virgin females were assigned to the nonmating treatment, where each female was isolated without males on one newly rooted host leaf. Another group of 20 females was assigned to a mating treatment. Each female in the mating treatment was paired with three newly emerged adult males to ensure fertilization. The preoviposition time, defined as the duration between adult molt and first day of egg production, was recorded for all ovipositing females. Ovisacs were collected daily for egg counts. The survival and fecundity of females subjected to daily egg collection were not significantly different from that of the females subjected to egg collection at the end of their life (J.-H.C. unpublished data). The duration of reproduction was determined by the duration between the start and the end of egg production. At the end of egg production, all female mealybugs ceased responses (contractions of abdomen and movements of limbs) to probing and were considered dead.

**Statistical Analyses.** Individual females used for egg collection had different reproductive periods; thus, the numbers of cohorts prepared each day were different among the treatments. The numbers of cohorts in each temperature treatment were 152 at 15°C, 151 at 20°C, 103 at 25°C, 169 at 30°C, 109 at 35°C, and 120 at 40°C. As a result of different sampling sizes among treatments, a general linear model procedure (PROC GLM) was performed to determine the temperature effect on all the parameters measured in the mealybug development and reproduction studies of *P. madeirensis* (SAS Institute 1985). The survival rates of individual instars (expressed as percent survival) and the proportion of females in each temperature treatment were arcsine transformed to normalize the variance before statistical analyses were performed. Where significant differences were detected, means of the variables were separated using Fisher protected significant difference (least significant difference [LSD]) test with the significance level at  $P = 0.05$ .

**Table 1.** Duration of development in days (means  $\pm$  SEM) of individual instars of male and female *P. madeirensis* at various constant temperatures

Temperature (°C)	Egg	Instars						Egg to adult	
		First	Second	Third		Fourth	Female	Male	
				Female	Male	Male			
15	19.9 $\pm$ 0.1a	20.8 $\pm$ 0.2a	13.3 $\pm$ 0.2a	13.7 $\pm$ 0.3a	6.5 $\pm$ 0.2a	13.0 $\pm$ 0.3a	66.2 $\pm$ 0.4a	74.8 $\pm$ 0.4a	
20	13.5 $\pm$ 0.1b	13.2 $\pm$ 0.1b	9.8 $\pm$ 0.1b	10.7 $\pm$ 0.2b	5.4 $\pm$ 0.2b	8.0 $\pm$ 0.2b	46.0 $\pm$ 0.2b	51.0 $\pm$ 0.2b	
25	8.2 $\pm$ 0.1c	9.1 $\pm$ 0.1c	6.5 $\pm$ 0.1c	6.6 $\pm$ 0.1c	2.9 $\pm$ 0.1c	5.6 $\pm$ 0.2c	29.8 $\pm$ 0.2c	32.6 $\pm$ 0.2c	
30	6.3 $\pm$ 0.1d	—	—	—	—	—	—	—	
35	6.1 $\pm$ 0.02e	—	—	—	—	—	—	—	
<i>F</i>	7208.76	1561.97	447.50	283.39	107.70	289.20	3494.18	5460.70	
<i>P</i> > <i>F</i>	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	

Means in columns followed by the same letter are not significantly different ( $P > 0.05$ ; Fisher's protected LSD).

**Results**

**Duration of Development.** Most eggs hatched at 30 and 35°C, but the resulting crawlers failed to develop into second-instar nymphs. No eggs hatched at 40°C, and these eggs had shriveled up and were brown in coloration instead of yellow in fresh eggs. From 15 to 25°C, higher temperature significantly shortened the duration of development of every developmental stage (Table 1). Eggs hatched in 19–20 d at 15°C. This was 2–3 times the duration required at 25 and 35°C, respectively (Table 1). The duration of development in every nymphal instar at 15°C was consistently more than twice as long as that at 25°C. The mean total duration of nymphal development of females was 48 d at 15°C, 34 d at 20°C, and 22 d at 25°C. A female completed development within 30 d at 25°C, which was less than one-half as long as a female at 15°C. Males required a longer duration (between 2 and 3 d) for nymphal development than females between 15 and 25°C (15°C,  $F = 129.34$ ,  $df = 1, 261$ ,  $P < 0.0001$ ; 20°C,  $F = 45.83$ ,  $df = 1, 264$ ,  $P < 0.0001$ ; 25°C,  $F = 43.52$ ,  $df = 1, 167$ ,  $P < 0.0001$ ). Within the same temperature range, the duration from egg to adult development for a female was also significantly shorter than that for a male (15°C,  $F = 278.40$ ,  $df = 1, 261$ ,  $P < 0.0001$ ; 20°C,  $F = 332.20$ ,  $df = 1, 264$ ,  $P < 0.0001$ ; 25°C,  $F = 80.03$ ,  $df = 1, 167$ ,  $P < 0.0001$ ). Adult males emerged 3–9 d after the adult molt of females, depending on the temperature. The differences between the mean total dura-

tion of development between males and females decreased with increased temperature (Table 1).

**Survival Rates.** Most eggs hatched from 15 to 35°C, with the highest percentage of hatching at 15 and 25°C (Table 2). The fate of the colonies in different temperature treatments, however, differed among the treatments. Eggs and nymphs in higher temperature treatments (30–40°C) suffered very high mortality. At 40°C, all eggs failed to hatch. At 35°C, 90% of the eggs hatched, but all crawlers were desiccated within 2 d. Desiccated crawlers had shriveled up and were brown in coloration. No feeding by the crawlers on the host leaves was observed at 35°C. These crawlers appeared to have difficulty in shedding their egg cases. Crawlers in the 30°C treatment settled and fed on the host leaves but grew very slowly and suffered high mortality. All crawlers at 30°C died before completing the first-instar nymphal development.

Survival rates of nymphal instars at 15, 20, and 25°C were very high, ranging between 92 and 100% (Table 2). Almost all prepupal males (99%) inside the tests survived to the next instar (pupal). More than 95% of male pupae successfully emerged as adults from their tests. On average, >95% of third-instar females survived to adulthood. Survival rates between males and females within the corresponding developmental stages were not significantly different.

The proportion of eggs that survived to adult male (slightly >40%) was highest at 25°C (Table 2). The

**Table 2.** Survival rates in percent survival (means  $\pm$  SEM) of individual instars of male and female *P. madeirensis* at various constant temperatures

Temperature (°C)	Egg	Instars						Egg to adult <sup>a</sup>	
		First	Second	Third		Fourth	Female	Male	
				Female	Male	Male			
15	93.5 $\pm$ 1.2a	91.8 $\pm$ 1.1a	95.8 $\pm$ 1.5a	93.2 $\pm$ 1.4a	99.5 $\pm$ 2.0a	94.9 $\pm$ 1.6a	39.2 $\pm$ 2.1a	36.6 $\pm$ 2.0b	
20	88.6 $\pm$ 1.8b	95.1 $\pm$ 1.2a	97.4 $\pm$ 1.1a	97.7 $\pm$ 0.7a	99.9 $\pm$ 1.4a	97.3 $\pm$ 1.7a	44.3 $\pm$ 2.2a	35.2 $\pm$ 1.8b	
25	92.9 $\pm$ 1.7a	92.9 $\pm$ 1.5a	96.7 $\pm$ 1.1a	96.0 $\pm$ 1.8a	99.9 $\pm$ 1.8a	97.2 $\pm$ 1.8a	39.9 $\pm$ 2.9a	41.7 $\pm$ 2.9a	
30	89.4 $\pm$ 1.5b	0b	—	—	—	—	—	—	
35	90.0 $\pm$ 1.7b	0b	—	—	—	—	—	—	
<i>F</i>	4.39	1145.76	1.96	2.12	2.20	0.85	1.25	3.90	
<i>P</i> > <i>F</i>	0.0017	0.0001	0.1858	0.1212	0.1120	0.4266	0.3510	0.0218	

Means in columns followed by the same letter are not significantly different ( $P > 0.05$ ; Fisher's protected LSD).

<sup>a</sup> Survival rate of female (or male) from egg to adult was calculated by dividing the total number of adult female (or male) emerged by the total number of eggs used in the initial infestation, then multiplied by 100%.

**Table 3.** Proportion of females and adult male and female longevity at various constant temperatures

Temperature (°C)	Proportion of females	Male longevity (days)		Mated female longevity (days)		Virgin female longevity (days)	
	Means ± SEM	n	Means ± SEM	n	Means ± SEM	n	Means ± SEM
15	0.51 ± 0.02a	129	3.8 ± 0.2a	19	33.1 ± 0.9a	20	56.6 ± 3.2a
20	0.53 ± 0.02a	133	3.7 ± 0.2a	18	23.9 ± 0.8b	20	41.2 ± 3.5b
25	0.49 ± 0.03a	83	2.7 ± 0.2b	12	19.0 ± 1.3c	20	37.8 ± 1.8b
F	0.17		53.45		11.13		11.69
P > F	0.85		0.0001		0.0001		0.0001

Means in columns followed by the same letter are not significantly different ( $P > 0.05$ ; Fisher's protected LSD).  
n, number of adults.

survival rates from egg to adulthood were not significantly different among females in the three lower temperature treatments.

**Proportion of Females and Adult Longevity.** Secondary sex ratio, measured as the proportion of adult females, did not seem to differ among the temperature treatments (15, 20, and 25°C). Overall, ≈50% of all individuals in the cohorts were females (Table 3).

Adult longevity was significantly shortened at higher temperature (Table 3). A male lived for an average of  $3.7 \pm 0.1$  d at 15 and 20°C. The life span of adult males decreased to  $2.7 \pm 0.2$  d at 25°C. Ovipositing females in the mating treatment died immediately after the end of oviposition. The longevity of ovipositing females decreased from 33 d at 15°C to 19 d at 25°C. Virgin females in the nonmating treatment lived almost twice as long as the ovipositing females. A virgin female could live up to 2 mo at 15°C.

**Reproduction.** *P. madeirensis* reproduced sexually. None of the virgin females assigned to the nonmating treatment produced eggs. The percentages of females in the mating treatments that had produced eggs were 95% ( $n = 19$ ) at 15°C, 90% ( $n = 18$ ) at 20°C, and 60% ( $n = 12$ ) at 25°C. The females appeared to be receptive 1 d after adult molt and remained so up to 1 mo. A 1-mo-old virgin female could produce eggs 2 d after copulation with an adult male (J.-H.C., unpublished data).

Temperature had a strong influence on fecundity, preoviposition time, and the duration of reproduction (Table 4). Per capita lifetime fecundity was highest at 20°C, with an average of 491 eggs, which was equal to 27 eggs/d for 13 d. Females at 25°C had the lowest

fecundity and the shortest preoviposition time and duration of reproduction. A female at 25°C produced  $288 \pm 31$  eggs in 8 d, which averaged 36 eggs per day. The preoviposition time decreased from 19 d at 15°C to 11 d at 25°C.

## Discussion

Temperature had pronounced effects on the development, survival, and reproduction of *P. madeirensis*. In western Sicily, Sinacori (1995) found that *P. madeirensis* completed five to six generations per year in the field, with the first generation females appearing in May and June. The summer population of *P. madeirensis* consisted of overlapping generations, with individuals of various developmental stages. *P. madeirensis* generally overwintered as first- or second-instar nymphs on the underside of leaves or in crevices of bark. In the laboratory, the developmental time of female *P. madeirensis* on sprouted potatoes (*Solanum tuberosum* L.) ranged from 22 to 31 d (average, 26 d) at  $30 \pm 2^\circ\text{C}$  (Sinacori 1995). We cannot compare our results to those of Sinacori (1995) because we failed to establish colonies at 30°C. In a separate study, we reported that the total duration of development of female *P. madeirensis* on chrysanthemums plants were on average  $20.8 \pm 0.4$  d at 30°C,  $28.5 \pm 0.2$  d at 25°C, and  $47.3 \pm 0.6$  d at 20°C (Chong 2001).

Developmental time and reproduction capacity of *P. madeirensis* fall between two mealybug species of the same genus. Between 20 and 25°C, the cassava mealybugs, *P. manihoti* Matile-Ferrero and *P. herreni* Cox and Williams, completes development within 36–46 d (Lema and Herren 1985) and 41–91 d (Herrera et al. 1989), respectively. At 20°C, a female *P. manihoti* lived for ≈38 d and produced 585 eggs in 37 d of oviposition period (Lema and Herren 1985).

We failed to establish colonies of *P. madeirensis* at 30–40°C. In these temperature treatments, the eggs failed to hatch, and the crawlers died before molting. These eggs and crawlers may have suffered from physiological stresses caused by high temperature. One of the possible causes of mortality is the increase of vapor pressure deficit (VPD) at high temperature. VPD is the difference in the amount of moisture in the air and the amount of moisture in saturated air at a particular temperature (Prenger and Ling 2001). A higher VPD indicates that the plants or insects will lose more

**Table 4.** Fecundity, pre-oviposition time, and duration of reproduction (means ± SEM) of female *P. madeirensis* at various constant temperatures

Temperature (°C)	n	Fecundity (number of eggs)	Pre-oviposition time (days)	Duration of reproduction (days)
15	19	378 ± 31b	19.1 ± 0.7a	14.0 ± 0.9a
20	18	491 ± 38a	11.3 ± 0.3b	12.7 ± 0.8a
25	12	288 ± 31b	10.6 ± 0.8b	8.4 ± 1.0b
F		7.96	59.99	9.17
P > F		0.0011	0.0001	0.0004

Means in columns followed by the same letter are not significantly different ( $P > 0.05$ ; Fisher's protected LSD).  
n, number of ovipositing females.

moisture to the air. Percentage survival of western flower thrips, *Frankliniella occidentalis* (Pergande), was significantly lower in treatments of high VPDs and temperatures (Shipp and Gillespie 1993). The predatory mites, *Amblyseius cucumeris* (Oudemans) and *Neoseiulus fallacis* (Garman), also showed reduced survival rates at high VPDs (Kramer and Hain 1989, Shipp and van Houten 1997).

An understanding of the life history of *P. madeirensis* is crucial to the integrated management of this pest. In a typical greenhouse situation, with temperature ranging from 20 to 30°C, a female can complete its development in about a month and produces as many as 300 eggs in 1 wk. With rapid development, high survival rates, enormous reproductive capacity, and lack of early management, a *P. madeirensis* population could potentially reach a high level and cause significant economic damage to greenhouse ornamental production within an average crop cycle of 3 mo. Successful management of *P. madeirensis* depends on the early detection and control of the mealybug population.

Adult mealybugs are difficult to control because of the thick waxy secretion surrounding the body. Repeated applications of chemicals targeting immatures are required in suppressing the mealybug populations (Townsend et al. 2000). Control programs could take advantage of the fact that the development of *P. madeirensis* is temperature-dependent. At lower temperatures, the immatures have a longer duration of development and thus a wider window of opportunity for management. Because many insecticides are only effective against a specific developmental stage, development of a rotation schedule relies on the developmental rates and duration of exposure of susceptible stages (Townsend et al. 2000). Most natural enemies employed in biological control programs also prefer specific developmental stages of the mealybugs. Knowing the life history of *P. madeirensis*, pest managers can time the insecticide applications and releases of natural enemies against the most susceptible immature stages. Manipulating the temperature inside a greenhouse whenever possible may facilitate management of *P. madeirensis*.

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