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## EFFECTS OF TEMPERATURE AND RELATIVE HUMIDITY ON THE LIFE TABLE OF *PHENACOCCLUS SOLENOPSIS* TINSLEY (HEMIPTERA: PSEUDOCOCCIDAE) ON COTTON

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### ABSTRACT

*Phenacoccus solenopsis*, the cotton mealy bug, has emerged as a serious pest of cotton in India, necessitating basic studies on its development and survival at different temperatures (20, 25, 30 and 35 °C) and relative humidities (RH) (65, 75 and 85 ± 1 %) levels to ascertain optimal population growth. A life table was constructed using temperature and humidity. The nymphal duration was 20.2 d at 35 ± 1 °C and 65 ± 1% RH, but lengthened to 26.6 days at 20 ± 1 °C and both RH combinations. Adult longevity was 16.4 days at 20 ± 1 °C and 65% RH, but 10.8 days at 35 °C at the same RH; however it was 6.4 days at a temperature of 20 ± 1 °C and 75% RH. Fecundity was at its maximum (489 nymphs/female) at 35 ± 1 °C and 65% RH, with lower fecundity at 75% RH across all temperature levels. The net reproductive rate ( $R_0$ ) and finite rate of increase ( $\lambda$ ) were 141.3 females/female/generation and 1.24 fold per female per day, respectively at 35 ± 1 °C and 65% RH suggesting that the population would increase more than 140 times per generation and 1.24 times per female per day. The rates of increase at higher relative humidities were generally lower than at 65% RH. Nymphs failed to complete development at 85% RH at all temperature levels. The intrinsic rate of increase ( $r_m$ ) was the highest (0.215) at 35 °C in combination with 65% RH. Our results suggest that 35 ± 1 °C and 65% RH is the most favorable temperature and RH combination for the optimal population growth of the Punjab strain of *P. solenopsis*. Our study also predicts the expansion of this pest to other parts of the world in which the average temperature equals to 35 °C with 65% RH.

Key Words: net reproductive rate ( $R_0$ ), development, cotton, temperature, survival

### RESUMEN

*Phenacoccus solenopsis*, la cochinilla harinosa de algodón, se ha convertido en una plaga seria de algodón en la India, que requiere de estudios básicos sobre su desarrollo y supervivencia a diferentes temperaturas (20, 25, 30 y 35 °C) y niveles de humedad relativa (HR) (65, 75 y 85 ± 1%) para determinar las condiciones óptimas para el crecimiento de su población. Se construyó una tabla de vida basada en datos de temperatura y humedad. La duración del estadio ninfal fue 20.2 días a 35 ± 1 °C y 65 ± 1% HR, pero se extendió a 26.6 días a 20 ± 1 °C y a las dos combinaciones de HR. La longevidad del adulto fue 16.4 días a 20 ± 1 °C y 65% de HR, pero 10.8 días a 35 °C y la misma HR; sin embargo, fue de 6.4 días a 20 ± 1 °C y 75% RH. La fecundidad máxima fue 489 ninfas/hembra a 35 ± 1 °C y 65% de HR, con una menor fecundidad al 75% HR en todos los niveles de temperatura. La tasa neta de reproducción ( $R_0$ ) y la tasa finita de crecimiento ( $\lambda$ ) fue 141.3 hembras/hembra/generación y 1.24 veces por hembra por día, respectivamente, a 35 ± 1 °C y 65% de humedad relativa lo que sugiere que la población aumentaría más de 140 veces por generación y 1.24 veces por hembra por día. La tasa de incremento en humedades relativas más altas fue generalmente menor que en el 65% de HR. Las ninfas no se pueden completar el desarrollo a 85% de humedad relativa a todos los niveles de temperatura estudiados. La tasa intrínseca de crecimiento ( $r_m$ ) fue la más alta (0.215) a 35 °C en combinación con 65% de HR. Nuestros resultados sugieren que 35 ± 1 °C y 65% HR es la combinación de temperatura y HR más favorable para el crecimiento óptimo de la población de la cepa Punjab de *P. solenopsis*. Nuestro estudio también predice la expansión de esta plaga a otras partes del mundo en el que la temperatura media es igual a 35 °C con 65% de humedad relativa.

Palabras Clave: *Phenacoccus solenopsis*, tasa neta de reproducción ( $R_0$ ), desarrollo, algodón, temperatura, supervivencia

Cotton (*Gossypium* spp.; Malvales: Malvaceae) is an important cash crop in India. Cotton yields have gone up almost 70%, and cotton has an export potential greater than US\$ 100 billion (Business Standard 2012). Its production accounts for 9% of the total area under agriculture in India, which is also the largest in the world (Agarwal 2007). As of 2008-09, India was the 2nd largest cotton producer and consumer. In 2008, the textile industry accounted for 14.4% of the country's export earnings (Emeka 2009).

In India, 162 species of insects attack cotton at different plant stages (Dhawan 2004). The bollworm complex [*Helicoverpa armigera* Hubner, *Spodoptera litura* Fabricius (Noctuidae) and *Pectinophora gossypiella* Saunders (Gelechiidae)], *Bemisia tabaci* Gennadius (Aleyrodidae) and *Amrasca bigutulla bigutulla* Ishida (Hemiptera: Cicadellidae) are considered key pests, resulting in 50-60% loss in seed-cotton yield (Dhawan 2004). With the introduction of *Bt* cotton in 2002, the pest complex has changed considerably. Presently, a mealy bug species, *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae), has emerged as a major pest of cotton, vegetables and fruits (Tanwar et al. 2008). In India, *P. solenopsis* has been reported on many crops (Suresh & Kaviatha 2008) and is found to cause economic losses in various states including Punjab, Haryana, Rajasthan, Gujarat, Maharashtra, Andhra Pradesh and Tamil Nadu (Nagrare et al. 2009). Tanwar et al. (2008) has also reported this species on various non-crop hosts, such as *Parthenium hysteroporus* L. (Congress grass), *Trianthema monogyne* L. (Shanti or itsit), *Xanthium strumarium* L. (Gutputna), *Achyranthus aspera* L. (Puthkanda), *Hibiscus rosa-sinensis* L. (China rose), *Abelmoschus esculentus* (L.) Moench (okra), *Solanum lycopersicum* L. (tomato), *Solanum melongena* L. (eggplant) and *Capsicum* spp. (chilli pepper). There have been reports of another species of mealy bug, *Maconellicoccus hirsutus* (Green), infesting cotton in Punjab (Dhawan et al. 1980) and Gujarat (Muralidharan & Badaya 2000). Abbas et al. (2009) reported yet another invasive mealy bug, *Phenacoccus gossypiphilus* (Stanley), often indistinguishable from *P. solenopsis*, in India, New Caledonia, Thailand and Taiwan. Because of the polyphagous nature of *P. solenopsis*, previous researchers have used different host plants when investigating the biology of this species (David et al. 2009; Abbas et al. 2010; Sana-Ullah et al. 2011). The variations in methodologies have complicated efforts in estimating the life table parameters of *P. solenopsis*. Economic damage to a wide variety of crops makes it necessary to identify important ecological factors associated with this pest.

Temperature influences everything that an organism does (Clark 2003) including its biology, ecology and population dynamics. Temperature

is a major factor that influences the survival and abundance of mealybugs (Arai 1996; Chong et al. 2003, 2008; Amarasekare et al. 2008; Kim et al. 2008). In general, when temperature is low, insect development slows (Jarosik et al. 2004). Fecundity of an insect is influenced by different abiotic factors like RH, and temperature as well as the age and development of the females.

As of yet, no studies have been conducted on the survival and development of *P. solenopsis* at various combinations of temperature and RH. This is the first study presenting a concise life table of *P. solenopsis* on cotton at 4 temperatures (20, 25, 30 and 35 ± 1°C) along with 3 levels of RH (65, 75 and 85%). We determined the life table parameters, age-schedule of survival ( $l_x$ ), age-schedule of female births ( $m_x$ ), net reproductive rate ( $R_0$ ), mean length of generation ( $T$ ), intrinsic rate of increase ( $r_m$ ) and the finite rate of increase per day ( $\lambda$ ) of *P. solenopsis* under laboratory conditions. The goal of this research was to observe the effect of temperature and RH on development and survival of *P. solenopsis* under laboratory conditions in order to predict its distribution in the cotton producing regions of India.

## MATERIALS AND METHODS

### Cultivation of Test Plants

Seeds of a *Bt* cotton hybrid, RCH-134, were obtained from Rasi Seeds Pvt. Ltd., Tamil Nadu, India, and were sown in 20.3 cm diam ceramic pots in a screen house at the Entomological Research Farm, Department of Entomology, Punjab Agricultural University (PAU), Ludhiana, Punjab, India. Pots were filled with soil and buffalo farm yard manure mixture (1:1) up to 2 cm from the upper edge and watered as required. Thirty-day-old potted plants (12-18 leaves, 45-50 cm in height, vegetative stage) were used for conducting various laboratory experiments.

### Insect Rearing

Nymphs and adults of *P. solenopsis* were collected from different hosts including cotton, *Abutilon theophrasti* L., *A. aspera* L., *P. hysteroporus* L. and *Sida acuta* L. around cotton fields in the Punjab cotton belt and Punjab Agricultural University of Ludhiana. These fields were visited regularly to collect *P. solenopsis*. Insects were reared on different hosts (*P. hysteroporus*, *Xanthium* spp., *H. rosa-sinensis* and *G. arboreum*) in 20.3 cm diam ceramic pots from Apr to Dec in a screen house at the Entomological Farm of PAU in Ludhiana. The first generation was completed on the above mentioned hosts in order to exclude parasitized females from the experiment. Second generation, non-parasitized females were transferred to cotton plants for conditioning for 3 to

4 days. The conditioning was done because the adults were reared on different hosts prior to transfer on cotton to keep the colony uniform. During Dec to Feb (off-season), *P. solenopsis* was reared on cuttings of *H. rosa-sinensis* L. because cotton plants were not available during this period. These cuttings were replaced every 3 days. Adults and nymphs were transferred to new cuttings using a camel hair brush. The temperature up to 25 °C was maintained using an electrical heater in the laboratory.

#### Effect of Constant Temperature and RH

Age-specific life-tables of *P. solenopsis* on cotton were generated from data recorded from an experiment carried out in programmable environmental test chamber incubators (6 modes, REMI, Model CHM10S) at 12 combinations of temperature (20, 25, 30 and 35 ± 1 °C) and RH (65, 75 and 85 ± 1%) utilizing a completely randomized design (CRD) with 3 replications. Five adults were released on excised cotton leaves in a Petri dish containing agar film to keep the leaves turgid. Leaves from the canopy were replaced every 3 days. Ten newly eclosed nymphs produced from the 5 adults were transferred to a new set of Petri dishes where development and mortality were observed and recorded daily until the death of each individual. Newly oviposited nymphs in ovisacs from each of the gravid females were removed daily and the total number of immature per ovisac was counted. Ovisacs were removed from each female's abdomen with the help of a camel hair brush when it was ready to detach from the abdomen every 2 days during the initial ovipositional period or/and whenever the next ovisac developed. This process continued until the death of female occurred. The parameters recorded were:

- x = Pivotal age
- $l_x$  = Age specific survivorship for immature and female adults
- $m_x$  = age schedule for female birth

#### Statistical Analysis

Data on nymphal duration, adult longevity and fecundity were analyzed as a completely randomized design using one way analysis of variance (ANOVA) in SAS Enterprise Guide 4.2 and JMP 8.0 software (SAS 2010). Means were compared at  $\alpha = 0.05$  significance level using Duncan's Multiple Range Test (DMRT). The fecundity/female/generation was calculated by multiplying ovisac numbers with fecundity per ovisac.

The data on development, survival and reproduction of *P. solenopsis* at various levels of temperature and RH were used to compute the net reproductive rate ( $R_0 = \sum l_x m_x$ ), mean generation length ( $T = \sum x l_x m_x / R_0$ ), finite rate of increase ( $\lambda = e^{r_m}$ ) and intrinsic rate of increase ( $r_m = \log_e R_0 / T$ )

of *P. solenopsis* as per Atwal & Bains (1974). To calculate the precise value of  $r_m$ , we followed the graphical method outlined by Southwood (1978). The graph was constructed by plotting the value of  $e^{(7-r_m)x} (l_x m_x)$  on the x-axis and the  $r_m$  value on the y-axis. The points were plotted against the value of  $r_m$  and 2 other  $r_m$  values on its lower and upper side and these were joined by a line. A perpendicular line from the x-axis against the value of 1097 was drawn to join the y-axis. The point where the perpendicular line joined was taken as the precise value of  $r_m$ . Alternatively, in the above equation, 2 values of  $r_m$  were substituted and then the precise value of  $r_m$  was calculated via transposition method (Atwal & Bains (1974) as follows:

$$\sum e^{(7-r_m)x} (l_x m_x) = 1097$$

## RESULTS

### Nymphal Development

Variation in temperature and RH significantly affected the developmental rate of *P. solenopsis* on cotton. Development from newly laid nymph to adult was significantly faster at 35 ± 1 °C and 65 ± 1% RH (20.2 days) or 75% RH (20.8 days) (Table 1). There was a progressive lengthening of development duration as temperatures decreased at both levels of RH. Development time was the longest (26.6 days) at 20 ± 1 °C with RH levels of 65% and 75% (Table 1). At 25, 30 and 35 °C, nymphs developed more quickly at 65% RH than at 75% RH. At 85% RH, the development of nymphs was not completed due to a fungal infection which was not identified in this study.

### Adult Longevity

The longevity of the adult stage was significantly affected by different combinations of temperature and RH. At 65% RH adult longevity was shortest (10.8 days) at 35 °C, and at 75% RH, it was shortest (6.4 days) at 20 °C (Table 1). The adults survived longer at other combinations of temperatures and 65 % RH with the longest survival (16.4 days) at 20 °C. At 75% RH, adult longevity was relatively shorter at 20 °C (6.4 days) than at 25 °C (10.4 days) and 30 °C (12.2 days).

### Fecundity

The fecundity of *P. solenopsis* was significantly affected by different temperatures and RH combinations. Adults produced 81.0 and 73.8 nymphs per female per ovisac at 35 ± 1 °C at 65 ± 1% RH ( $F = 32.85$ ,  $df = 3$ ,  $N = 34$ ,  $P = <0.0001$ ) and 75% ( $F = 53.00$ ,  $df = 3$ ,  $N = 45$ ,  $P = <0.0001$ ) RH, respectively (Table 1). Fecundity declined progressively as temperatures decreased from 35 °C to 20 °C at both 65% RH and 75% RH. The lowest number of

TABLE 1. EFFECT OF DIFFERENT TEMPERATURES AND RELATIVE HUMIDITIES ON THE DEVELOPMENT AND FECUNDITY OF *PHENACOCCLUS SOLENOPSIS*.

Constant temperature (°C)	20 ± 1 °C	25 ± 1 °C	30 ± 1 °C	35 ± 1 °C	N	df	F-value	Pr
<b>At 65±1% RH</b>								
Nymphal duration(days)	26.6 ± 0.40 a (25-28)	24.0 ± 0.42 b (22-26)	21.0 ± 0.39 c (19-23)	20.2 ± 0.37 c (19-22)	34	3	32.85	< 0.0001
Female adult longevity (days)	16.4 ± 0.24 a (16-17)	13.4 ± 0.37 b (12-15)	14.0 ± 0.39 b (12-16)	10.8 ± 0.58 c (9-12)	34	3	16.67	< 0.0001
Fecundity (Nymphs/ovisac)	54.4 ± 3.73 b (34.00-72.00)	63.6 ± 3.27 b (47.00-79.00)	77.4 ± 3.26 a (63.00-99.00)	81.0 ± 3.02 a (79.00-103.00)	60	3	13.70	< 0.0001
Number of ovisacs/ female	3.0 ± 0.17 b	3.0 ± 0.17 b	4.0 ± 0.16 a	4.0 ± 0.24 a	60	3	9.33	< 0.0001
Total fecundity/female	167.4 ± 18.94 b	186.6 ± 9.95 b	315.6 ± 26.21 a	327.6 ± 27.82 a	60	3	14.71	< 0.0001
<b>At 75±1% RH</b>								
Nymphal duration(days)	26.6 ± 0.27 a (25-28)	25.0 ± 0.29 b (23-27)	22.2 ± 0.44 c (20-24)	20.8 ± 0.39 d (19-22)	45	3	53.00	< 0.0001
Female adult longevity (days)	6.4 ± 0.16 a (6-7)	10.4 ± 0.13 b (10-11)	12.2 ± 0.25 b (11-13)	10.8 ± 0.38 c (9-12)	45	3	101.31	< 0.0001
Fecundity (nymphs/ovisac)	39.2 ± 4.81 c (21.00-48.00)	54.6 ± 5.01 b (38.00-66.00)	68.8 ± 7.63 a (52.00-94.00)	73.8 ± 7.04 a (54.00-98.00)	80	3	29.46	< 0.0001
Number of ovisacs/female	2.0 ± 0.31 c	3.0 ± 0.44 b	4.0 ± 0.32 a	4.0 ± 0.32 a	80	3	34.83	< 0.0001
Total fecundity/female	73.4 ± 8.67 c	162.8 ± 29.51 b	273.2 ± 32.82 a	300.0 ± 49.85 a	80	3	46.00	< 0.0001

Means within a row followed by the same letters are not significantly different at  $\alpha = 0.05$  (Duncan's Multiple Range Test (DMRT)); N = number of observations and df = degree of freedom. Value in parentheses indicates the range.

At 85 ± 1% RH development was not completed

nymphs (54.4 and 39.2) per female per ovisac was produced at  $20 \pm 1$  °C at 65 and 75% RH, respectively (Table 1). Total numbers of ovisacs produced per female ranged between 3 to 4 at  $65 \pm 1\%$  RH, however, this range was 2 to 4 at all temperatures and  $75 \pm 1\%$  RH. Total fecundity per female was the highest (327.6) at 35 °C and 65% RH, which was statistically at par with total fecundity 30 °C and 65% RH (316.6). A similar trend toward high total fecundity at high temperatures was seen at 75% RH.

#### Life Table Parameters at 65% RH

The commencement of reproduction varied substantially with temperature (Table 2). Adults were found after only 21 days at 35 °C, compared to 30 days at 20 °C. Females reproduced early (21st day) and also stopped reproducing early (27th day) at 35 °C. At 20 °C, oviposition did not begin until the 30th day of the life cycle and it terminated on the 37th day.

The net reproductive rate ( $R_0$ ) was lowest at  $20 \pm 1$  °C (i.e., 59.25), and highest (141.31) at  $35 \pm 1$  °C (Table 2). The population increased by 122.9 and 141.3 times at  $30 \pm 1$  °C and  $35 \pm 1$  °C, respectively (Table 3), suggesting that 30 °C and 35 °C are the most favorable temperatures for population growth of *P. solenopsis* at 65% RH.

The finite rate of increase ( $\lambda$ ) of *P. solenopsis* was highest at  $35 \pm 1$  °C, which means that its population multiplied 1.24 times per female per day (Table 4). The respective values of  $\lambda$  were lower (1.14 and 1.15 times, respectively) at  $20 \pm 1$  °C and  $25 \pm 1$  °C. The mean length of generation (T) was the lowest (23.0 days) at  $35 \pm 1$  °C (Table 1), showing a progressive increase with a decrease in temperature.

The intrinsic rate of increase (approximate  $r_m$ ) of *P. solenopsis* on cotton was the lowest (0.125) at  $20 \pm 1$  °C, but increased as temperature increased, with its maximum (0.215) at  $35 \pm 1$  °C. The precise value of  $r_m$  was the highest at 35 °C, suggesting this is the most suitable temperature for the multiplication of *P. solenopsis* when the RH is 65% (Table 4; Fig. 1).

#### Life Table Parameters at 75% RH

Adults started to eclose on the 22nd day at 35 °C, while eclosion did not begin until day 27 and day 28 at 20 °C and 25 °C, respectively (Table 3). At 20 °C, however, nymphs took a shorter time (27 days) to develop into adults at 75% RH than at 65% RH (30 days). Oviposition took place over a period of 6 days at 25 °C, and 7 days at 30 °C and 35 °C, but at 20 °C, it was only 2 days. The adults stopped ovipositing at day 28 at 35 °C, while oviposition was extended up to day 33 at 25 °C.

The net reproductive rate ( $R_0$ ) was the lowest and merely marginal (1.57) at  $20 \pm 1$  °C, while

TABLE 2. AGE-SCHEDULE TABLE OF SURVIVAL AND BIRTHS OF *PHENACOCCLUS SOLENOPSIS* ON BT COTTON VARIETY 'RCH-134' AT 4 DIFFERENT TEMPERATURES AND 65% RH.

Pivotal age in days (x)	Age-schedule of survival ( $l_x$ )	Age-schedule of female births ( $m_x$ )	$l_x m_x$	$x l_x m_x$
<b>20 ± 1 °C</b>				
0.5-28.5	Immature stages			
29.5	0.31	53.80	16.68	492.06
30.5	0.19	0.00	0.00	0.00
31.5	0.18	47.13	8.48	267.12
32.5	0.18	45.60	8.21	266.83
33.5	0.16	49.87	7.98	267.33
34.5	0.16	47.20	7.55	260.54
35.5	0.16	44.00	7.04	249.92
36.5	0.08	41.39	3.31	120.82
37.5	0.05	0.00	0.00	0.00
38.5	0.04	0.00	0.00	0.00
39.5	0.02	0.00	0.00	0.00
40.5	0.02	0.00	0.00	0.00
41.5	0.02	0.00	0.00	0.00
			$\sum l_x m_x (= R_0) = 59.25$	$\sum x l_x m_x = 1924.62$
<b>25 ± 1 °C</b>				
0.5-26.5	Immature stages			
27.5	0.26	60.67	15.78	433.84
28.5	0.26	0.000	0.00	0.00
29.5	0.19	69.91	13.28	391.82
30.5	0.19	65.13	12.37	377.44
31.5	0.18	0.000	0.00	0.00
32.5	0.18	63.13	11.36	369.29
33.5	0.11	63.20	6.95	232.89
34.5	0.08	0.00	0.00	0.00
35.5	0.02	0.00	0.00	0.00
			$\sum l_x m_x (=R_0) = 60.02$	$\sum x l_x m_x = 1805.28$
<b>30 ± 1 °C</b>				
0.5-22.5	Immature stages			
23.5	0.44	79.04	34.78	817.28
24.5	0.41	0.00	0.00	0.00
25.5	0.36	75.69	27.25	694.82
26.5	0.29	78.31	22.71	601.79
27.5	0.29	76.09	22.07	606.82
28.5	0.24	0.00	0.00	0.00
29.5	0.20	80.63	16.13	475.72
30.5	0.11	0.00	0.00	0.00
31.5	0.06	0.00	0.00	0.00
32.5	0.03	0.00	0.00	0.00
33.5	0.03	0.00	0.00	0.00
			$\sum l_x m_x (=R_0) = 122.93$	$\sum x l_x m_x = 3196.43$
<b>35 ± 1 °C</b>				
0.5-19.5	Immature stages			
20.5	0.51	78.93	40.26	825.23
21.5	0.35	71.14	24.89	535.33
22.5	0.35	0.00	0.00	0.00
23.5	0.27	87.33	23.58	554.11
24.5	0.24	80.68	19.36	474.40
25.5	0.21	81.85	17.19	428.31
26.5	0.18	89.20	16.06	425.48

TABLE 2. (CONTINUED) AGE-SCHEDULE TABLE OF SURVIVAL AND BIRTHS OF *PHENACOCOCCUS SOLENOPSISON* BT COTTON VARIETY 'RCH-134' AT 4 DIFFERENT TEMPERATURES AND 65% RH.

Pivotal age in days (x)	Age-schedule of survival ( $l_x$ )	Age-schedule of female births ( $m_x$ )	$l_x m_x$	$x l_x m_x$
27.5	0.012	0.00	0.00	0.00
28.5	0.11	0.00	0.00	0.00
29.5	0.04	0.00	0.00	0.00
30.5	0.02	0.00	0.00	0.00
			$\sum l_x m_x (= R_0) = 141.31$	$\sum x l_x m_x = 3252.86$

at  $35 \pm 1$  °C it was the highest (89.43) (Table 3), suggesting that *P. solenopsis* populations will increase a maximum of 86.4 times per generation at 35 °C. The  $R_0$  values under 75% RH were much lower than those under 65% RH. Furthermore, nymphs failed to complete development and no adult eclosion was observed at any temperature in combination with 85% RH (Table 4).

The finite rate of increase ( $\lambda$ ) was the highest at 35 °C (1.2) and showed a progressive decline with a decrease in temperature (Table 4). This suggests that the *P. solenopsis* population would increase 1.2 times per female per day. The mean generation time (T) was the longest at  $25 \pm 1$  °C (29.3 days), while it was the shortest at  $30 \pm 1$  °C (23.9 days).

A similar trend was observed for the intrinsic rate of increase (approximate  $r_m$ ) of *P. solenopsis* at 65% RH with different temperature combinations. The  $r_m$  value was the lowest (0.02) at  $20 \pm 1$  °C and the highest (0.18) at  $35 \pm 1$  °C (Table 4; Fig. 1). The precise value of  $r_m$  was the highest at 30 °C (0.25), suggesting that 30 °C is the most favorable temperature for reproduction when the RH is 75%.

#### Life Table Parameters at 85% RH

At 85% RH, *P. solenopsis* nymphs survived for 6, 7, 14 and 15 d at 20, 25, 30, 35 °C, respectively, with the shortest duration of survival at 35 °C and the longest at 20 °C. Compared with the other RH percentages, the immature stages persisted for a longer period at 65% RH (20-29 days) and 75% RH (21-27 days) than at 85% RH under which they died before eclosing to adults.

#### DISCUSSION

*Phenacoccus solenopsis* has recently become a serious pest in Asia. Little work on the effect of temperature and RH on its development, fecundity and life history parameters on cotton have been carried out. This study was conducted to describe the life history of *P. solenopsis*, and it was focused on its development, multiplication and birth rate on cotton under laboratory conditions. This study also investigated the effects on reproductive success of *P. solenopsis* of combinations of

temperature and RH. Our results indicate that age-specific development and fecundity increase with temperature up to  $35 \pm 1$  °C at 65% RH. A similar trend was observed in net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r_m$ ), finite rate of increase ( $\lambda$ ) and precise value of  $r_m$ . Overall, life cycle duration decreased as temperature increased and was the lowest at 35 °C.

Very little work has been undertaken to quantitatively describe the basic life table parameters of *P. solenopsis*. As a result, it is difficult to correlate this research with published literature, although related species will be discussed for the support of this research. Fand et al. (2010) investigated the life history parameters of *P. solenopsis* at  $27 \pm 2$  °C and  $65 \pm 5\%$  RH, and their values for net reproductive rate ( $R_0$ ), mean generation time (T) and fecundity per female were higher than we found, while their values for intrinsic rate of increase ( $r_m$ ) and finite rate of increase ( $\lambda$ ) were lower than we observed at either of 25 °C or 30 °C combined with 65% RH.

While no life table research work has been performed previously on *P. solenopsis*, such research on congeneric species has shown that 25 °C was the optimum temperature for the development of *P. solani* (Nakahira & Arakawa 2006), and the population growth rate of *P. manhoti* increased between 20 °C and 30.5 °C (Lemma & Herren 1985). In addition, a life table of *P. parvus* was constructed on 7 plant species, out of which *Lantana camara* L. (Lamiales: Verbenaceae) afforded the maximum net reproductive rate, and while *Phaleria clerodendron* (F. Muell.) Benth. (Malvales: Thymelaeaceae) afforded the lowest (Marohasy 1997).

However, there are also studies with findings different from our results. Chong et al. (2003) reported no colony of *P. madeirensis* on chrysanthemum (*Dendrathermum × grandiflora* Kitam.) between 30 °C and 40 °C. We found that the maximum development of *P. solenopsis* occurred at 35 °C, the highest temperature employed in our experiments. In contrast *Paracoccus marginatus* has maximum fecundity at 25 °C on *H. rosa-sinensis* L., while adult longevity, pre-oviposition and oviposition period increased with a decrease in temperature to 25 °C (Amarasekare et al. 2008). This research on *P. marginatus* was conducted near the southern tip of the Florida

TABLE 3. AGE-SCHEDULE TABLE OF SURVIVAL AND BIRTHS OF *PHENACOCCLUS SOLENOPSIS* ON BT COTTON VARIETY 'RCH-134' AT DIFFERENT TEMPERATURES AND 75% RH.

Pivotal age in days (x)	Age-schedule of survival ( $l_x$ )	Age-schedule of female births ( $m_x$ )	$l_x m_x$	$x l_x m_x$
<b>20 ± 1 °C</b>				
0.5-25.5	Immature stages			
26.5	0.02	40.00	0.80	21.20
27.5	0.02	38.40	0.77	21.12
			$\sum l_x m_x (R_0) = 1.57$	$\sum x l_x m_x = 42.32$
<b>25 ± 1 °C</b>				
0.5-26.5	Immature stages			
27.5	0.12	53.10	6.37	175.23
28.5	0.12	0.00	0.00	0.00
29.5	0.12	76.63	9.22	271.24
30.5	0.09	36.73	3.30	100.81
31.5	0.09	0.00	0.00	0.00
32.5	0.03	52.80	1.58	51.48
33.5	0.02	0.00	0.00	0.00
34.5	0.01	0.00	0.00	0.00
			$\sum l_x m_x (=R_0) = 20.47$	$\sum x l_x m_x = 599.16$
<b>30 ± 1 °C</b>				
0.5-22.5	Immature stages			
23.5	0.44	79.04	34.78	817.28
24.5	0.41	0.00	0.00	0.00
25.5	0.36	75.69	27.25	694.82
26.5	0.29	78.31	22.71	601.79
27.5	0.29	76.09	22.07	606.82
28.5	0.24	0.00	0.00	0.00
29.5	0.20	80.63	16.13	475.72
30.5	0.11	0.00	0.00	0.00
31.5	0.06	0.00	0.00	0.00
32.5	0.03	0.00	0.00	0.00
33.5	0.03	0.00	0.00	0.00
			$\sum l_x m_x (=R_0) = 62.89$	$\sum x l_x m_x = 1500.13$
<b>35 ± 1 °C</b>				
0.5-20.5	Immature stages			
21.5	0.36	63.49	22.86	491.38
22.5	0.36	0.00	0.00	0.00
23.5	0.25	75.01	18.75	440.66
24.5	0.24	79.30	19.03	466.30
25.5	0.23	64.63	14.87	393.94
26.5	0.21	0.00	0.00	0.00
27.5	0.13	84.00	10.92	300.30
28.5	0.11	0.00	0.00	0.00
29.5	0.08	0.00	0.00	0.00
30.5	0.05	0.00	0.00	0.00
31.5	0.04	0.00	0.00	0.00
32.5	0.02	0.00	0.00	0.00
			$\sum l_x m_x (=R_0) = 86.43$	$\sum x l_x m_x = 2092.58$

peninsula, where temperatures rarely reach 35 °C and development occurs year round, whereas temperatures in Punjab may exceed 45 °C in summer and plunge to single digits in winter. Clearly

the differences in temperature effects on development and reproduction between various species may be caused either by adaptations to local temperatures or to a different choices of host plant,



TABLE 4. EFFECT OF DIFFERENT CONSTANT TEMPERATURES AT EITHER 65% OR 75% RH ON THE MULTIPLICATION OF *PHENACOC-CUS SOLENOPSIS*.

Temperature (°C)	Net reproductive rate ( $R_0$ )	Mean length of generation ( $T = \sum l_x m_x / R_0$ )	Intrinsic rate of increase ( $r_m = \log_e R_0 / T$ )	Precise value of $r_m$	Finite rate of increase/day ( $\lambda = e^{r_m}$ )
<b>65% RH</b>					
20 ± 1 °C	59.25	32.48	0.125	0.129	1.139
25 ± 1 °C	60.02	30.08	0.136	0.137	1.146
30 ± 1 °C	122.93	26.00	0.185	0.188	1.203
35 ± 1 °C	141.31	23.02	0.215	0.221	1.240
<b>75% RH</b>					
20 ± 1 °C	1.57	26.96	0.020	0.015	1.020
25 ± 1 °C	20.47	29.28	0.103	0.108	1.108
30 ± 1 °C	62.89	23.85	0.174	0.147	1.190
35 ± 1 °C	86.43	24.21	0.184	0.188	1.202

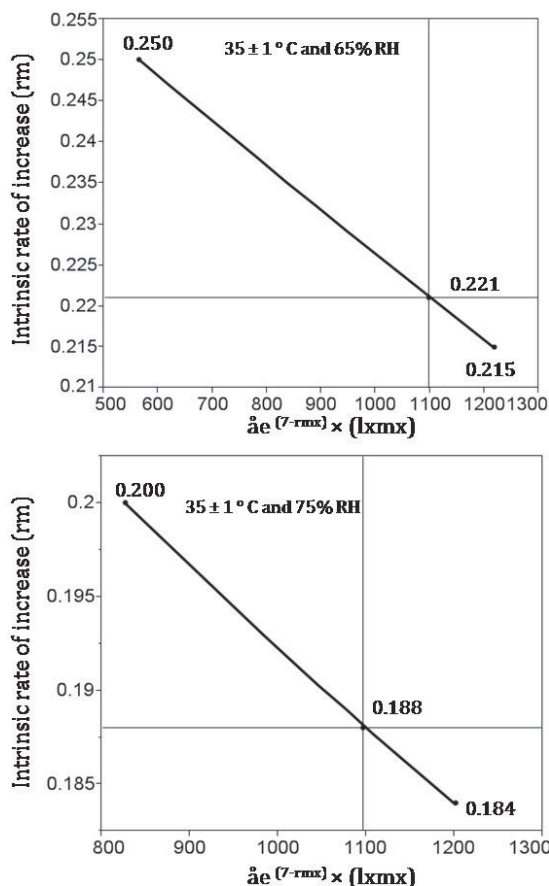


Fig. 1. Determination of precise value of  $r_m$  of *Phenacoccus solenopsis* on Bt cotton variety 'RCH-134' at 35 °C in combination with 65% and 75% RH under laboratory conditions (analysis with JMP8 software). Upper panel: value of  $r_m$  at 35 °C and 65% RH; Lower panel: value of  $r_m$  at 35 °C and 75% RH.

TABLE 5. MEAN DURATION OF DIFFERENT LIFE STAGES AT DIFFERENT COMBINATIONS OF TEMPERATURE (°C) AND RH.

Temperature (°C) + % RH	Duration (days)		
	Immature stages	Adult stage	Oviposition period
20 + 65%	29	13	8
75%	26	3	2
85%	6	—	—
25 + 65%	27	9	7
75%	27	9	6
85%	7	—	—
30 + 65%	23	11	7
75%	21	11	7
85%	14	—	—
35 + 65%	20	11	8
75%	21	12	7
85%	15	—	—

—No adults formed at 85% RH

because host plant profoundly affect insect physiology and development.

Previous studies that investigated the development of *Maconellicoccus hirsutus* on *H. rosa-sinensis* L. at 6 constant temperatures (15, 20, 25, 27, 30 and 35 ± 1 °C) revealed that female longevity decreased with an increase in temperature (Chong et al. 2008) and the development period decreased with an increase in temperature (Persad & Khan 2002). A similar trend was observed in another study using *M. hirsutus* on pumpkin (*Cucurbita moschata* Duchesne ex Poir.; Cucurbitales: Cucurbitaceae), where this species of mealy bug completed development in 48 days and 29 days at 25 °C and 27.2 °C, respectively (Babu & Azam 1987). The data gathered from this research will be helpful to narrow down the information gap on

the development and survival of *P. solenopsis* at different temperature and RH combinations.

The information presented in the life tables provides a foundation for subsequent computation and comparison of the development threshold and thermal constant of *P. solenopsis*. In addition to temperature and RH, photoperiod/fertility/sex ratio/plant type can influence the survival and development of *P. solenopsis*. Further experiments designed to investigate the effect of photoperiod and other biotic factors on the development of this pest, along with temperature and RH, may be the next step in this process. At high temperatures, *P. solenopsis* completes a life cycle approximately twice as fast as compared to lower temperatures, which may reduce the exposure time to insecticides and/or natural enemies, or both. This study may also be valuable in predicting the distribution and abundance of *P. solenopsis* in the state of Punjab and help in the timely and effective management of this pest.

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