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A temperature-based phenology model for predicting development, survival and population growth potential of the mealybug, *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae)

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ABSTRACT

The temperature-dependent population growth potential of *Phenacoccus solenopsis* Tinsley, a highly polyphagous and invasive mealybug species, was studied on sprouted potatoes under laboratory conditions at six constant temperatures (15–40 °C). Several non-linear equations were fitted to the obtained data to model temperature-dependent population growth and species life history. The established equations for each life age/stage of the species were compiled to obtain an overall temperature-dependent phenology model. The life table parameters of *P. solenopsis* were estimated using stochastic simulation centred on a rate summation and cohort up-dating approach. The theoretical lower development threshold temperatures estimated using linear regressions applied to mean development rates were 11.2, 8.9, 9.8 and 12.7 °C, and the thermal constants for development were 93.7, 129.8, 97.1 and 100.0 degree days (DD) for nymph 1, nymph 2, nymph 3 and male pupa stages, respectively. The developed phenology model predicted temperatures between 25 and 35 °C as the favourable range for *P. solenopsis* development, survival and reproduction. *P. solenopsis* population attained a maximum net reproductive rate (107–108 females/female/generation) and total fecundity (216.6–226.5 individuals/female/generation) at temperatures between 25 and 30 °C. Mean length of generations decreased from 75.6 days at 15 °C to 21 days at 40 °C. The maximum finite rate of increase (1.12–1.16 females/female/day) and shortest doubling time (4.3–6.1 days) were also observed at temperatures between 25 and 35 °C. The simulation of phenology model at fluctuating temperatures indicated that *P. solenopsis* populations might potentially increase with a finite rate of 1.06 females/female/day with an average generation time of 58.7 days and a doubling time of 12.1 days. The obtained life table parameters were reasonably similar when compared with literature data. The present model can be simulated spatially for estimating the pest risk and undertaking agro-ecoregion specific pest management strategies.

1. Introduction

The mealybug, *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae), native to North America (Williams and Granara de Willink, 1992) is a highly invasive and serious pest of cotton and vegetables of economic importance in tropical and subtropical parts of the world. *P. solenopsis* is distributed over a wide range of agro-ecological zones and presently has been reported from more than 24 countries worldwide where it causes significant crop losses (Williams and Granara de Willink, 1992; Abbas et al., 2005; Akintola and Ande, 2008; Nagrare et al., 2009; Wang et al., 2010). Recent outbreak of *P. solenopsis* in India caused large scale devastation in cotton resulting in 30–40% yield losses in both *Bt* and non-*Bt* cotton crops (Dhawan et al., 2007; Jhala et al., 2008; Nagrare et al., 2009; Tanwar et al., 2011). After its first documentation in 2005 in the North-Western parts of Gujarat State (Jhala et al., 2008), *P. solenopsis* has spread to almost all the nine major cotton growing States of India (Nagrare et al., 2009; Vennila et al., 2010b). The pest is reported to infest several other crops of economic importance such as okra (*Abelmoschus esculentus* Linn.), chilli (*Capsicum annum* Linn.), brinjal (*Solanum melongena* Linn.), tomato (*Solanum lycopersicum* Linn.), pomegranate (*Punica granatum* Linn.), guava

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(*Psedium guajava* Linn.), grapes (*Vites vinifera* Linn.), ornamentals like *Hibiscus rosa-sinensis* Linn., as well as various weeds (Nagrare et al., 2009; Vennila et al., 2010b; Tanwar et al., 2011).

The behaviour, biology and ecology of *P. solenopsis* have been extensively studied in different parts of the world, in both field and laboratory (Abbas et al., 2005; Dhawan et al., 2007; Akintola and Ande, 2008; Fand et al., 2010; Wang et al., 2010; Vennila et al., 2010a; Tanwar et al., 2011; Asifa et al., 2012; Prasad et al., 2012). A linear degree-day model based on the accumulation of heat units above a lower temperature threshold has been developed for *P. solenopsis* (Prasad et al., 2012). However, due to non-linearity of the development curve, especially under fluctuating temperature regimes, linear models produce errors at temperature extremes and hence are considered poor predictors of insect development (Stinner et al., 1974). The non-linear relationship between rate of insect development and temperature existing at higher temperatures can be used to estimate the optimum temperature for development (Briere et al., 1999). Earlier studies predicting temperature-dependent population growth potential of *P. solenopsis* have largely focused on the use of developmental thresholds and thermal constants (Prasad et al., 2012), but no emphasis was given to the simulation of variability in development times, mortality and fecundity with temperature changes. Phenology models that use non-linear functions of higher biological significance and include stochastic functions for simulating variability in development times within a population can provide better results than linear models (Logan et al., 1976; Sharpe et al., 1977; Sporleder et al., 2004).

Knowledge of the temperature-dependent population growth potential is imperative for understanding population dynamics and implementing agro-ecoregion specific pest control strategies, especially in the context of predicted global climate change. The global climate change is predicted to raise the mean surface temperature of earth by 1.5–5.8 °C by the end of 2100 (Govindasamy et al., 2003; Hijmans et al., 2005; IPCC, 2007). Temperatures throughout the tropics and subtropics have been found to be highly congenial for the spread and multiplication of *P. solenopsis*, and these are the regions of the world which will be at the greatest risk of looming climate change. Thus, future temperature increases in these areas due to climate change are expected to exacerbate damage due to *P. solenopsis*. The risk for *P. solenopsis* invasion has been modelled to some extent. However, previous models have addressed only its geographical distribution based on the relationship between occurrence data and climatic factors (Wang et al., 2010; Fand, 2012), and estimation of development thresholds (Prasad et al., 2012). The objective of this study was to develop a comprehensive temperature-based population model for *P. solenopsis* that permits prediction of population growth potential and seasonal dynamics in various agro-ecological zones of India and the world at large, and will also aid in forecasting the probable pest aggravation due to climate change. The Insect Life Cycle Modelling (ILCYM) software developed by the International Potato Centre (CIP), that supports the development of process-based temperature-driven and age-stage structured insect phenology models was used (Tonnang et al., 2013).

2. Materials and methods

2.1. Maintenance of *P. solenopsis* culture

The mealybugs collected from the infested plants in the field *S. lycopersicum* Linn. (tomato), *H. rosa-sinensis* Linn. (china rose) and *Parthenium hysterophorous* Linn. (carrot weed) were cultured in the laboratory on sprouted potato tubers at room temperature (27 ± 2 °C), 65 ± 5% RH and natural photoperiod (Gautam, 2008). About 2-3 gravid females of *P. solenopsis* were released on the sprouted potato tubers kept in plastic jars (20 × 10 cm diameter) with the help of a camel hairbrush (No. 000). The jars were covered with clean black muslin cloth tied with rubber band. The mealybug culture that developed after 10–12 days was used for subsequent studies.

2.2. Experimental procedures for data collection

2.2.1. General rearing conditions

The effects of temperature on the behavioural biology of *P. solenopsis* were studied in cohorts of single life stages in controlled incubation chambers at six constant temperatures i.e. 15, 20, 25, 30, 35 and 40 °C. The required temperatures inside the incubators were regularly monitored using a standard thermometer. The experiments in which temperatures fluctuated more than ±1.0 °C were discarded and not included in the analysis. The relative humidity was maintained between 60 and 80% and photoperiod regime was kept at 10L:14D h.

2.2.2. Cohort life table studies at constant temperatures

2.2.2.1. Development of immature life stages. A group of 25 newly emerged crawlers (0–24 h old) of *P. solenopsis* from the stock colony was transferred into a small plastic jar (10 × 7.5 cm size) containing a medium sized sprouted potato tuber. The jar was covered with muslin cloth tied with a rubber band. The experiment was replicated 12 times, a total of 300 crawlers being observed at each tested temperature. The insects were observed daily under a stereomicroscope for subsequent development and survival. A similar procedure was followed for the cohorts of second and third instar mealybugs. The development time and mortality of nymphs during each instar were recorded daily. The sex of cohort individuals was determined after the occurrence of the second moult. The development of females and males was tracked separately from this point onward. Ten newly woven cocoons (10 replicates) were separated and observed until completion of the immature male development of the species.

2.2.2.2. Adult longevity and reproduction. Six newly moulted adult females (0–24 h old) from the colony of *P. solenopsis* were confined to a plastic jar (10 × 7.5 cm size) containing a sprouted potato tuber. The total daily fecundity of surviving females in the cohort was recorded and the average fecundity per female was calculated. A total of 30 individual females were observed in five replicates at each temperature. Similarly, freshly emerged winged adults from puparia were observed for their longevity at respective temperatures. The survival time was recorded separately for males and females.

2.3. Model parameterization and analysis

2.3.1. Modelling software

The life table data collected at different constant temperatures were used to develop a temperature-dependent phenology model of *P. solenopsis* using the Insect Life Cycle Modelling (ILCYM, version 3.0) software developed by International Potato Centre (Freely available at the CIP web-site: http://www.cipotato.org) (Tonnang et al., 2013). The present study applied two modules of ILCYM i.e. the 'model builder' for development of the phenology model, and the 'validation and simulation' for estimation of the life table parameters. The model builder component of the software contains a library of several empirical linear and nonlinear models proposed to define critical temperature effects in the insect's development. The validation and simulations module demonstrates the application of the phenology models for estimating and simulating insect

population abundance under constant and fluctuating temperatures.

2.3.2. Development time and its distribution

To estimate the distribution of development rates of *P. solenopsis* immature stages at various constant temperatures, we used the hypothesis that the standard deviation of the development time is proportional to the mean or median of each distribution. This means the intrinsic distributions of development times of an insect at different temperatures fall on top of each other (same shape property) when normalized by the mean or median of each distribution (Sharpe et al., 1977; Curry et al., 1978). Thus, the median rate of development in relation to temperature can be rationalized as a lognormal distribution of tolerances among individuals of cohort.

To accounting for variability among individuals, the concepts of rate summation (Curry et al., 1978) and same shape (Sharpe et al., 1977) are included into the formulation of developmental time. Accordingly, the cumulative probability distributions of *P. solenopsis* development times under different temperatures were estimated and normalized. The normalised development times were arranged in frequency distributions and cumulative density functions were fitted to each developmental time for determining the relation between temperature-dependent and cumulated developmental time relative frequency. The median development time (d) and cumulative frequencies of survivorship for each life stage at different temperatures were calculated. The cumulative frequencies of developmental times of each life stage and temperatures were plotted against normalized developmental times by fitting a normal (probit) distribution curve for nymph 1 and nymph 2 life stages, a complementary log–log (CLL) distribution curve for nymph 3 and logit distribution curve for male pupae. The mathematical expressions of these distribution functions are given below (Tonnang et al., 2013):

$$\text{Probit distribution}: F(x) = \phi(a_i + b\ln x) \tag{1}$$

$$\text{Logit distribution}: F(x) = 1/(1+\exp(-(a_i + b\ln x))) \tag{2}$$

$$\text{CLL distribution}: F(x) = 1-\exp(-\exp(a_i + b\ln x)) \tag{3}$$

where, *F(x)* is the probability to complete development at time *x*, ln*x* is the natural logarithm of the days observed, *a* is the intercept corresponding to temperature *i*, and *b* is the common slope of the regression model. The best fit model was selected based on Akaike's Information Criterion (AIC), a well-known goodness of fit indicator (Akaike, 1973).

2.3.3. Development rate

The linear regression model was fitted to establish the relationship between development rate and temperature (Zajac et al., 1989). Theoretical lower development threshold temperatures and thermal constants (k) for *P. solenopsis* immature life stages were estimated from the slope and intercept of the model. The equation used for estimating the linear relationship is:

$$r(T) = a + bT \tag{4}$$

where, $r(T)$ is the rate of development ($1/d$) at temperature T (°C), and, a and b represent the intercept and the slope of the equation, respectively.

The modified version of the biophysical Sharpe and DeMichele model (Sharpe and DeMichele, 1977; Schoolfield et al., 1981) was used for estimating the non-linearity in development at temperature extremes. The choice of this model was oriented by its biological significance to the species development which stipulates that, the development of poikilotherms is driven by a rate determining enzyme or enzyme complex which has three basic reversible energy rates: inactive at cold temperatures, active at optimum temperatures and inactive at high temperatures. For the immature stages, four parameter version of the Sharpe and DeMichele model was applied (Schoolfield et al., 1981):

$$r(T) = \frac{p\cdot\frac{T}{T_o}\cdot e^{\left[\frac{\Delta H_a}{R}\left(\frac{1}{T_o}-\frac{1}{T}\right)\right]}}{1+\exp\left[\frac{\Delta H_h}{R}\left(\frac{1}{T_h}-\frac{1}{T}\right)\right]} \tag{5}$$

where, $r(T)$ is the development rate at temperature T (°K), R is the universal gas constant (1.987 cal degree^{-1} mol^{-1}), P represents the development rate at optimum temperature To (°K) assuming no enzyme inactivation, ΔH_a is the enthalpy of activation of reaction catalysed by enzyme (cal mol^{-1}), ΔH_h is the change in enthalpy at high temperature (cal mol^{-1}), and T_h is the high temperature at which enzyme is half active.

The choice of best-fit function in ILCYM was done via Akaike's Information Criterion (Akaike, 1973) or other inbuilt statistics (R^2, Adjusted R^2, MSE). The smaller the value of the AIC, the better the model fitted. However, for predicting the species behaviour under a wide range of environmental conditions, the statistics and the species biology were combined. A Least Square Design (LSD) test was applied at $P = 0.05$ significance level for probability thresholds and hypothesis testing in all the regressions.

2.3.4. Survivorship

Survivorship was calculated from the cumulative frequency of cohort survivors and mortality was estimated by the 1-survivorship. The mortality in first and second nymphal instar was described by Wang model (Wang et al., 1982). The following equation of the model was used:

$$m(T) = 1 - \frac{1}{e\left\{\left[1+e\left(-\frac{T-T_{opt}}{B}\right)\right]\left[1+e\left(-\frac{T_{opt}-T}{B}\right)\right]\times H\right\}} \tag{6}$$

where, $m(T)$ is the rate of mortality at temperature T (°C), T_{opt} is the optimum temperature for survival (°C), and B and H are the fitted parameters.

A second order exponential polynomial function was fitted to describe the temperature dependence of mortality in third nymphal instar and male pupae. The following expression of polynomial model was used (Sporleder et al., 2004; Tonnang et al., 2013):

$$m(T) = e^{\left(a+bT+cT^2\right)} \tag{7}$$

where, $m(T)$ is the rate of mortality at temperature T (°C), and a, b, and c are the equation parameters.

2.3.5. Adult life span

The mean survival time of adults was recorded for both sexes and the inverse of it was plotted against respective temperature. A modified four parameter Stinner model (Stinner et al., 1974) was fitted to determine the relationship between senescence rate of female adults and temperature.

$$r(T) = \frac{c_1}{1+e(k_1+k_2\times T)} + \frac{c_2}{1+e(k_1+k_2(2\times T_o - T))} \tag{8}$$

where, $r(T)$ is the senescence rate at temperature T (°C), To is the optimum temperature (°C), c_1 and c_2 are the maximum and minimum temperatures (°C) when $T \leq T_o$ and $T >$ To, respectively, and k_1 and k_2 are constants representing the slope and the intercept, respectively.

A cubic equation (Tanigoshi and Browne, 1978) was used to describe temperature dependent senescence rate of male adults.

$$r(T) = a_0 + a_1 T + a_2 T^2 + a_3 T^3 \quad (9)$$

where, $r(T)$ is the senescence rate at temperature T (°C), and a_0, a_1, a_2 and a_3 are constants.

2.3.6. Temperature-dependent reproduction

A Gaussian equation (Taylor, 1981) was applied to determine the effects of temperature on the total number of eggs laid per female. The expression of the model is:

$$f[T] = \frac{1}{1 + R_{\max} \cdot e^{-a\left(\frac{T - T_{\max}}{b}\right)^2}} \quad (10)$$

where, $f(T)$ is the fecundity at temperature T (°C), $R_{\max}$ is the maximum fecundity, $T_{\max}$ is the temperature at which maximum fecundity occurs, and a and b are the fitted parameters representing intercept and slope of the equation, respectively.

An exponential model was fitted to describe the age-specific fecundity rate at each of the test temperatures. The cumulative oviposition rate was plotted against normalized female age expressed as ratio of age in days divided by mean survival time. Below is the formula of the exponential equation which was used for assessing the relative oviposition frequency:

$$y = 1 - e^{-(aX + bX^2 + cX^3)} \quad (11)$$

where, y is the cumulative oviposition frequency, X is the normalised age of female expressed as a ratio of age in days and mean survival time, and a, b and c are the equation parameters.

2.3.7. Life table parameters

Using 'stochastic simulation tool' in ILCYM, the life table parameters *viz*., gross reproductive rate (GRR), net reproductive rate (R_0), mean generation time (T), intrinsic rate of natural increase (r_m), finite rate of increase, (λ) and doubling time (D_t) of *P. solenopsis* were estimated. The estimates were based on the developed phenology model at six constant temperatures ranging from 15 to 40 °C with ten repetitions each. The simulation method employed rate summation and cohort updating approaches (Curry et al., 1978). The sex of an emerging adult was determined through generation of a random value between 0 and 1. The sex ratio observed in *P. solenopsis* is 0.9:0.1 and is highly skewed towards female (Vennila et al., 2010a; Prasad et al., 2012). The proportion of females in the progeny was not significantly affected by temperature or age of the ovipositing female. Hence, for simulation of population growth rates, we assumed a constant female rate of 0.9 in progeny while fitting the model parameters. We set the initial number of first instar nymphs to 100 for the simulations at each of the tested temperatures. The estimated life table parameters were plotted against respective temperatures and fitted to a quadratic equation.

$$Lp(T) = a + bT + cT^2 \quad (12)$$

where, $Lp(T)$ represents the respective life table parameters (GRR, R_0, T, r_m, λ, D_t) at temperature T (°C), and a, b, and c are the model parameters.

2.3.8. Model validation

For validation of the developed phenology model within the temperature range 15–40 °C, life table parameters at fluctuating temperatures were estimated. Daily data on minimum and maximum temperatures for each Julian day obtained from four locations across cotton growing areas of India *viz*; Ludhiana (Punjab State, Coordinates: 75° 54′ E, 30° 55′ N, Alt.: 250 m); Hisar (Haryana state, Coordinates: 76° 23′ E, 29° 19′ N, Alt.: 215 m); Junagadh (Gujarat state, Coordinates: 70°36'E, 21° 31′ N; Alt.: 179 m) and Akola (Maharashtra State, Coordinates: 77° 02′ E, 20° 42'N, Alt.: 282 m) were used in stochastic simulation. The results obtained were compared with life table parameter values of *P. solenopsis* described in other studies. As an example, the results for only one location i.e. Akola were discussed here. The location Akola was chosen because the annual maximum and minimum temperatures at this place ranged between 29.6 and 42.5 °C and 10.8–27.3 °C, respectively, and daily maximum temperatures are often in the range where detrimental development effects may occur.

3. Results

3.1. Development time and its distribution

The temperatures within the evaluation range have a profound influence on the development of the immature life stages of *P. solenopsis*. The frequency distributions of *P. solenopsis* development times were inclined toward the longer times. Development time decreased significantly with increasing temperatures within the tested temperature range (Table 1). The variability in the development times of immature stages of *P. solenopsis* was described by a cumulative probit distribution (nymph 1 and 2), a complementary log–log distribution (nymph 3) and a logit distribution (male pupae) (Table 2).

3.2. Development rate

Linear equations were used to describe the temperature-dependent development of immature life stages of *P. solenopsis* (all stages, $P < 0.001$; df = 1, 4; nymph 1: $F = 72.89$; nymph 2: $F = 146.11$; nymph 3: $F = 97.77$; male pupa: $F = 54.71$) (Table 3). The theoretical lower development threshold temperatures estimated from the slope and intercepts of the linear regressions (LTT = intercept/slope), were 11.3, 8.9, 9.8 and 12.7 °C for nymph 1, nymph 2, nymph 3 and male pupae, respectively. Based on these thresholds, the thermal constants (k) for the development, expressed in degree days (DD = 1/slope), were 93.7 (with confidence limits at 70.7 and 138.9 by using upper and lower confidence limits of the slope in the equation), 129.8 (105.9–169.2), 97.1 (75.8–135.0) and 100.0 (72.4–159.3) for nymph 1, nymph 2, nymph 3 and male pupa, respectively.

However, the linear model is not well suited for predicting non-linearity in development rate of *P. solenopsis* that may exist at extreme temperatures reported in previous studies (Kumar and Kontodimas, 2012; Prasad et al., 2012). The modified Sharpe and DeMichele model allowed precise estimation of the predicted drop in development rates at temperatures higher than 40 °C (Table 3; Fig. 1). This was possible through the use of "additional values", a feature inbuilt in the ILCYM software which allowed more data points obtained from literature reports on *P. solenopsis* biology and behaviour under varied temperature conditions to be included (Kumar and Kontodimas, 2012; Prasad et al., 2012) for better fitting of the curves.

3.3. Mortality response of immature life stages

The temperature dependent mortality of first and second instar nymphs of *P. solenopsis* was described by the Wang model whereas

Table 1
Mean development time and survival of *P. solenopsis* life stages at different constant temperatures in laboratory.

Temperature (°C)	Immature stages								Adults	
	Nymph1		Nymph2		Nymph3		Male pupae		Female	Male
	Mean development time (days)	Survival (%)	Mean development time (days)	Survival (%)	Mean development time (days)	Survival (%)	Mean development time (days)	Survival (%)	Survival time (days)	Survival time (days)
15	14.5 (0.11)	41.6 (1.82)	16.5 (0.12)	77.0 (1.67)	13.9 (0.12)	87.0 (1.13)	18.9 (0.10)	71.0 (2.07)	50.5 (0.59)	3.8 (0.06)
20	11.9 (0.10)	47.7 (1.95)	12.2 (0.10)	86.0 (1.21)	10.0 (0.10)	91.0 (0.83)	14.8 (0.08)	81.0 (1.91)	44.4 (0.51)	2.9 (0.05)
25	6.7 (0.06)	71.3 (2.40)	7.8 (0.06)	93.0 (0.87)	5.8 (0.06)	94.0 (0.85)	9.0 (0.06)	90.0 (0.91)	29.5 (0.40)	2.7 (0.05)
30	5.5 (0.05)	76.7 (1.60)	6.3 (0.05)	95.0 (0.86)	5.6 (0.06)	96.3 (0.91)	6.9 (0.05)	93.0 (0.81)	30.8 (0.35)	1.8 (0.04)
35	3.9 (0.05)	55.3 (1.46)	4.9 (0.05)	75.3 (1.51)	3.3 (0.04)	89.7 (1.01)	3.8 (0.04)	84.0 (1.05)	23.8 (0.19)	1.8 (0.04)
40	3.0 (0.04)	29.3 (1.50)	3.5 (0.04)	54.0 (1.28)	3.0 (0.05)	85.0 (1.05)	3.5 (0.00)	79.0 (1.11)	18.4 (0.11)	1.4 (0.01)

Numbers in parentheses are standard errors.

Table 2
Estimated parameters of the cumulative distribution functions fitted to normalized development time frequencies for immature life stages of *P. solenopsis*. Fitted functions: probit model (nymph 1 and 2), CLL model (nymph 3) and logit model (male pupae).

Temperature (°C) life stage	Intercepts (a_i)						Slope (b)	AIC	R^2
	15	20	25	30	35	40			
Nymph 1	−32.63 (0.958)	−30.36 (0.892)	−23.28 (0.686)	−20.72 (0.611)	−16.62 (0.505)	−12.99 (0.416)	12.22 (0.357)	235.131	0.984
Nymph 2	−37.65 (0.870)	−33.56 (0.776)	−27.55 (0.639)	−24.75 (0.575)	−21.45 (0.505)	−17.75 (0.440)	13.43 (0.309)	217.341	0.994
Nymph 3	−32.14 (0.784)	−28.26 (0.688)	−22.08 (0.540)	−21.22 (0.518)	−16.37 (0.407)	−13.68 (0.333)	12.05 (0.293)	436.251	0.980
Male pupa	−100.10 (5.341)	−91.65 (4.892)	−74.82 (3.994)	−66.001 (3.533)	−46.037 (2.524)	−42.245 (2.433)	34.00 (01.81)	117.004	0.993

Numbers in parentheses are standard errors.

a polynomial function offered the best fit for mortality of third instar nymphs and male pupae (Table 4; Fig. 2). The model predicted the optimum temperature for survival of immature life stages of *P. solenopsis* within the range of 25–35 °C (>70% survival of all the immature stages). The first instar nymphs were highly sensitive to the temperature extremes; however, later instars had a better survival at all the test temperatures. The effect of temperature was less pronounced on the mortality of the immature males developing inside the puparial protection.

3.4. Adult life span

Longevity of both male and female adults decreased significantly with increasing temperature. The Stinner equation (Stinner et al., 1974) offered a good fit to the observed mean senescence rates of females (df = 4, 4; $F = 70.43$, $P = 0.0006$). The temperature dependence of mean senescence rates of male adults was described by the Tanigoshi equation ($P = 0.002$; df = 3, 4; $F = 39.67$) (Table 5; Fig. 3). Differences in longevity between adult males and females were highly significant (paired *t*-test: $P = 0.001$, df = 5; $t = 6.537$; Pearson $r = 0.932$).

3.5. Temperature-dependent reproduction

The results revealed significant effects of temperature on the reproductive life of *P. solenopsis*. The reproductive period shortened with increasing temperatures as female life span abridged. The pre-oviposition period ranged from 4 to 17 days for the evaluated temperature range. The Gaussian denominator function described the temperature dependence of *P. solenopsis* fecundity ($P = 0.098$; df = 3, 2; $F = 9.32$) (Table 6; Fig. 4a). The model predicted the favourable temperature range for *P. solenopsis* reproduction to be between 20 and 35 °C with maximum fecundity at 30 °C. The relationship between cumulative oviposition rate and female age was well described by the exponential function ($P < 0.001$; df = 2, 387; $F = 7960.3$) (Table 7; Fig. 4b). The 50% oviposition was completed by the time female reached a normalized age of 0.607.

3.6. Life table parameters

P. solenopsis population attained a maximum net reproductive rate (107–108 females/female/generation) at temperatures between 25 and 30 °C. The total fecundity was maximal (216.6 – 226.5 individuals/female/generation) in this temperature range. Values estimated for 'T' indicate that the mean length of generations decreased with increase in temperatures from low to high within the evaluation range (Table 8). Fitting of a polynomial model to the estimated life table parameters predicted temperatures between 25 and 35 °C as a favourable range for *P. solenopsis* development, survival and reproduction with shorter generation length and high reproductive potential (Fig. 5). Stochastic simulation of the phenology model of *P. solenopsis* at fluctuating temperatures with an initial population of 100 crawlers using the cohort updating and rate summation approach indicated that *P. solenopsis*

Table 3
Estimated parameters of the linear and non-linear models fitted to median development rate (1/*d*) for immature life stages of *P. solenopsis*.

Life stage	Linear model				Modified sharpe and DeMichele model						
	Intercept (*a*)	Slope (*b*)	R^2	T_{min} (°C)[a]	*P*	T_o	H_a	H_h	T_h	AIC	R^2
Nymph 1	−0.120 (0.033)	0.011 (0.001)	0.959	11.3	0.240	307.01 (1.06)	11215.74 (676.84)	220244.25 (1.62)	316.98 (0.170)	−39.03	0.995
Nymph 2	−0.071 (0.018)	0.008 (0.001)	0.978	8.9	0.200	307.62 (1.20)	9581.10 (543.26)	226302.90 (0.69)	317.35 (0. 200)	−44.04	0.995
Nymph 3	−0.098 (0.029)	0.010 (0.001)	0.963	9.8	0.105	290.03 (2.89)	10342.98 (1009.98)	164117.57 (7.65)	316.81 (0.310)	−33.39	0.979
Male pupa	−0.127 (0.039)	0.010 (0.001)	0.934	12.7	0.125	298.16 (1.13)	12428.68 (1916.76)	76061.35 (78.97)	316.88 (1.52)	−25.34	0.965

Numbers in parentheses are standard errors.
[a] Theoretical lower development threshold (T_{min}), calculated by intercept/slope, ignoring minus sign.

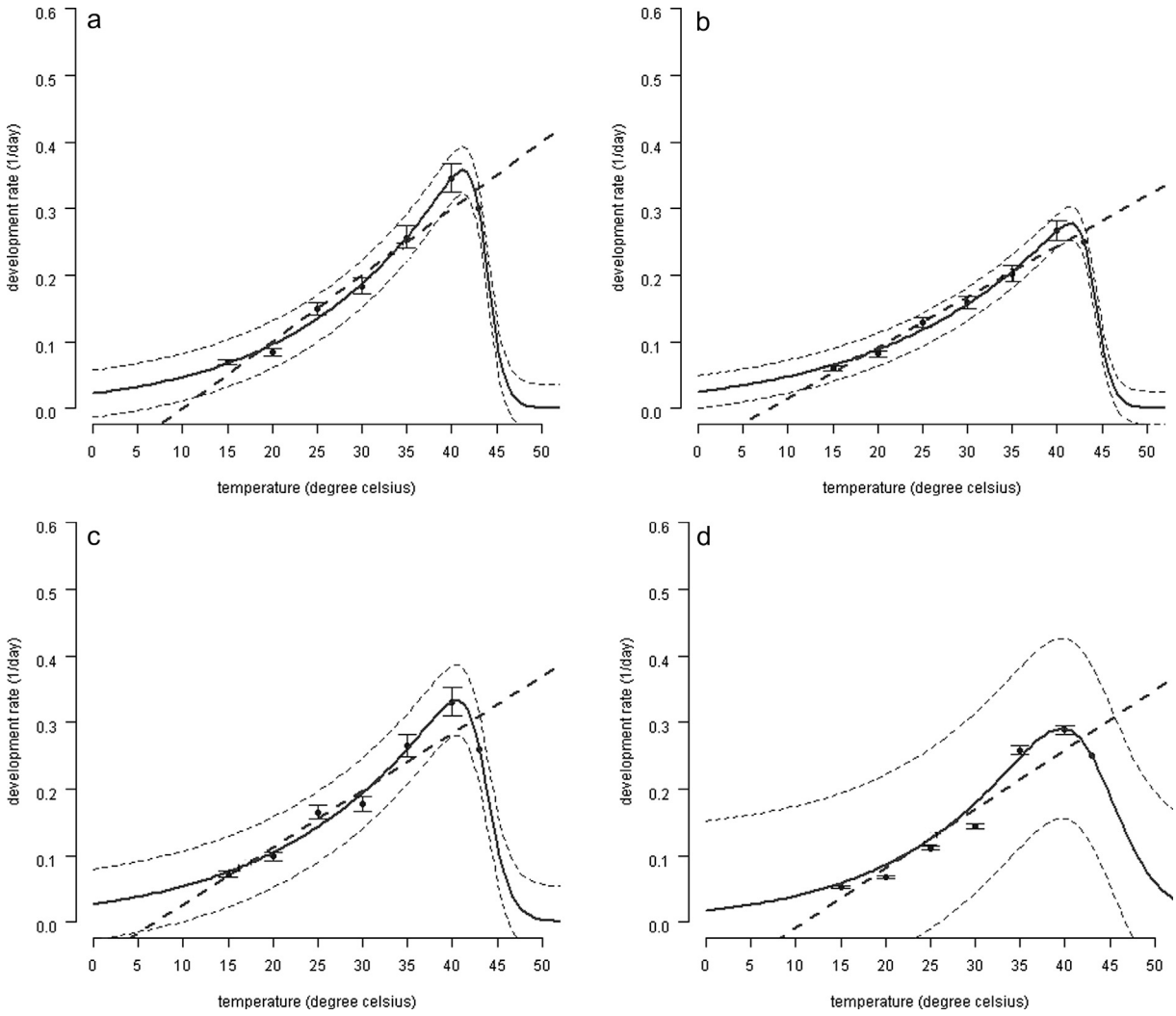

Fig. 1. Temperature-dependent developmental rates (1/day) for immature stages of *P. solenopsis*: nymph 1 (a), nymph 2 (b), nymph 3 (c) and male pupae (d) (Modified Sharpe and DeMichele model). The bold solid line is the selected model output and dashed lines above and below represents the upper and lower 95% confidence bands. Bars represent standard deviation of the mean.

populations potentially might increase with a finite rate of 1.06 females/female/day. Accordingly, the populations can double within 12.1 days with a mean generation time of 58.7 days (Table 9).

4. Discussion

4.1. Rearing techniques for P. solenopsis

In the present study, we used sprouted potatoes for rearing of *P. solenopsis*, unlike detached cotton leaves in previous studies (Vennila et al., 2010a; Prasad et al., 2012). The sprouted potatoes were used for rearing *P. solenopsis* because its development on cotton and sprouted potato tubers proceeds equivalently with no significant deviations in the life table parameters (Gautam, 2008; Fand et al., 2010) and thus results can be extrapolated. The development time in *P. solenopsis* eggs from oviposition until hatching of nymphs is relatively short ranging from few minutes to a maximum of 2 h (Nikam et al., 2010; Vennila et al., 2010a; Asifa et al., 2012; Prasad et al., 2012). Hence, the egg stage of *P. solenopsis* was not included in the present study for modelling the temperature-dependent life table for *P. solenopsis*. *P. solenopsis* exhibits sexual dimorphism; the adult sexes have distinct morphological

Table 4
Estimated parameters of the non-linear models fitted to mortality rate for immature life stages of *P. solenopsis*.

Life stage	Parameters of the Wang model: $m(T) = 1 - 1/(\exp((1 + \exp(-(x - T_{opt})/B)).(1 + \exp(-(T_{opt}-x)/B)).))$							
	T_{opt}	B	H	AIC	R^2	F	df	P
Nymph 1	27.10 (0.908)	5.29 (0.814)	0.086 (0.019)	−8.27	0.856	8.89	(2,3)	0.054
Nymph 2	25.40 (0.663)	4.36 (0.525)	0.021 (0.005)	−17.07	0.953	30.19	(2,3)	0.010
Life stage	Parameters of the exponential polynomial function: m $(T) = \exp.(a + bT + cT^2)$							
	a (Intercept)	b	c	AIC	R^2	F	df	P
Nymph 3	1.25 (0.001)	−0.302 (0.012)	0.006 (0.0003)	−26.43	0.873	10.33	(2,3)	0.045
Male pupa	2.27 (0.0008)	−0.315 (0.010)	0.005 (0.0003)	−20.02	0.895	12.80	(2,3)	0.034

Numbers in parentheses are standard errors.

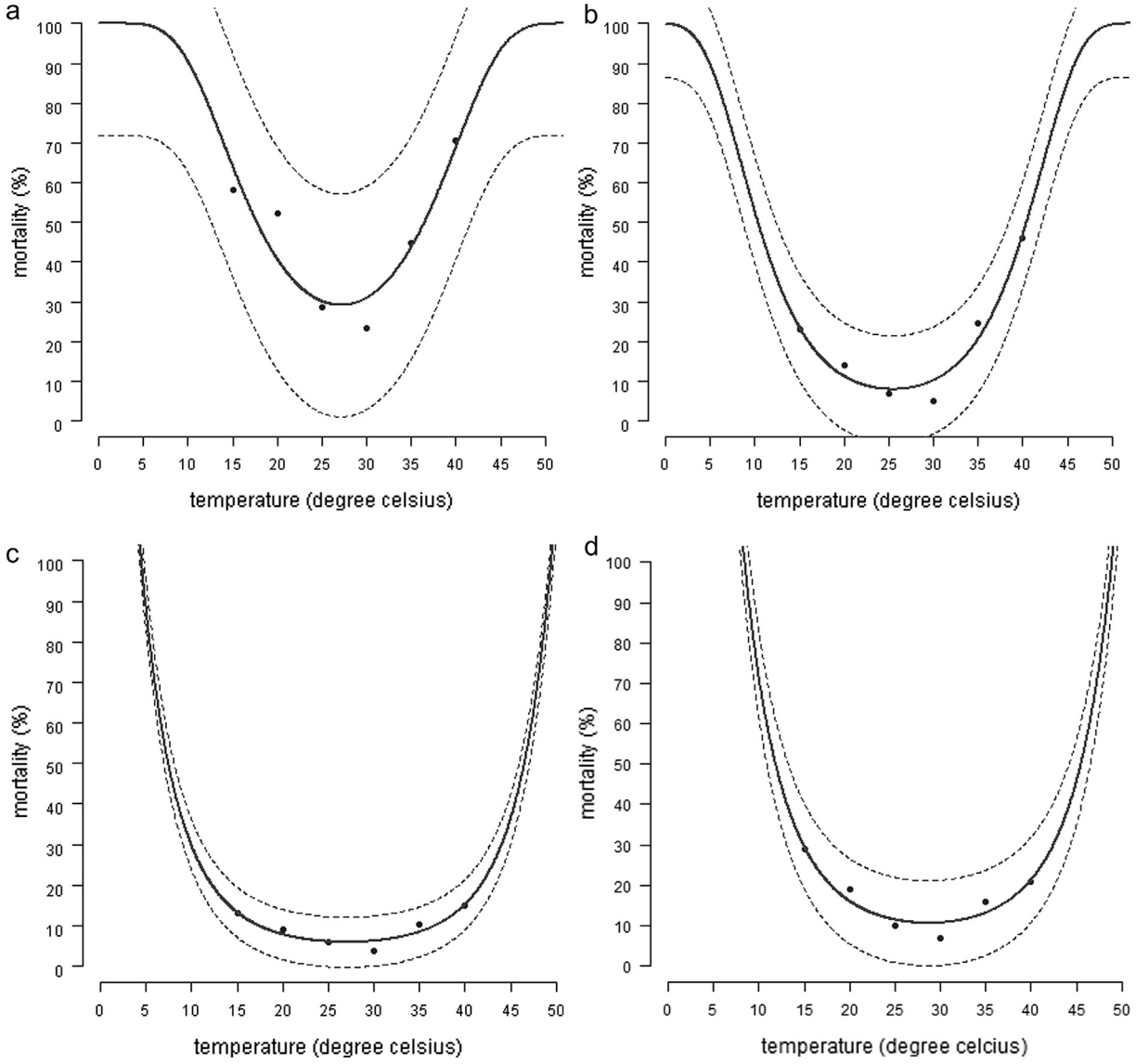

Fig. 2. Temperature-dependent mortality rates of immature life stages *P. solenopsis*: nymph 1 (a), nymph 2 (b), nymph 3 (c) and male pupae (d). Fitted curves, Wang model (a and b) and polynomial model (c and d); the upper and lower 95% confidence intervals of the model are indicated. Markers are observed means; bars represent standard deviation.

differences. The immatures destined to develop as males construct a loosely woven silky filamentous cocoon after the second moult and undergo two moults inside with a prepupal stage, before emerging as winged adults (Vennila et al., 2010a; Prasad et al., 2012). Hence, for the second instar onwards the development was observed separately for immature females and males, and the combined development duration of third and fourth instars was considered for male pupa.

4.2. Temperature-dependence of P. solenopsis life cycle

Temperature had significant influences on the *P. solenopsis* life cycle. The developmental durations of all the life stages of *P. solenopsis* decreased linearly with increasing temperatures within the evaluation range, as increasing temperatures accelerated development rates. The linear decrease in development times of the immature stages of *P. solenopsis* have been reported for a

Table 5
Estimated parameters of the non-linear functions fitted to the mean senescence rates for adult life stages of *P. solenopsis*.

Life stage	Stinner function: $r(T) = c_1/(1 + \exp(k_1 + k_2 \cdot x)) + c_2/(1 + \exp(k_1 + k_2 \cdot (2 \cdot T_o - x)))$						
	$c1$	$c2$	$k1$	$k2$	T_o	AIC	R^2
Female	42.26 (0.47)	15.50 (0.038)	3.58 (2.86)	0.216 (0.030)	25.14 (0.203)	−34.84	0.986
Tanigoshi model: $r(T) = a_0 + a_1 \cdot T + a_2 \cdot T^2 + a_3 \cdot T^3$							
	a_0	a_1	a_2	a_3		AIC	R^2
Male	0.652 (1.17)	−0.047 (0.00001)	0.002 (0.0001)	0.000 (0.0001)		−20.88	0.966

Numbers in parentheses are standard errors.

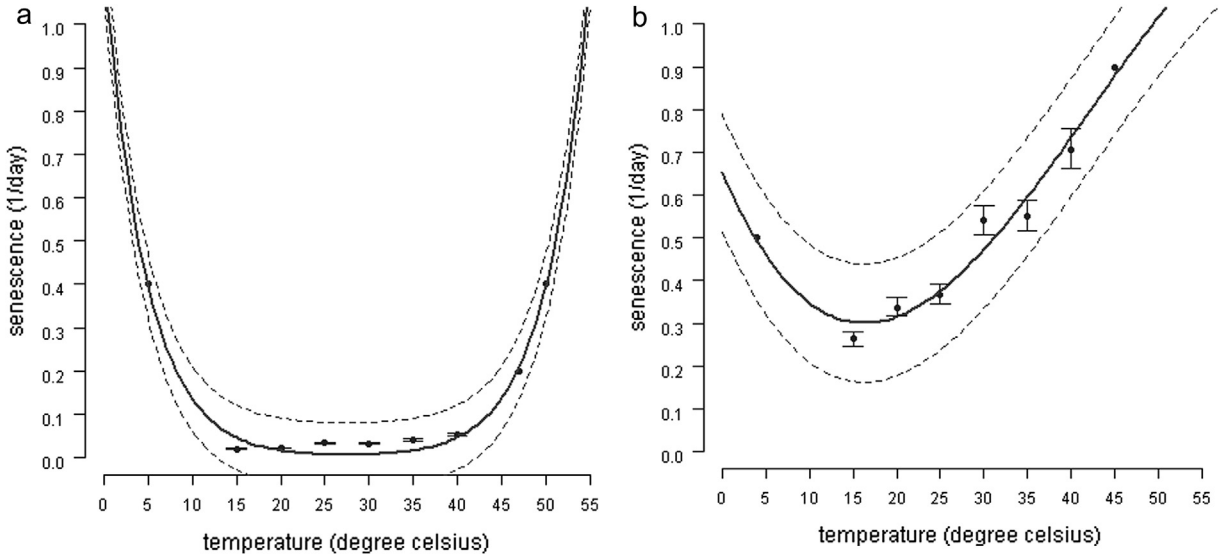

Fig. 3. Temperature-dependent senescence rates (1/day) for adults of *P. solenopsis*: female (a) and male (b). Fitted curves, Stinner model (a) and Tanigoshi model (b); the upper and lower 95% confidence intervals of the model are indicated. Bars represent standard deviation of the mean.

Table 6
Estimated parameters of the Gaussian denominator function fitted to fecundity of *P. solenopsis*.

Response variable	Gaussian denominator function: $f(T) = y0 + a \cdot \exp(-0.5((T - T_0)/b)^2)$					
	a	*b*	*c*	*d*	AIC	R^2
Fecundity/female	−0.996 (0.0003)	4273.98 (0.00004)	28.84 (0.810)	−9016.75 (0. 00004)	61.18	0.933

Numbers in parentheses are standard errors.
*$f(T)$, fecundity at temperature T (°C).

temperature range 20–40 °C (Asifa et al., 2012). Prasad et al. (2012) also reported a similar trend for a temperature range of 18–32 °C. However, they found non-linear development for temperatures above 32 °C. Previous studies (Kumar and Kontodimas, 2012; Prasad et al., 2012) indicated that the development rate in *P. solenopsis* starts decreasing above 40 °C. Hence, in order to obtain a curve that descends after reaching this temperature, the "additional value" feature in ILCYM was used to add more data points obtained from the literature (Kumar and Kontodimas, 2012; Prasad et al., 2012). Based on this, the immature development rates at 45 °C, the female senescence rates at 5, 45 and 50 °C, and the male senescence rates at 5 and 45 °C were included in the model. This gave realistic fitting of mathematical equations to explain biological phenomena.

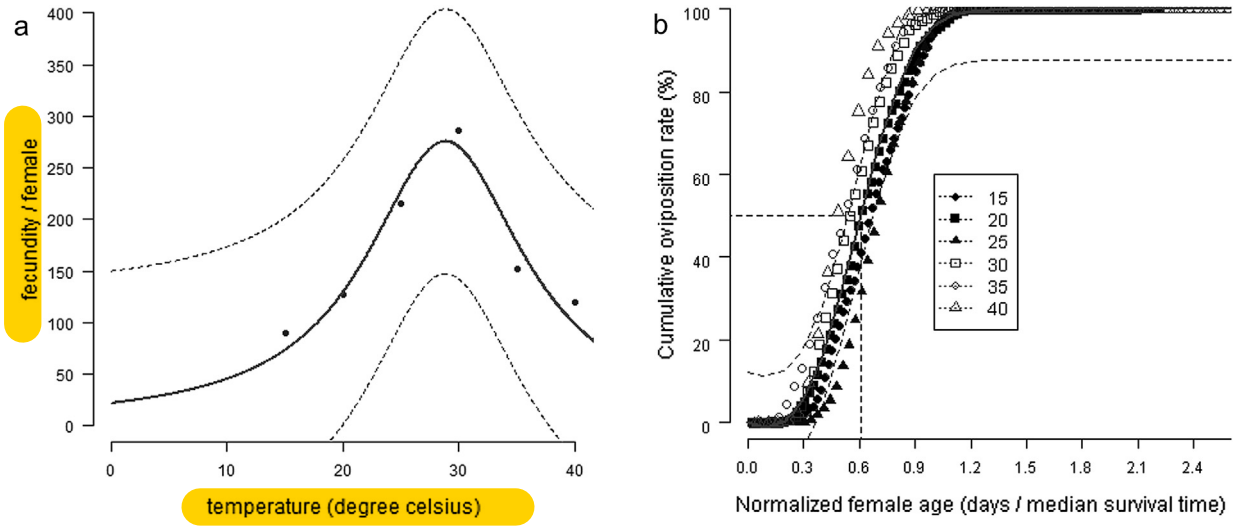

Fig. 4. a. Temperature-dependent total egg production curve. Fitted curve, Gaussian denominator model; the upper and lower 95% confidence intervals of the model are indicated. The dots are observed data points. b. Cumulative proportion of egg production in relation to female age expressed as normalized time (senescence/mean senescence time). Fitted curve: exponential function; the upper and lower 95% confidence intervals of the model are indicated. The dots are observed data points at each of the test temperatures. Age of the female at 50% oviposition is indicated.

Table 7
Age-related oviposition rate of *P. solenopsis* described by exponential model.

Response variable	Model coefficients ($y = (1 - \exp(-(ax + bx^2 + cx^3)))^*$				
	a	*b*	*c* (Intercept)	AIC	R^2
Cumulative oviposition rate	−0.156 (0.116)	0.198 (0.487)	3.2 (0.481)	−1058.49	0.976

Numbers in parentheses are standard errors.
*Normalized female age, expressed as a ratio of age in days and median survival time.

A relatively longer duration of development was observed in second instar nymphs compared to first and third instar nymphs at all the test temperatures; it is in agreement with the reports of Vennila et al. (2010a) and Prasad et al. (2012). However, our results were not consistent with those of Nikam et al. (2010) who mentioned that first instar nymphs had longer developmental duration compared to second and third instar nymphs. Unlike our results, Asifa et al. (2012) also reported uniform developmental durations for all the three nymphal instars. The thermal constants and lower development threshold temperatures estimated from the linear model are relatively similar to those mentioned by Prasad et al. (2012). However, the variability in the development times at extreme low and high temperatures were described more precisely by modified Sharpe and DeMichele model due to non-linearity at the temperature extremes.

In the present study, the mortality rate was relatively higher for the first instar crawlers but the mortality declined sharply in subsequent instars. This may be attributed to the absence of the protective wax coating on younger stages of the mealybug, making them more liable for desiccation (Persad and Khan, 2002; Fand et al., 2010). Very few data on immature mortality of *P. solenopsis* at constant temperatures was available for comparisons with the results of the present study. Our findings differ from Vennila et al. (2010a) who reported higher mortality in second instar nymphs compared to first and third instar nymphs. Comparatively better survival of *P. solenopsis* life stages at 40 °C observed in this study over earlier reports (Asifa et al., 2012; Prasad et al., 2012) may be due to differences in rearing procedures and food source/host plant used for rearing of test insect, that seriously affect survival of the organisms. Better survival observed in immature males of *P. solenopsis* developing inside the puparia is reported in mealybugs (Chong et al., 2003; Prasad et al., 2012).

The longevity and fecundity of adults were significantly affected by the temperature. At higher temperatures, the life span of female adults was approximately three times less than the life span at low temperatures leading to substantial shortening of reproductive phase. The lifetime fecundity and cumulative oviposition rate were temperature-dependent. A curvilinear response for fecundity with a maximum at 30 °C (286.4 eggs/female) and decreasing at temperatures below and above this temperature. This is consistent with the findings of Prasad et al. (2012). However, it is not consistent with Asifa et al. (2012) who reported linear decrease of *P. solenopsis* fecundity from low to high (20–35 °C) temperatures. Fecundity was highly variable at different temperatures as reported by previous authors (Vennila et al., 2010a; Asifa et al., 2012; Prasad et al., 2012). The cumulative development rate represents physiological age of female adults and this gives a clear idea of age-related fecundity. Oviposition and its rate are crucial components on which an insect population dynamics depend and hence detailed knowledge on age-dependent fecundity is imperative for developing precise pest forecasting models (Wagner et al., 1984; Sporleder et al., 2004). This study presents only the effect of temperature on *P. solenopsis* fecundity when reared on sprouted potatoes; however fecundity is also influenced by several other factors such as host nutritional quality, food availability, nutrition of immature stages, light intensity, relative humidity (Akintola and Ande, 2008; Vennila et al., 2010a,b; Asifa et al., 2012) and natural enemies like predators and parasitoids (Gautam et al., 2009; Pala and Saini, 2010; Fand et al., 2011). Hence, the total fecundity of *P. solenopsis* presented here should be compared cautiously with previous studies.

The present study reports the life table parameters estimated at constant temperatures ranging between 15 and 40 °C based on the simulation of *P. solenopsis* phenology model. All the equations representing life history of the species are non-linear mathematical expressions and can be used for estimating lower and upper limits of various life cycle parameters such as development, mortality, etc. The effects of temperature on the life table parameters of *P. solenopsis* under laboratory conditions have been reported (Fand et al., 2010; Asifa et al., 2012; Prasad et al., 2012; Kumar et al., 2013). Our results are largely consistent with earlier reports. However, discrepancies occurred between predicted life table parameters from this study and those reported in literature, mostly for r_m and R_o (r_m is a function of R_o). It seems that, these discrepancies are attributed largely to the deviations from the selected sub-model for development and mortality of immature stages and total fecundity per female, which are considered to be the most variable factors. Besides, host material i.e. sprouted potatoes used in rearing *P. solenopsis* adds further to the variability in life cycle of *P. solenopsis*. Such a difference in phenology model formulation and structure may be responsible for the overall discrepancy between the results presented here and those reported by previous authors (Fand et al., 2010; Asifa et al., 2012; Prasad et al., 2012; Kumar et al., 2013). Increased reproductive potential coupled with shorter generation length and doubling time due to increasing temperatures within the evaluation range implies for the more number of generations and increased abundance of *P. solenopsis* due to climate change. This may pose a serious threat to agricultural production systems, especially in the tropics and sub-tropics.

Table 8
Life table parameters for *P. solenopsis* estimated at different constant temperatures.

Parameter	Temperature (°C)					
	15	20	25	30	35	40
r_m	0.03 (0.002)^a	0.08 (0.000)^b	0.11 (0.000)^c	0.15 (0.001)^d	0.16 (0.002)^e	0.10 (0.005)^f
R_o	14.0 (1.52)^a	67.0 (1.79)^b	108.9 (2.73)^c	107.5 (3.15)^c	58.4 (2.51)^d	9.0 (0.93)^a
GRR	67.7 (1.20)^a	167.4 (2.93)^b	216.6 (3.39)^c	226.5 (3.72)^c	192.5 (3.39)^d	111.1 (4.85)^e
T	75.6 (0.32)^a	54. 4 (0.14)^b	41.0 (0.05)^c	30.2 (0.07)^d	25.2 (0.07)^e	21.2 (0.15)^f
λ	1.03 (0.002)^a	1.08 (0.000)^b	1.12 (0.000)^c	1.16 (0.001)^d	1.17 (0.002)^e	1.11 (0.006)^f
D_t	20.3 (1.08)^a	9.0 (0.049)^b	6.1 (0.031)^{cf}	4.7 (0.037)^{cde}	4.3 (0.053)^{de}	6.8 (0.39)^f

Numbers in parentheses are standard errors.
Means followed by the different letters within rows are significantly different ($P \leq 0.05$, LSD test).
r_m, intrinsic rate of natural increase; R_o, net reproductive rate; T, mean generation time (days); λ, finite rate of increase; D_t, doubling time (days).

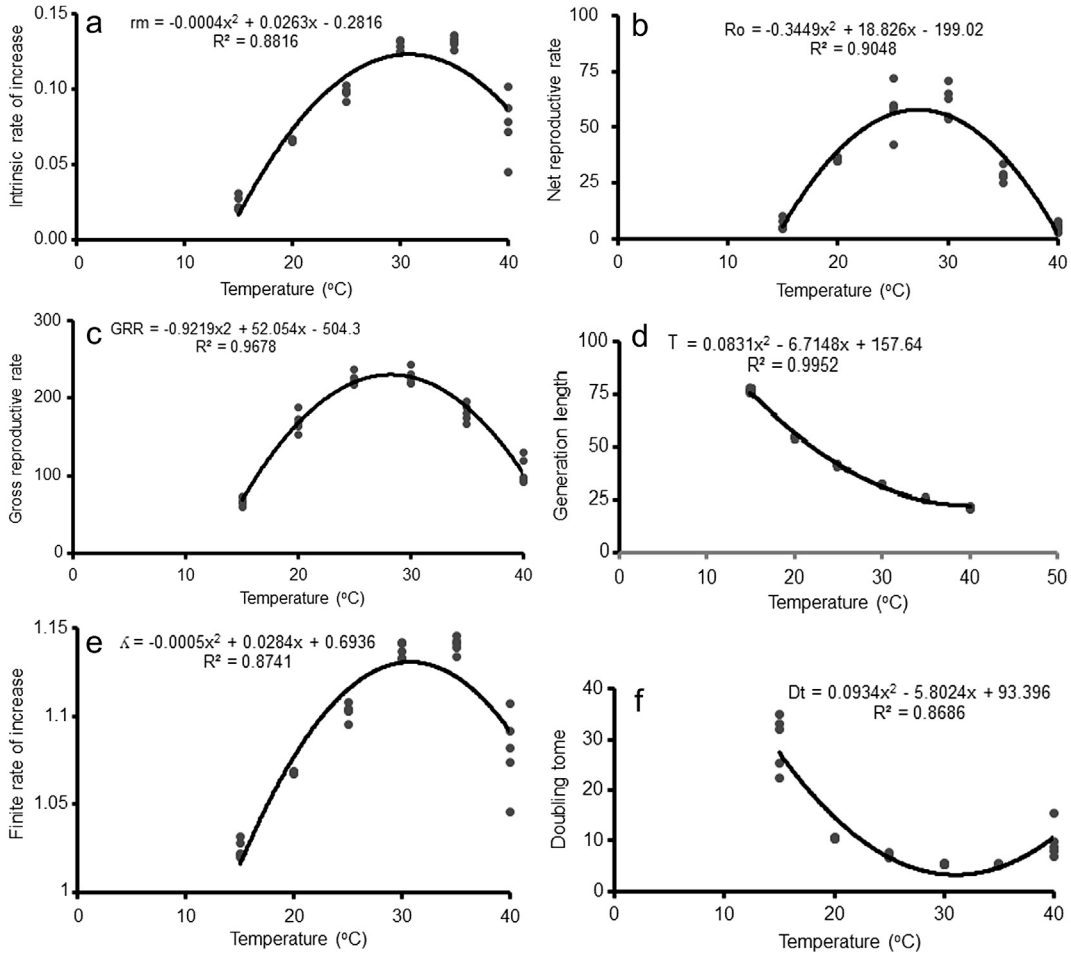

Fig. 5. Life table parameters of *P. solenopsis* estimated through model prediction over a range of six constant temperatures: Intrinsic rate of natural increase, rm (a); net reproduction rate, R_o (b); gross reproductive rate, GRR (c); mean generation time, T (d); finite rate of increase, λ (e); and doubling time, D_t (f).

In conclusion, the life table parameters estimated for *P. solenopsis* at constant temperatures in this study reflect its temperature-dependent growth potential which can further be employed in geographic information systems (GIS) for predicting its behaviour under fluctuating temperatures in different agro-ecologies. Estimated development rates and population growth potential at various temperatures may also help in comprehending seasonal dynamics of *P. solenopsis* in relation to initiation of its peak abundance. Geospatial modelling of *P. solenopsis* risk based on outputs of temperature-driven phenology model linked to GIS will allow a detailed analysis of the impact of climate change on future invasiveness and spread of this pest in various parts of the world.

Table 9
Statistical summary of life table parameters for *P. solenopsis* simulated at fluctuating temperatures.

Sr. No	Parameter	Observations
1.	Initial number of insects	100.0
2.	Number of repetitions for simulation	10
3.	Numbers developed to II instar	46.0 ± 1.16 (46.0)[a]
4.	Numbers developed to III instar	40.0 ± 1.43 (86.96)[a]
5.	Numbers developed to adult females	36.0 ± 0.707 (90)[a]
6.	Average fecundity per female	172.5 ± 2.68
7.	Sex ratio (proportion of females)	0.90 ± 0.06
8.	Net reproductive rate (R_o) (Females/female/generation)	29.3 ± 1.83
9.	Gross reproductive rate (GRR) (Females/female/generation)	193.1 ± 1.39
10.	Intrinsic rate of natural increase (r_m) (Females/female/day)	0.06 ± 0.002
11.	Finite rate of increase (λ) (Females/female/day)	1.06 ± 0.001
12.	Mean generation time (T) (Days)	58.7 ± 1.07
13.	Doubling time (D_t) (Days)	12.1 ± 0.26

[a] Figures in parentheses are survival (%).

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