

Effect of temperature on biology and population growth parameters of *Aphis gossypii* Glover (Hom., Aphididae) on greenhouse cucumber

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Abstract: Temperature-dependent development, survivorship and reproduction of the cotton aphid, *Aphis gossypii* on *Cucumis sativus* L. were evaluated at six constant temperatures (10, 15, 20, 25, 30 and 35°C). Developmental periods of immature stages varied from 20.70 days at 10°C to 3.81 days at 30°C. The population failed to survive at 35°C. As temperature increased, the intrinsic rate of increase (r_m) followed a typical asymmetrical dome-shape pattern, with maximum value of 0.419/day at 25°C. Survival of immature stages differed from 55.97% to 93.14% within the range of 10–30°C. The average adult longevity ranged from 8.56 days at 30°C to 17.00 days at 25°C. Three mathematical models were compared for accuracy in predicting the developmental rate of *A. gossypii*, and estimating its temperature thresholds and optima. The developmental threshold was estimated to be 6.19°C, and the thermal constant was 97.09 degree-days, using the linear model. The Briere 2 and Lactin 2 models were accepted for success to satisfy criteria of goodness-of-fit (residual sum of square and coefficient of determination) and estimable temperature threshold parameters and highly recommended for the description of temperature-dependent development of *A. gossypii*. No other data are available in using nonlinear models to describe the relationship between temperature and *A. gossypii* development.

Key words: cotton aphid, degree-days, nonlinear models, temperature-dependent development

1 Introduction

The cotton aphid, *Aphis gossypii* Glover (Hom., Aphididae), is a cosmopolitan, polyphagous species and widely distributed in tropical, subtropical and temperate regions (Kersting et al. 1999). It is a major pest of cultivated plants such as Cucurbitaceae, Rutaceae and Malvaceae. Damage caused by this species include reduction in fruit quantity and quality and virus transmission (Roistacher et al. 1984). In Iran, *A. gossypii* is one of the most important pests of greenhouse plants (Baniaméri and Nasrollahi 2003). It is variable not only in its morphology, but also in its life cycle and its ecological characteristics (Havelka 1978). Therefore, for each pest management programme, an exact determination of the population parameters is required. Temperature is a key abiotic factor that regulates insect population dynamics, developmental rates and seasonal occurrence (Campbell et al. 1974; Logan et al. 1976). The intrinsic rate of increase, upper and lower developmental threshold, fecundity and survivorship schedules are essential for describing temperature effects on aphid population dynamics (McCornack et al. 2004). A variety of temperature-dependent models have been proposed

to describe the relationship between temperature and insect development (Briere and Pracros 1998). They vary with respect to parameter number and basic assumptions about temperature effects near lower and upper limits (Roy et al. 2002). Temperature-driven rate models are most often used to predict the activity and seasonal population dynamics of pests and natural enemies in field situations (Lamb 1992). Data on temperature-dependent development and fecundity of the cotton aphid reported in the literature suggest important differences with regard to host plant and geographical region (van Steenis and El-Khawass 1995; Kersting et al. 1999). Therefore, the development and fecundity data for *A. gossypii* on one crop and from one region should be used with caution if applied to different crops and regions (Akey and Butler 1989).

In order to analyse the biological control of *A. gossypii* with the aphid parasitoids in cucumber greenhouses, reliable and site-specific information on the development time and population growth parameters is important. Several factors have major consequences for the growth potential of aphids as measured in laboratory studies. These include geographical origin, host plant, fertilization levels and temperature (Kersting et al. 1999; Perng 2002; Rohne 2002; Du et al. 2004;

Chau et al. 2005). Several studies provided strong evidence that genetically distinct host races exist in *A. gossypii*. Cotton aphid clones from cucumber performed badly on cotton and similarly those from cotton developed poorly on cucumber (Guldemon et al. 1994; Du et al. 2004). Genetically distinct forms of *A. gossypii* were also reported from chrysanthemum and cucumber (Guldemon et al. 1994; Satar et al. 1999). Published studies on the biology of *A. gossypii* were difficult to extrapolate in Tehran cucumber greenhouses because either the studied aphids were from a different geographical origin (e.g. Komazaki 1982; Aldyhim and Khalil 1993; Xia et al. 1999) or the aphids were reared on another host plant (e.g. Liu and Perng 1987; Kersting et al. 1999; Xia et al. 1999) or the temperature response was not studied or investigated over a limited range of temperature (most studies). We therefore decided to do this study.

Thus, the objective of this study was to develop knowledge of the thermal requirements of populations of *A. gossypii* in Tehran province, as a prerequisite to developing a biological programme in greenhouse cucumber. Several experiments were designed to provide data on the effect of temperature on the development, intrinsic rate of increase and reproduction of *A. gossypii*. The developmental rate of all stages of *A. gossypii* was determined at six constant temperatures. However, several studies have been conducted on the thermal requirement of *A. gossypii* (Komazaki 1982; Aldyhim and Khalil 1993; van Steenis and El-Khawass 1995; Kersting et al. 1999), but for the first time, using the data obtained in this study we tested two nonlinear regression equations to model effects of temperature on the development of *A. gossypii*. These models will provide basic information for predicting the emergence date of *A. gossypii* from overwintering sites in the spring and for the establishment of a pest management programme for the cotton aphid that integrates the use of insecticides, natural enemies and cultural practices.

2 Materials and Methods

2.1 Rearing methods and experimental conditions

The aphids used in the experiments were originally collected from cucumber grown in greenhouses in Tehran, Iran, in June 2004. Aphids were reared on cucumber (*Cucumis sativus* L. cv. Negin) in growth chamber at $25 \pm 1^\circ\text{C}$, relative humidity (r.h.) of $65 \pm 5\%$ and a photoperiod of L16:D8 h. Aphids were reared on cucumber in the laboratory for six generations before they were used in the experiments. Seedlings of *C. sativus* were grown to the four to five leaf stage in a mixture of sand (33%), clay (33%) and peat moss (33%) in 25 cm pots.

2.2 Development and mortality

Developmental time of *A. gossypii* was studied at six constant temperatures (10, 15, 20, 25, 30 and 35°C) in separate growth chambers, with $65 \pm 5\%$ r.h. and a photoperiod of L16: D8 h. The experiment followed a randomized complete block design with temperatures randomly assigned to a chamber. The experiments were blocked

at two points in time with chamber temperatures randomized in each block. At the beginning of experiments for each temperature, newly emerged nymphs (within 12 h) were individually transferred into excised cucumber leaf discs placed upside-down on wet cotton wool in Petri dishes (5 cm-diameter) and then transferred to growth chambers. To reduce the effects of plant age on aphid development and survivorship, the cotton wool in the Petri dishes was wetted daily and aphids were transferred every 3 days to new cucumber leaf discs (McCornack et al. 2004). For each block (time), the number of aphids in a growth chamber varied between 45 and 80. For the entire experiments, 69 aphids were examined at 10°C , 76 at 15°C , 83 at 20°C , 102 at 25°C , 109 at 30°C and 72 at 35°C . Developmental times of individuals were determined for each nymphal instar (N_1 – N_4), total pre-imaginal development, pre-reproductive, reproductive and post-reproductive periods. Aphids were observed every 24 h at 10 – 25°C and every 12 h at 30 – 35°C . The presence of exuviae was used to verify moulting.

2.3 Reproduction and population growth parameters

Aphis gossypii reproduction was studied at five constant temperatures. Reproduction at 35°C was not included because primary observation showed there was no survival at this temperature. For each temperature 15 wingless adult females (replicates) were collected from stock colony and put separately into detached cucumber leaf discs placed upside-down on wet cotton wool in Petri dishes (5 cm diameter). After 1 day, all aphids except one young nymph per cage were removed. Nymphs were followed in their development, and the instar was recorded daily. After nymphs developed to adults and during the reproductive period, newborn nymphs were counted daily and then removed. Different parameters such as pre-reproduction period, reproduction period, post-reproduction period, age-specific fecundity, pre-adult mortality and female longevity were determined. Fresh leaf discs were provided every 3 days during the course of the 30- to 45-day experiments. From the fertility and survivorship schedules, the following population growth parameters were calculated using formula suggested by Carey (1993): intrinsic rate of increase (r_m), mean generation time (T_c), finite rate of increase (λ), net reproduction rate (R_0) and doubling time (d_t). Because insect development is dependent on temperature, insect age (day) does not realistically describe an insect's physiological maturity (McCornack et al. 2004). To integrate time and temperature, we plotted survivorship and fecundity against physiological time, measured in degree-days (DD). For survivorship we calculated the cumulative degree-days (CDD) for each aphid at time of death using the following equation (McCornack et al. 2004):

$$\text{CDD} = (T - T_0) \times n, \quad (1)$$

where T is chamber temperature, T_0 is lower developmental threshold, and n is number of days alive at the chamber temperature. The lower developmental threshold was estimated by linear regression between developmental rate and temperature (Muniz and Nombela 2001). Fecundity (m_x) schedules were also developed on physiological time scales. Physiological time was estimated by substituting calendar age for n in equation (1).

2.4 Developmental rate models

We compared the performance of one linear and two nonlinear developmental rate models (table 1). These models are most commonly used for this purpose. Evaluation of each model was based on the following criteria:

Table 1. Mathematical models that were used to describe the effect of temperature on the development of *Aphis gossypii*

Equation	Model	Reference
$Y = a + bx^*$	Linear regression	Muniz and Nombela (2001)
$R(T) = \exp(\rho T) - \exp\left[\rho T_{\max} - \left(\frac{T_{\max} - T}{\Delta T}\right)\right] + \lambda^\dagger$	Lactin 2	Lactin et al. (1995)
$R(T) = aT(T - T_0)^{\frac{1}{m}} / (T_{\max} - T)^{\frac{1}{m}}$	Briere 2	Briere et al. (1999)

* a and b are equation constants.
 $^\dagger T$ is the rearing temperature ($^\circ\text{C}$), ρ is a constant defining the rate at optimal temperature, T_{\max} is the lethal maximum temperature, ΔT is the temperature range over which physiological breakdown becomes the overriding influence and λ forces the curve to intercept the Y -axis at a value below zero.
 $^\ddagger T$ is the rearing temperature ($^\circ\text{C}$), a and m are empirical constants, T_0 is the lower developmental temperature threshold and T_{\max} is the lethal maximum temperature.

(a) The model should describe the data accurately. Two statistics were used to evaluate accuracy, the adjusted coefficient of determination (R^2) and the residual sum of squares, which provides complementary information on goodness-of-fit and usefulness for predicting observation (Roy et al. 2002).

(b) The model should allow estimation of parameters with biological significance. For development, the key biological parameters needed are the developmental threshold temperature, optimal temperature and high temperature threshold (Roy et al. 2002).

A good model must explicitly include a thermal maximum or thermal minimum, or both (Logan and Hilbert 1983; Kontodimas et al. 2004).

Developmental rate is the reciprocal of development time in days and ranges between 0 and 1. These rates are used in models of developmental rate summation in which daily estimates of developmental rates are needed. The development of an organism is completed when the sum of its daily developmental rates reaches the value of 1 (Curry and Feldman 1987).

2.5 Statistical analysis

For statistical analysis, each mean value is given with its standard error (\pm SEM). Effect of temperature on the developmental time, reproduction period and adult longevity were analysed with one-way ANOVA. If significance differences were detected, multiple comparisons were made using the SNK procedure ($P < 0.05$). Statistical analysis was carried out using Minitab software (MINITAB 2000). Differences in R_0 , T_c , λ , d_i and r_m values were tested for significance by estimating variances through the jackknife procedure (Meyer et al. 1986; Maia et al. 2000). We used the jackknife procedure to estimate the variance for r_m and the other population parameters (Meyer et al. 1986). This procedure is used mostly to estimate variance and bias of estimators. It is based on repeated recalculation of the required estimator, missing out each sample in turn (Maia et al. 2000). It is used to quantify uncertainty associated with parameter estimates, as an alternative to analytical procedures, in cases for which the analytical methods require very complicated mathematical derivation (Maia et al. 2000).

Algorithms for jackknife estimation of the means and variances are described only for r_m . Similar procedures were used for the other parameters (R_0 , T_c , λ and d_i). The steps for the application of the method are the following (Maia et al. 2000):

(a) Estimation of r_m , R_0 , T_c , λ and d_i considering the survival and reproduction data for all the n females, referred to as true calculation. At this point, called step zero, estimates obtained are denoted as $r_{m(\text{all})}$, $R_{0(\text{all})}$, $T_{c(\text{all})}$, $\lambda_{(\text{all})}$ and $d_{i(\text{all})}$ (Maia et al. 2000).

(b) Repeat the procedure described in part (a) for n times, each time excluding a different female. In so doing, in each step i , data of $n - 1$ females are taken to estimate parameters for each step, now named $r_{m(i)}$, $R_{0(i)}$, $T_{c(i)}$, $\lambda_{(i)}$ and $d_{i(i)}$ (Maia et al. 2000).

(c) In each step i , pseudo-values are calculated for each parameter, subtracting the estimate in step zero from the estimate in step i . For instance, the pseudo-values of r_m , $r_{m(j)}$, was calculated for the n samples using the following equation (Maia et al. 2000):

$$r_{m(j)} = n \times r_{\text{all}} - (n - 1) \times r_{m(i)} \quad (2)$$

d) After calculating all the n pseudo-values for r_m , jackknife estimate of the mean ($r_{m(\text{mean})}$), variance ($\text{VAR } r_{m(\text{mean})}$) and standard error ($\text{SEM } r_{m(\text{mean})}$) calculated, respectively, by the following equations (Maia et al. 2000):

$$r_{m(\text{mean})} = \frac{\sum_{j=1}^n r_{m(j)}}{n} \quad (3)$$

$$\text{VAR } r_{m(\text{mean})} = \frac{\sum_{j=1}^n (r_{m(j)} - r_{m(\text{all})})^2}{n - 1} \quad (4)$$

$$\text{SEM } r_{m(\text{mean})} = \sqrt{\frac{\text{VAR}(r)(r_{m(\text{mean})})}{n}} \quad (5)$$

The mean values of $(n - 1)$ jackknife pseudo-values for each temperature were subjected to analysis of variance (Kersting et al. 1999). The temperature-dependent models were analysed with the Levenberg-Marquardt algorithm using the JMP (V. 5.0.1; SAS Institute 2003) and SPSS (SPSS 2004) statistical programs.

3 Results

3.1 Development and mortality

Aphis gossypii successfully developed to adulthood from 10 to 30°C. At 35°C, there was 25% survival to the third instar but no survival to the fourth instar. The developmental times of *A. gossypii* reared on various temperatures differed significantly ($F = 180.8$, $P < 0.0001$). The effect of temperature on the development of *A. gossypii* is presented in table 2. Developmental time was inversely related to temperature.

Table 2. Developmental time, mortality and population parameters of *Aphis gossypii* on cucumber at five different temperatures

	Temperature				
	10°C	15°C	20°C	25°C	30°C
Developmental time (days \pm SEM)					
Instar I	4.30 \pm 0.47 c	2.18 \pm 0.29 b	1.43 \pm 0.22 ab	1.23 \pm 0.13 ab	0.90 \pm 0.03 a
Instar II	4.82 \pm 0.49 c	3.18 \pm 0.35 b	1.92 \pm 0.23 a	1.41 \pm 0.22 a	1.05 \pm 0.09 a
Instar III	5.81 \pm 0.35 d	2.90 \pm 0.28 c	1.90 \pm 0.23 b	1.83 \pm 0.13 ab	0.94 \pm 0.02 a
Instar IV	5.82 \pm 0.66 c	2.81 \pm 0.29 b	2.21 \pm 0.20 b	1.25 \pm 0.13 ab	0.92 \pm 0.04 a
Total	20.70 \pm 0.79 d	11.09 \pm 0.61 c	7.44 \pm 0.30 b	5.60 \pm 0.37 ab	3.81 \pm 0.11 a
Immature mortality (%)					
Instar I	18.84 \pm 4.35 b	10.53 \pm 2.63 ab	6.02 \pm 1.20 ab	2.94 \pm 0.50 a	16.51 \pm 1.83 b
Instar II	8.69 \pm 2.90 a	2.63 \pm 2.63 a	2.40 \pm 1.20 a	1.96 \pm 0.39 a	12.84 \pm 3.67 a
Instar III	4.35 \pm 1.45 ab	6.58 \pm 1.32 ab	1.20 \pm 0.96 a	0.98 \pm 0.59 a	9.17 \pm 1.83 b
Instar IV	5.79 \pm 2.90 a	1.31 \pm 0.79 a	3.61 \pm 0.96 a	0.98 \pm 0.39 a	5.50 \pm 0.92 a
Total	37.68 \pm 5.80 b	21.05 \pm 5.26 ab	13.22 \pm 3.61 a	6.86 \pm 0.98 a	44.03 \pm 3.67 b
Adult life history					
Reproduction period(days \pm SEM)	6.60 \pm 1.61 b	10.81 \pm 0.95 ab	10.10 \pm 1.10 ab	13.80 \pm 1.19 a	4.67 \pm 0.71 b
Adult longevity (days \pm SEM)	14.90 \pm 1.39 a	14.45 \pm 1.32 a	14.00 \pm 1.24 ab	17.00 \pm 1.80 a	8.56 \pm 0.91 b
Reproduction					
Intrinsic rate of increase (r_m)	0.064 \pm 0.000 e	0.180 \pm 0.000 d	0.325 \pm 0.001 c	0.419 \pm 0.001 a	0.363 \pm 0.003 b
Net reproduction rate (R_0)	5.42 \pm 0.08 e	23.29 \pm 0.26 c	35.98 \pm 0.47 b	57.07 \pm 0.95 a	7.76 \pm 0.16 d
Generation time (T_c)	26.14 \pm 0.11 a	17.43 \pm 0.04 b	11.02 \pm 0.02 c	9.66 \pm 0.02 d	5.63 \pm 0.02 e
Finite rate of increase (λ)	1.06 \pm 0.00 e	1.20 \pm 0.00 d	1.38 \pm 0.00 c	1.52 \pm 0.00 a	1.48 \pm 0.00 b
Doubling time (d_t)	10.73 \pm 0.08 e	3.84 \pm 0.01 d	2.13 \pm 0.01 c	1.66 \pm 0.01 a	1.91 \pm 0.02 b

Mean values followed by the same letter in the same row are not significantly different ($P < 0.05$, SNK after one-way ANOVA)

The total nymphal period decreased significantly with increasing temperature. Development from birth to adult stage required 20.70 ± 0.79 days at 10°C but only 3.81 ± 0.11 days at 30°C. Adult longevity was not significantly different at temperatures ranging from 10 to 25°C (table 2). Adult longevity was the longest at 25°C (17.00 days) and the shortest at 30°C (8.56 days).

Mortality of the juvenile stage of *A. gossypii* at 20 and 25°C was remarkably low (table 2). At all temperatures, mortality was higher in the first instar than in subsequent instars.

3.2 Reproduction and population growth parameters

Age-specific survivorship of *A. gossypii* reared at five constant temperatures is presented in fig. 1a. The linear regression equation (table 1) for the developmental rate in relation to temperature is $Y = 0.0103X + 0.0638$, where Y is developmental rate and X is temperature. The lower developmental threshold (T_0) was estimated from this equation to be 6.19°C. Thus, all remaining DD calculations use the combined lower developmental estimate of 6.19°C. When survivorship (l_x) was expressed in DD (physiological time scale), survivorship curves were nearly similar at 15, 20, 25 and 30°C (fig. 1a). The lowest survivorship period of *A. gossypii* was at 10°C. Complete mortality for aphids reared at 10, 15, 20, 25 and 30°C was observed after 167, 471, 529, 564 and 496 DD respectively (fig. 1a). At all temperatures, the survival rate of *A. gossypii* adults sharply decreased immediately after the reproduction period.

The reproduction period in physiological time scale (DD) is presented in fig. 1b. Aphids reared at 25°C spent significantly more physiological time reproducing than aphids reared at 10, 15, 20 and 30°C. There

was no significant difference in the number of DD, spent reproducing at 15, 20 and 30°C. On a calendar basis, cotton aphid spent more time producing

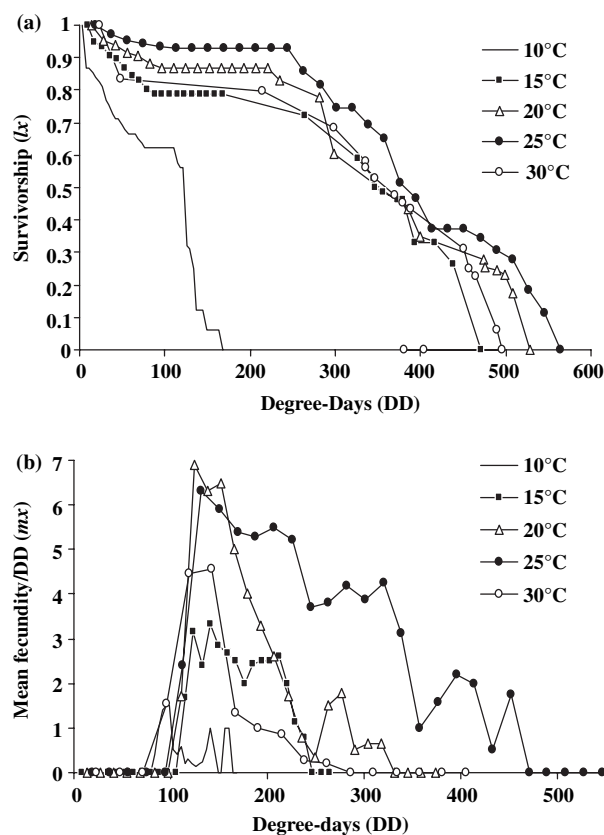


Fig. 1. Age-specific survivorship (a) and age-specific fecundity (b) of *Aphis gossypii* as a function of physiological time (degree-days, base 6.19°C) reared at five constant temperatures on greenhouse cucumber

offspring at 15 and 20°C (10.81 and 10.10 days respectively) than at 30°C (4.67 days) (table 2). Whereas, when we compare reproduction periods in physiological time scale, aphids spent an equal amount of DD reproducing at 15, 20 and 30°C (fig. 1b).

The intrinsic rate of increase (r_m) of *A. gossypii* increased almost linearly with temperature to reach a maximum at 25°C and then decreased at 30°C, displaying an asymmetrical dome-shaped pattern. The highest r_m of *A. gossypii* was $0.419 \pm 0.001/\text{day}$ and was recorded at 25°C. The effect of temperature on net reproductive rate (R_0), mean generation time (T_c), finite rate of increase (λ) and doubling time (d_t) is presented in table 2. The net reproductive rate was the highest at 25°C with 57.07 offspring per aphid and lowest at 10°C with 5.42 offspring per aphid. Increasing temperature resulted in shorter generation times of *A. gossypii* with 26.14 days at 10°C and 5.63 days at 30°C.

3.3 Model evaluation

Results of parameter estimation of linear, Briere 2 and Lactin 2 models for the developmental rate of *A. gossypii* are presented in table 3. All models had R^2 higher than 0.95. The thermal constant has been estimated from the linear equation to be 97.08 DD. Between 15 and 25°C the development was linearly related to

temperature. The lower developmental threshold estimated by the Briere 2 and Lactin 2 models was 5 and 5.5°C respectively (fig. 2). The lower developmental threshold predicted by Briere 2 and Lactin 2 models was lower than the estimated developmental threshold derived from the linear regression equation (6.19°C), because at low temperatures, the curves overestimate the developmental rate and do not respect the nonlinear form. The linear model does not provide both the optimal and the high temperature thresholds (table 3). The Briere 2 and Lactin 2 models provide estimates for low and high temperature threshold and optimal temperature. The estimated optimal temperature by these models was between 30 and 35°C.

4 Discussion

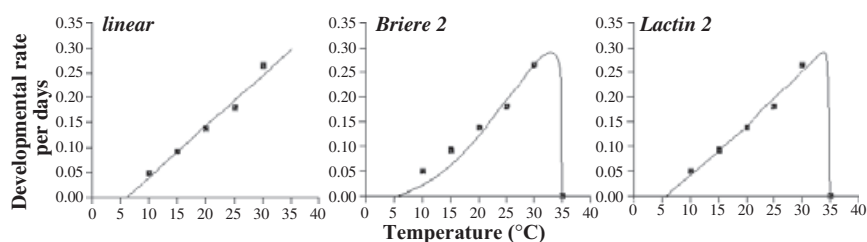
The results revealed the obvious effects of temperature on the developmental time, mortality, survival and fecundity of *A. gossypii*. No other study has covered the full range of temperatures that are suitable to the development and survival of *A. gossypii* in Tehran.

Effects of temperature on the biology of *A. gossypii* have been studied on cucumber (van Steenis and El-Khawass 1995) and on other host plants such as cotton (Attia and El-Hamaky 1987; Akey and Butler 1989; Xia et al. 1999), cucurbit (Liu and Perng 1987), squash (Aldyhim and Khalil 1993) and citrus (Komazaki 1982). Among these studies, there is considerable variation in developmental time and the intrinsic rate of natural increase. *Aphis gossypii* survival and developmental data reported here partially agree with Kersting et al. (1999) and Aldyhim and Khalil (1993). The optimum temperature for development of *A. gossypii* was 30°C and thus, slightly higher than the 27.5°C reported by Akey and Butler (1989) on cotton, although it was essentially the same as the 29.7°C observed for *A. gossypii* on citrus (Komazaki 1982). Temperature had a significant influence on the demographic parameters of *A. gossypii* (table 2). Comparison of data in the literature with the results presented here revealed many differences among the various population parameters for *A. gossypii* collected in different geographical areas and from different host plants. In particular, the optimum temperature of 25°C for population growth rate in this study was considerably lower than the 30°C reported by Liu and Perng (1987) on cucurbit and the 30°C reported by Kocourek et al. (1994) on cucumber and the temperatures given for *A. gossypii* on cotton (Akey and Butler 1989; Kersting et al. 1999), but was greater than the 19.8°C reported by Komazaki (1982) for a Japanese

Table 3. Parameters estimated for the three temperature-dependent models for describing total development of *Aphis gossypii*

Model type	Parameters	Estimates
Linear regression	a	-0.0638 ± 0.019
	b	0.0103 ± 0.000
	R^2	0.976
	RSS	0.657×10^{-3}
Lactin 2	ρ	0.009 ± 0.000
	T_{\max}	35.299 ± 0.010
	Δ	0.201 ± 0.000
	λ	-1.049 ± 0.015
	T_0	5.512
	T_{opt}	35.091
	R^2	0.989
	RSS	0.487×10^{-3}
Briere 2	a	0.000 ± 0.000
	m	2.820 ± 0.276
	T_0	5.000 ± 0.001
	T_{\max}	35.001 ± 0.000
	T_{opt}	32.71
	R^2	0.955
	RSS	2.093×10^{-3}

Fig. 2. Fitting of equations of table 1 on data of table 2 for the pre-imaginal developmental time of *Aphis gossypii*



cotton aphid colony obtained from citrus. At low temperatures, the r_m of aphid populations from Saudi Arabia fed on squash (Aldyhim and Khalil 1993) and from Japan fed on citrus (Komazaki 1982) and from Turkey fed on cotton (Kersting et al. 1999) was greater than for our *A. gossypii* source fed on cucumber. The r_m values of *A. gossypii* in our study at 10, 15, 20, 25 and 30°C were 0.064 ± 0.000 , 0.180 ± 0.000 , 0.325 ± 0.001 , 0.419 ± 0.001 and 0.363 ± 0.003 /day (table 2), respectively, whereas these values for the sources studied by Xia et al. (1999), fed on cotton, were 0.033, 0.142, 0.255, 0.386 and 0.360/day respectively. However, both *A. gossypii* populations showed similar trends in relation to temperature. At all temperatures, the r_m of aphid populations reared on cucumber were greater than aphids reared on cotton. Our source of *A. gossypii* was more susceptible to high temperatures than the aphids examined by Xia et al. (1999). As our source was not able to complete its life cycle and give birth to offspring at 35°C (table 2), whereas the source studied by Xia et al. (1999) had this ability, this indicates that there is different thermal compatibility between cotton aphid populations reared on various host plants and originating from different geographical regions.

Therefore, although *A. gossypii* is known as a polyphagous species, it seems widely accepted in the literature that its performance varies widely among different host plants (Kersting et al. 1999; Perng 2002; Rohne 2002; Du et al. 2004; Chau et al. 2005). There are three possible reasons for the observed differences: (1) host plants vary widely in their nutritional value for *A. gossypii*; (2) the utilization of a new host plant depends on the experience of the aphid in that *A. gossypii* needs time to adapt to a new host; and (3) genetically distinct forms or host races exist in *A. gossypii*, which differ in their ability to colonize various host plants (Satar et al. 1999; Perng 2002; Du et al. 2004). Even different biological features of cotton aphid has been observed among populations reared on various variety of the same host plant. Du et al. (2004) studied the effects of three cotton cultivars with different gossypol contents on the development, reproduction and survival of *A. gossypii* and its predator *Propylaea japonica* (Thunberg). Their results indicated that high gossypol content in host cotton had an antibiotic effect on *A. gossypii* and showed a positive effect on growth and development of *P. japonica* at the third trophic level. Such differences affect the potential of natural enemy populations to prevent pest population increase on different host plants and at various temperatures.

Fecundity rate and net reproductive rate of *A. gossypii* were greater at 20°C than at 30°C (table 2), but the intrinsic rate of increase at 30°C was greater than that at 20°C. Thus, the difference between the r_m of *A. gossypii* at 20 and 30°C is mainly due to its pre-imaginal developmental time. Because of the minus sign in the intrinsic rate of increase equation (Carey 1993), $\Sigma l_x m_x e^{-r_m x} = 1$, increasing the pre-imaginal developmental time leads to more x value, so $e^{-r_m x}$ decreases. From the productivity study of *A. gossypii* reared at 20, 25 and 30°C on two cucumber cultivars

conducted by van Steenis and El-Khawass (1995), a rough estimate of r_m of 0.426, 0.556 and 0.510/day, respectively, can be obtained. These results agree with our data for *A. gossypii* at the same temperatures. A moderate temperature of 25°C appeared to be the most suitable for cotton aphid survival and reproduction (table 2). This result may explain the fact that *A. gossypii* increased to a high population density in spring when the ambient temperature in Tehran province is near 25°C.

The theoretical development threshold of 6.19°C computed from the linear equation was similar to the 6.4°C obtained from data reported by Akey and Butler (1989), but quite different from the -0.4°C estimated by Komazaki (1982), 1.25°C estimated by Aldyhim and Khalil (1993) and 7.9°C estimated by Xia et al. (1999), suggesting differing temperature adaptations among various populations.

The thermal constant in our study was estimated to be 97.08 DD that was nearly similar to the 90.1 DD on cucumber reported by Kocourek et al. (1994) and quite different from the 168.8 DD estimated by Xia et al. (1999) on cotton. These differences may be explained by the existence of two genetically distinct host races of *A. gossypii* on cotton and cucumber.

The linear model is the simplest description of the developmental rate-temperature relationship, and it is widely used for calculating lower developmental temperature threshold and thermal constant (Dent and Walton 1997). However, as the curve over a wider temperature range is sigmoidal, the linear model will underestimate and overestimate the DD per unit time near lower and upper extreme for development respectively. Therefore, to describe the developmental rate more realistically and over a wider temperature range, several nonlinear models have been applied (e.g. Logan et al. 1976; Lactin et al. 1995; Briere et al. 1999). For *A. gossypii*, the Lactin 2 and Briere 2 models seem to be the best, and satisfactorily estimated the optimal temperature and the high temperature threshold. These two models were also highly efficient in modelling *Orius niger* Wolf (Baniamiri et al. 2005), *Tyrophagus putrescentiae* (Schrank) (Sanchez-Ramos and Castanera 2001), *Stethorus punctillum* and its prey *Tetranychus medaniali* (Roy et al. 2002). However, our results were obtained from studies of fitted models, and we are cautious in applying these findings to actual aphid populations. Furthermore, the models fitted might not be robust to extrapolations to temperatures outside the observed range.

The key to using environmental controls in an insect and mite management programme is to know how environmental conditions affect both the pest and their natural enemies. Temperature may strongly affect the relationship between a natural enemy and the target pest. Temperature records from computerized greenhouse provide a further opportunity to predict pest outbreaks and to track the population interplay between pest and natural enemy by computing the developmental times of both pest and parasitoid stages, measured in DD. This information can be useful in timing initial releases of the parasitoid, making natural enemy introductions more efficient

(Heinz et al. 2004). *Aphis gossypii* population from Tehran seems to perform better at high temperatures than other known populations; therefore, we must maintain the greenhouse temperature down to the range not unfavourable for crop growth and utilize the natural enemies, the development of which is faster than *A. gossypii* at lower temperatures. High greenhouse temperatures (over 28°C) were found to be unfavourable for *Aphidius colemani* Viereck (Goh et al. 2001), the aphid parasitoid in greatest use in greenhouse crops, and it is more effective at lower temperatures. Therefore, *A. colemani* is a good candidate for biological control of cotton aphid at lower temperature. Shipp et al. (1991) noted that manipulating the greenhouse environment, especially temperature and humidity, was probably the most underutilized tactic in insect and mite pest management.

Insect development is closely related to temperature and this must be taken into account in designing routine sampling programmes. Insect populations change faster in warm than in cold weather. It is therefore more appropriate to base sampling intervals on DD than on calendar days (Horn 1988). In addition, the monitoring DD can be used to predict when specific life stages of certain pests and natural enemies are most abundant. The required DD provide a practical application method based on the concept that phenological considerations are essential in the economically and environmentally prudent uses of chemical pesticides. In fact, pesticides can be applied timely and economically according to the prediction of the occurrence of certain phenological events (Briere and Pracros 1998). Consequently, the prediction of phenological events using DD is one of the most essential parts in an integrated pest management programme for *A. gossypii*.

This work described the temperature-dependent development of a Tehran population *A. gossypii* under the broad range of temperatures generally prevailing in this region. However, more knowledge of their adaptations at temperatures close to the low threshold would be important. Meanwhile, from the present knowledge, it may be concluded that the existence of host incompatibility and host races is a common phenomena in *A. gossypii*. To determine the importance of the host plant for the performance of the cotton aphid, its host plant relationship should be studied in more detail.

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