

Influence of temperature on bionomics of cotton aphid, *Aphis gossypii*, on cotton

J. Y. Xia^{1,2}, W. van der Werf¹ & R. Rabbinge¹

¹Department of Theoretical Production Ecology Wageningen Agricultural University P.O. Box 430, 6700 AK Wageningen, the Netherlands; ²Cotton Research Institute Chinese Academy of Agricultural Sciences Anyang, Henan 455112, China (E-mail: crixia@public.zz.ha.cn)

Accepted: October 27, 1998

Key words: *Aphis gossypii*, development, survival, fecundity, intrinsic rate of increase, life table, temperature

Abstract

Life table parameters of *Aphis gossypii* Glover (Homoptera: Aphididae) on *Gossypium hirsutum* L. were determined at six temperatures (10, 15, 20, 25, 30, and 35 ± 0.5 °C) in the laboratory. Relationships of life table parameters with temperature were described with mathematical equations. Development was fastest at 30 °C, with a pre-larviposition period of 4.6 d. Survival to adult was greatest at 25 °C (81%). Fecundity was highest at 25 °C, with a total fecundity of 28.3 nymphs per female and a mean reproductive rate of 3.1 nymphs per female per day. Threshold temperatures for development in the first through fourth instar and the adult were 8.2, 8.0, 7.2, 6.2 and 7.9 °C, respectively. The durations of these stages, expressed as temperature sums above these thresholds, were 24.2, 23.7, 23.0, 25.5 and 168.8 degree-days (D°), respectively. *A. gossypii* achieved its maximum net reproductive number (24.4 nymphs per female) and greatest intrinsic rate of increase (0.386 d⁻¹) at 25 °C. The high relative rate of population increase at 25 °C results in a daily population increase of 47% and a doubling time of only 1.8 d, illustrating the tremendous growth capacity of *A. gossypii* populations under favourable conditions. Compared to literature sources, our source of *A. gossypii*, fed on cotton, showed a comparatively great heat tolerance.

Introduction

Cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is the key pest of seedling cotton (*Gossypium hirsutum* L.) in China, particularly the North China cotton region (Fang et al., 1992; Xia, 1992). Seven-spot ladybird beetle (*Coccinella septempunctata* L.; Coleoptera: Coccinellidae) is the predominant natural enemy of cotton aphid in this region during the seedling stage of cotton (Xie & Sterling, 1987; Fang et al., 1992). The development of biological control requires insight into the bionomics and potential population growth of *A. gossypii* as affected by environmental conditions, notably temperature.

Effects of temperature on the bionomics of *A. gossypii* have been studied on cotton in the USA (Akey & Butler, 1989) and Egypt (Attia & El-Hamaky, 1987), and on other host plants such as cucumber (Wyatt & White, 1977), cucurbit (Liu & Peng,

1987), squash (Aldyhim & Khalil, 1993) and citrus (Komazaki, 1982). Among these studies, there is considerable variation in life table statistics and resulting statistics describing potential population increase, such as the intrinsic rate of natural increase. There is no information on life table statistics and population growth parameters for Chinese sources of *A. gossypii*, fed on cotton.

In order to analyse biological control of *A. gossypii* with the seven-spot ladybird beetle in cotton-wheat intercropping in the North China cotton region, reliable and site-specific information on life table statistics and potential population growth is indispensable. This paper describes the effect of temperature on life table parameters and potential population growth of a Chinese population of *A. gossypii*, collected and reared on cotton.

Materials and methods

Experiments. The study was carried out at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07°N and 114.22°E) in 1993. The experiments were conducted in a Multi-Unit-Chamber (Messrs. Brabender, KSE-S 6-125/RN) at six temperatures (10, 15, 20, 25, 30 and 35 ± 0.5°C). All experiments were done at 70–90% r.h. and 14-h photoperiod.

A laboratory colony was started with field-collected aphids from CCRI 12, a cultivar of *Gossypium hirsutum* L. which is commonly cultivated in the North China cotton region. The colony was maintained in field cages (3 m × 3 m × 2 m high). Three generations were completed before tests were initiated. Adults from the colony served as the parent stock for all rearing experiments.

For each temperature, 100 adults collected in field cages were kept in 40 glass petri dishes (15 cm diameter and 2.5 cm deep) for 12 h to produce offspring. Around 100 newly born aphids were individually reared on cotton leaflets in glass tubes (2 cm diameter and 10 cm long). The third and fourth true leaves of cotton seedlings were used as rearing substrate in all tests. All cotton leaves were grown in field cages and free of aphid injury. Moulting and mortality were monitored every 24 h at 10, 15 and 20°C, and every 12 h at 25, 30 and 35°C. After each observation, the cotton leaf was replaced. During the adult stage, the aphids were individually reared on cotton leaves in glass petridishes (10 cm diameter and 2 cm deep), where newly born aphids were counted and then removed. Observations were continued until death of all adults.

Analysis. We estimated the following life history parameters: development time of the first to fourth nymphal instar; total nymphal period; pre-reproductive period; reproductive period; reproductive plus post-reproductive period; total adult longevity; time between birth and first larviposition, life span from birth to death; total fecundity (number of nymphs produced per female in her lifetime); and mean reproductive rate during the reproductive period (number of nymphs produced per female per day). Parameters were statistically compared among temperature treatments using the GLM procedure of SAS 6.1 for PC (SAS Institute, 1993–1995).

From the data collected, the age-specific survival (l_x) and age-specific fecundity (m_x) were calculated.

The intrinsic rate of increase (r_m , d⁻¹) was determined using the method of Birch (1948):

$$\Sigma l_x m_x \exp(-r_m x) = 1 \quad (1)$$

where x is the age. The net reproductive number (number of nymphs produced per capita, $R_0 = \Sigma l_x m_x$), generation time ($t = \ln(R_0)/r_m$, d), finite rate of increase [$\lambda = \exp(r_m)$, –] and population doubling time ($\tau = \ln 2/r_m$, d) were also calculated according to the method of Birch (1948).

Developmental rate (R_d , d⁻¹) of each life stage was calculated as the reciprocal of the stage duration. Logan et al.'s (1976) model was used to describe the response of the developmental rate to temperature (T , °C):

$$R_d = a_1 \{ \exp[a_2(T - T_l)] - \exp[a_2(T_u - T_l) - (T_u - T)/a_3] \} \quad (2)$$

where T_l is the lower threshold temperature (°C), T_u is the upper lethal temperature (°C); and a_1 , a_2 and a_3 are coefficients. The upper lethal temperature was assumed to be the same for all life stages: 38°C as estimated in growth chambers by Xie & Sterling (1987). The lower threshold temperature of each life stage was determined by linear regression, excluding the data for the higher temperature where the relationship becomes non-linear (Siddiqui et al., 1973):

$$T = b_1 + b_2 R_d \quad (3)$$

where T is the temperature (°C). The regression coefficients b_1 and b_2 represent the threshold temperature and the duration of the stage, expressed in degree-days, respectively.

Mortality and fecundity in the adult stage are not only temperature- but also age-dependent. Twenty age classes were discerned to describe the age dependency of fecundity and mortality with the method of Rabbinge (1976, pp. 58–61). The duration of each age class was determined by dividing the maximum life span by the total number of age classes. The maximum life span was defined as the mean life span plus 3 s.d. The relative mortality rate (R_m , d⁻¹) of each life stage and each adult age class was computed using the method of Rabbinge (1976, p. 57):

$$R_m = (\ln N_t - \ln N_{t+\Delta t})/\Delta t \quad (4)$$

where N_t is the number of insects at time t , $N_{t+\Delta t}$ is the number of insects at time $t + \Delta t$, and Δt is the time interval between observations (i.e., duration of a life stage or an age class). The relationship between the relative mortality rate and temperature (T , °C) was described with a parabola:

$$R_m = c_1 + c_2 T + c_3 T^2 \quad (5)$$

where c_1 , c_2 and c_3 are coefficients.

Weibull's (1951) model was used to describe the relationship of temperature with total fecundity (A), mean reproductive rate during the reproductive period (B) and the mean reproductive rate of each adult age class (C):

$$Y = d_2/d_1 d_3 [(T - T_l)/d_1]^{(d_2-1)} \exp\{-(T - T_l)/d_1\}^{d_2} \quad (6)$$

where Y stands for A, B or C; T and T_l have the same meaning as in Equation (2); and d_1 , d_2 and d_3 are coefficients. An equation modified from Bieri *et al.* (1983) was used to describe the relationship between the mean reproductive rate of each age class (R_q) and adult age (q):

$$R_q = e_1 q / (e_2)^q \quad (7)$$

where e_1 and e_2 are coefficients.

Model equations were selected to provide a biologically appropriate shape, minimum Root Mean Square Error (RMSE) and maximum coefficient of determination (r^2). All parameters in non-linear models or equations were estimated iteratively by minimisation of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

Results

Development. Development period of pre-reproductive stages of *A. gossypii* feeding on cotton decreased with temperature up to 25–30 °C and then increased (Table 1). The time from birth to first larviposition was shortest (4.6 d) at 30 °C, at which temperature it was one fifth of that at 10 °C (23.0 d). Duration of the reproductive, and reproductive plus post-reproductive adult stages decreased with temperature. The longest period of the reproductive plus post-reproductive adult (26.0 d), at 10 °C, was about 7 times that at 35 °C (3.8 d) (Table 1).

The response of the developmental rate (R_d) in all life stages to temperature was satisfactorily described by Logan *et al.*'s (1976) model (Figure 1). RMSE ranged from 0.040 to 0.046 d⁻¹ for the first through fourth instar, 0.17 d⁻¹ for the pre-reproductive adult, and 0.0053 d⁻¹ for the reproductive plus post-reproductive adult; and r^2 ranged from 0.94 to 0.99. Developmental rate of pre-reproductive stages increased exponentially from the lower threshold temperature to an optimum (around 30 °C) and then declined until the upper lethal temperature had been reached; while it increased exponentially up to 35 °C in the reproductive plus post-reproductive adult (Figure 1).

Survival. Survival in all pre-reproductive stages increased with temperature up to 25 °C and then decreased (Table 1). The greatest survival from birth to first larviposition was attained at 25 °C (81%), which was approximately 3 times that at 10 °C and 35 °C (26–33%) (Table 1).

A parabola adequately described the relationship between temperature and the relative mortality rate (R_m) of pre-reproductive stages (Figure 2). RMSE ranged from 0.0015 to 0.0073 d⁻¹, and r^2 from 0.95 to 0.99. The relative mortality rate was higher at 10 °C and 35 °C, while it was lower at 20–25 °C (Figure 2). Relationships between temperature and the relative mortality rate in adult age classes were also adequately described by parabolas (Appendix; Table A1). The relative mortality rate increased with adult age at all six temperatures, and it also increased with temperature in each adult age class (Figure 3).

Fecundity. Total fecundity and the mean reproductive rate were highest at 25 °C (Table 1). For instance, total fecundity (28.3 nymphs per female) at 25 °C was about 5 times that at 10 °C (6.1 nymphs per female) and 7 times that at 35 °C (4.0 nymphs per female). The mean reproductive rate (3.1 nymphs per female per day) at 25 °C was about 8 times that at 10 °C (0.4 nymphs per female per day) and 2 times that at 35 °C (1.7 nymphs per female per day) (Table 1).

Weibull's (1951) model adequately described the relationships between temperature and total fecundity and the mean reproductive rate (Figure 4). RMSE was 2.9 nymphs per female for the total fecundity (Figure 4A) and 0.4 nymphs per female per day for the mean reproductive rate (Figure 4B), and r^2 exceeded 0.95. Total fecundity and the mean reproductive rate increased from the lower threshold temperature to an

Table 1. Effect of temperature on life history parameters (means \pm s.e.) of *A. gossypii* on cotton^a

	Temperature (°C)					
	10	15	20	25	30	35
Nymphs (d)						
First instar	4.6 \pm 0.24 (99) ^b a [67.7] ^c	3.5 \pm 0.23 (54) b [75.9]	2.9 \pm 0.19 (51) c [84.3]	1.4 \pm 0.08 (68) d [92.6]	1.1 \pm 0.04 (66) d [92.4]	1.3 \pm 0.06 (87) d [86.2]
Second instar	5.3 \pm 0.25 (67) a [71.6]	3.5 \pm 0.19 (41) b [85.4]	2.0 \pm 0.13 (43) c [93.0]	1.3 \pm 0.06 (63) de [93.7]	1.0 \pm 0.06 (61) e [91.8]	1.6 \pm 0.09 (75) cd [77.3]
Third instar	5.8 \pm 0.29 (48) a [72.9]	2.7 \pm 0.14 (35) b [85.7]	2.0 \pm 0.14 (40) c [90.0]	1.3 \pm 0.05 (59) de [96.6]	1.0 \pm 0.06 (56) e [91.1]	1.6 \pm 0.12 (58) cd [70.7]
Fourth instar	6.8 \pm 0.38 (35) a [74.3]	3.0 \pm 0.27 (30) b [86.7]	1.9 \pm 0.11 (36) c [91.7]	1.3 \pm 0.05 (57) de [96.5]	1.1 \pm 0.07 (51) e [90.2]	1.7 \pm 0.11 (41) cd [70.7]
Total nymphal stage	23.0 \pm 0.9 (26) a [26.3]	13.0 \pm 0.5 (26) b [48.2]	8.5 \pm 0.20 (33) c [64.7]	5.0 \pm 0.10 (55) d [80.9]	4.6 \pm 0.09 (46) d [69.7]	5.4 \pm 0.20 (29) d [33.3]
Adults (d)						
Pre-reproductive	3.2 \pm 0.28 (26) a [76.9]	2.4 \pm 0.24 (26) b [88.5]	1.0 \pm 0.10 (33) c [97.0]	0.6 \pm 0.04 (55) cd [96.4]	0.6 \pm 0.06 (46) d [95.7]	0.9 \pm 0.10 (29) c [82.8]
Reprod. plus post-reprod.	26.0 \pm 2.9 (20) a	23.0 \pm 2.6 (23) a	14.2 \pm 1.5 (32) b	10.3 \pm 1.0 (53) bc	6.8 \pm 0.69 (44) cd	3.8 \pm 0.40 (24) d
Entire adult stage	29.0 \pm 3.2 (20) a	25.4 \pm 2.4 (23) a	15.6 \pm 1.4 (32) b	10.9 \pm 1.0 (53) c	7.4 \pm 0.70 (44) cd	4.7 \pm 0.40 (24) d
Age at first larviposition (d)	25.9 \pm 1.1 (20) a	15.1 \pm 0.4 (23) b	9.7 \pm 0.2 (32) c	5.6 \pm 0.08 (53) e	4.9 \pm 0.13 (44) e	7.2 \pm 0.32 (24) d
Age at death from aging (d)	53.4 \pm 3.6 (20) a	38.4 \pm 2.5 (23) b	24.2 \pm 1.5 (32) c	15.8 \pm 1.0 (53) d	12.0 \pm 0.7 (44) d	10.2 \pm 0.4 (24) d
Fecundity per female	6.1 \pm 1.69 (20) d	21.4 \pm 2.5 (23) b	24.6 \pm 2.0 (32) ab	28.3 \pm 2.5 (53) a	14.6 \pm 1.4 (44) c	4.0 \pm 0.35 (24) d
Fecundity per female per day	0.4 \pm 0.14 (20) d	1.2 \pm 0.10 (23) c	2.2 \pm 0.12 (32) b	3.1 \pm 0.13 (53) a	2.7 \pm 0.20 (44) a	1.7 \pm 0.21 (24) b

^aMeans in each row followed by the same letter are not significantly different in ANOVA, using LSD-tests at P = 0.05.^bValues in parentheses are number of aphids tested.^cValues in square brackets are survival (%) from one stage to the next.

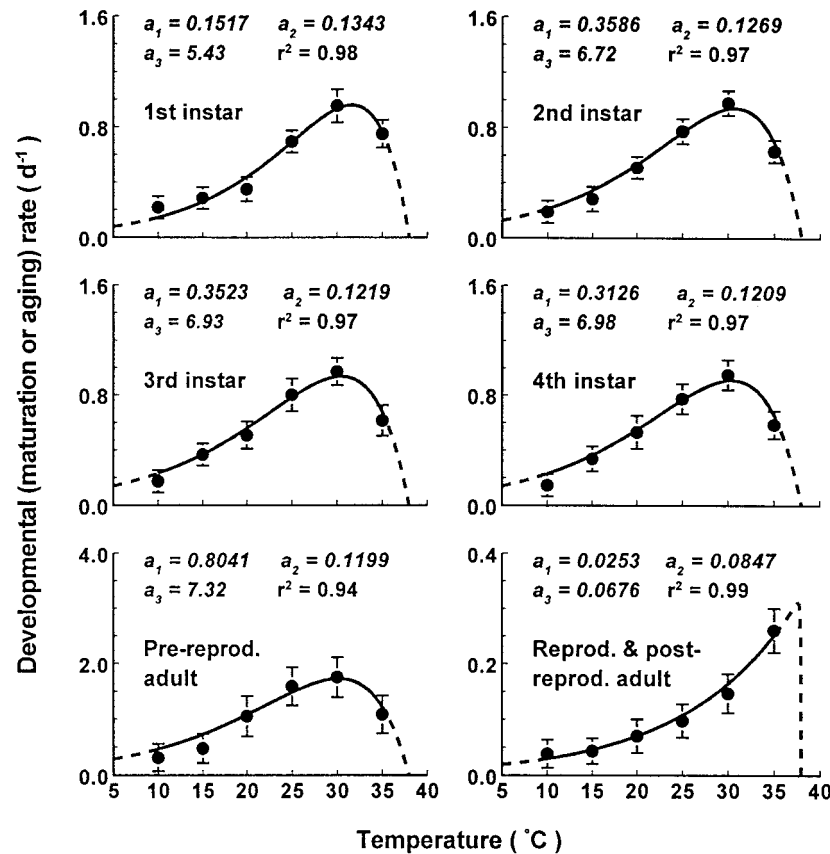


Figure 1. Relationship between temperature and the developmental (maturation or aging) rate of *A. gossypii* on cotton. Curves are described by Equation (2). The lower threshold temperature (T_l) is presented in Table 2, and the upper lethal temperature (T_u) is 38 °C. Bars represent observations with 95% confidence limits.

optimum and then decreased (Figure 4). The relationship between temperature and the mean reproductive rate of each adult age class was also satisfactorily described by Weibull's (1951) model (Appendix; Table A2).

The relationship between the mean reproductive rate of each age class (R_q) and adult age at each temperature was adequately described by Equation (7) (Figure 5). RMSE was 0.02, 0.08, 0.21, 0.24, 0.09 and 0.08 nymphs per female per day for 10 °C through 35 °C, respectively; and r^2 ranged from 0.94 to 0.98. The adult age-dependent mean reproductive rate was relatively low at 10 °C and 35 °C, with the reproduction terminated before age class 10; while it was relatively high at 20–30 °C, with the reproduction ending after age class 15 (Figure 5).

Threshold temperature. Threshold temperature decreased in successive nymphal instars from 8.2 °C in the first instar to 6.2 °C in the fourth instar and then

increased with adult age up to 7.9 °C in the reproductive plus post-reproductive adult (Table 2). The temperature sum above threshold, needed to complete the development of nymphal instars, ranged with narrow bounds: from 23.0 to 25.5 degree-days (D°). The duration of the adult stage, expressed in thermal time above the threshold, was 168.9 D°, which was about 2 times that for the entire nymphal period (99.4 D°) (Table 2).

Potential rate of population increase. The net reproductive number (R_0) had a maximum value of 24.4 nymphs per female at 25 °C, compared to 18.5 nymphs per female at 20 °C and 10.2 nymphs per female at 30 °C (Table 3). At the extreme temperatures of 10 °C and 35 °C, the net reproductive number was only 2.6 and 2.0 nymphs per female, respectively. The intrinsic rate of population increase (r_m) showed an optimum response to temperature, with a maximum of 0.386 d⁻¹ at 25 °C compared to 0.255 d⁻¹

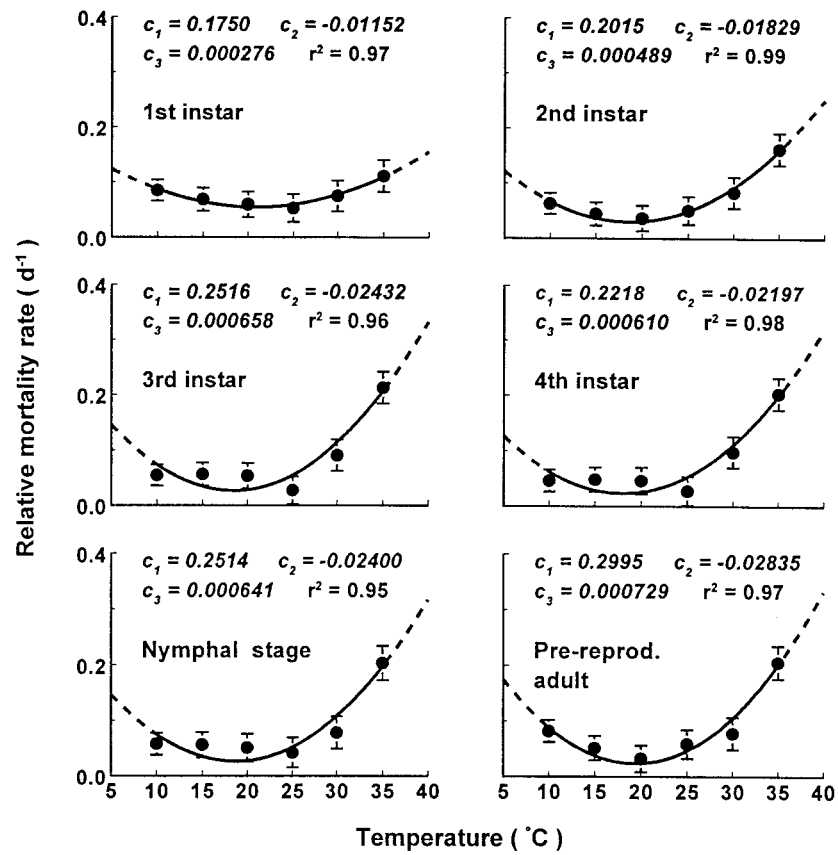


Figure 2. Relationship between temperature and the relative mortality rate of *A. gossypii* on cotton. Curves are described by Equation (5). Bars represent observations with 95% confidence limits.

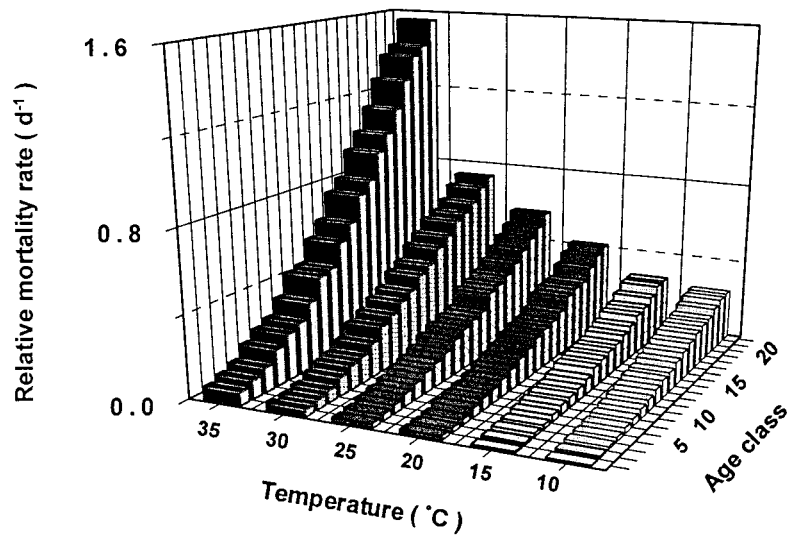


Figure 3. Age class-dependent relative mortality rate of *A. gossypii* adults on cotton at six temperatures.

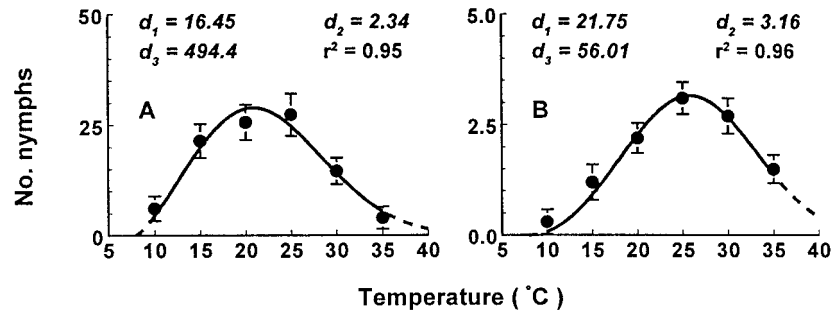


Figure 4A,B. Relationships between temperature and total fecundity (total nymphs per female, A), and the mean reproductive rate during the reproductive period (nymphs per female per day, B) of *A. gossypii* on cotton. Curves are described by Equation (6). The lower threshold temperature (T_l) is 7.9 °C (Table 1). Bars represent observations with 95% confidence limits.

Table 2. Threshold temperature and temperature sum (means \pm s.e.) of *A. gossypii* on cotton

Stage/period	Threshold temperature (°C)	Temperature sum (D°)	r^2
First instar	8.2 ± 2.5	24.2 ± 3.6	0.95
Second instar	8.0 ± 1.2	23.7 ± 1.5	0.99
Third instar	7.2 ± 1.1	23.0 ± 1.5	0.99
Fourth instar	6.2 ± 1.1	25.5 ± 1.5	0.99
Total nymphal stage	7.1 ± 2.5	99.4 ± 14.2	0.96
Pre-reproductive adult	6.3 ± 1.7	11.4 ± 2.0	0.91
Reprod. plus post-reprod. adult	7.9 ± 2.6	156.2 ± 30	0.95
Entire adult stage	7.9 ± 2.4	168.8 ± 24	0.96
Age at first larviposition	7.7 ± 2.2	105.3 ± 12	0.97
Age at death from aging	7.4 ± 1.5	275.4 ± 23	0.98

and 0.360 d^{-1} at 20 °C and 30 °C (Table 3). At the extreme temperatures of 10 °C and 35 °C, the intrinsic rate of population increase was 0.033 d^{-1} and 0.092 d^{-1} , respectively. The high relative rate of population increase at 25 °C would result in a daily population increase of 47% and a doubling time of only 1.8 d, illustrating the tremendous growth capacity of *A. gossypii* populations under favourable conditions.

Discussion

This study was initiated to ascertain the growth potential of *A. gossypii* populations in cotton fields in North China, in order to better understand possibilities and impossibilities of its biological control, using natural enemies. Three factors have major consequences for the growth potential of aphids as measured in laboratory studies: (1) the geographic origin and adaptation of the aphid population; (2) host plant; (3) tempera-

ture. Published studies on the bionomics of this aphid were difficult to extrapolate to *A. gossypii* in North Chinese cotton because either (1) the aphids were from a distinct geographical origin (e.g., Aldyhim & Khalil, 1993; Komazaki, 1982); or (2) the aphids were fed on another host plant (e.g., Liu & Peng, 1987); or (3) the temperature response was not studied or investigated over a limited range of temperature (most studies). We therefore decided to do this study.

The question is: does *A. gossypii* collected in cotton and reared on cotton in North China exhibit different population growth responses to temperature than other populations of this aphid? A monofactorial comparison with literature data cannot be made because in the two published studies that include a broad range of temperatures (Komazaki, 1982; Aldyhim & Khalil, 1993), both the aphid origin and host plant are different from our study. Komazaki (1982) collected *A. gossypii* in a citrus orchard in Japan, and determined life table statistics on *Citrus unshiu*. Aldyhim &

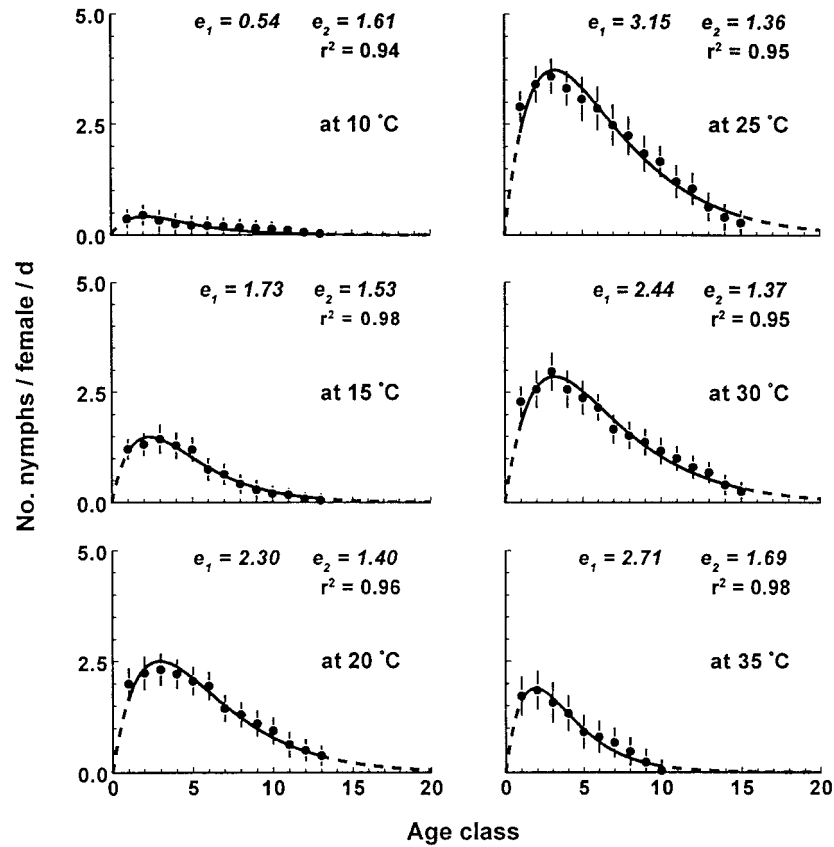


Figure 5. Relationship between adult age class and the mean reproductive rate (nymphs per female per day) of *A. gossypii* on cotton at six temperatures. Curves are described by Equation (7). Bars represent observations with 95% confidence limits.

Khalil (1993) collected *A. gossypii* on squash (*Cucurbita pepo*) in Saudi Arabia, and determined life table statistics on squash. Figure 6 compares our results with those of these two studies, taking the intrinsic rate of population increase, r_m , and the development rate from birth to first larviposition as the main indicators of aphid population performance. Arguably, the different host plants used in the three studies may have affected the absolute values of the development rates and intrinsic rates of increase, in relation to their nutritional suitability (Auclair, 1963); however, it is likely that the shape of the temperature response represents intrinsic properties of the different aphid populations studied.

The intrinsic rate of increase (r_m), especially, is a useful summary parameter to characterize the influence of abiotic factors, in particular temperature, on the growth potential of insect populations (Birch, 1948; Messenger, 1964; DeLoach, 1974; Wyatt & White, 1977; Nowierski et al., 1983). It should primarily be considered as a comparative figure, indicating

growth potentials, as the conditions under which its absolute value may be achieved (excellent host plant quality; no adverse weather conditions such as rain and wind; no natural enemy or disease impacts) are nearly never fully met.

The r_m -temperature response of the local population of *A. gossypii* near Anyang, Henan, in the middle of the North China cotton region, differed indeed from that of the other populations on other host plants. At low temperatures, the r_m of aphid populations from Saudi Arabia fed on squash (Aldyhim & Khalil, 1993) and from Japan fed on citrus (Komazaki, 1982) was greater than for our *A. gossypii* source, fed on cotton (Figure 6A). The maximum r_m was attained at 27 °C on cotton, at 25 °C on squash and at only 22 °C on citrus (Figure 6A).

Our source of *A. gossypii* was more tolerant to high temperatures than the sources examined by Komazaki (1982) and Aldyhim & Khalil (1993). Our source, for instance, was able to complete its life cycle and give birth to offspring at 35 °C (Table 1), whereas

Table 3. Effect of temperature on the rate of increase of *A. gossypii* populations on cotton

Parameters	Temperature (°C)					
	10	15	20	25	30	35
Net reproductive number (R_0)	2.6	13.8	18.5	24.4	10.2	2.0
Intrinsic rate of increase (r_m , d ⁻¹)	0.033	0.142	0.255	0.386	0.360	0.092
Finite rate of increase (λ , —)	1.03	1.15	1.29	1.47	1.43	1.10
Population doubling time (τ , d)	20.8	4.9	2.7	1.8	1.9	7.5
Generation time (t , d)	28.9	18.5	11.4	8.3	6.4	7.6

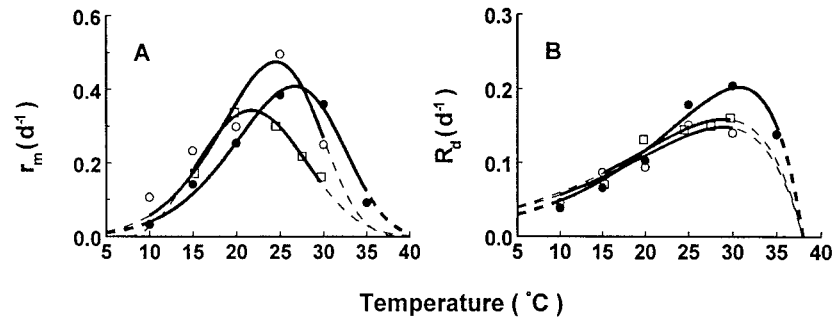


Figure 6. Comparison of the temperature responses of (A) the intrinsic rate of increase (r_m) and (B) the rate of development from birth to first larviposition (R_d) for *A. gossypii* reared on cotton (●) (this study), squash (○) (Aldyhim & Khalil, 1993) and citrus (□) (Komazaki, 1982).

the sources studied by Komazaki (1982) and Aldyhim & Khalil (1993) did not have this ability. The ability to survive at high temperatures also exceeds that of aphids studied on cotton in USA (Akey & Butler, 1989). Development rate at 30 °C was greater for our aphid population than for the other two sources (Figure 6B). High extreme and optimum temperatures for population growth and development (Figure 6) are adaptive traits, given the high temperatures in cotton fields in summer in North China. It would also contribute to the propensity of cotton aphid for outbreaks at the square-boll stage ('summer aphid') in North China, where the daily maximum temperature in the late summer fluctuates between 28 and 38 °C (Luo & Gao, 1986; Fang et al., 1992). *A. gossypii* obtained its highest rate of increase on cotton at 25–30 °C. This favours population growth on cotton seedlings during late May and early June in North China, when average daily temperatures are 20–30 °C. Cotton seedlings are vulnerable to aphid injury, and yield losses of 10–15% may result or it may be necessary to replant in some areas (Pan et al., 1986; Xia, 1992).

The differences in r_m among the three studies compared in Figure 6 may have major implications for population growth over time, due to the positive feedback between population size and population growth

in exponential growth. This can be illustrated by an example. After one week at 25 °C, a cotton aphid population would have increased by a factor $e^{7 \times 0.3} \approx 8$ according to the results of Komazaki (1982), by a factor $e^{7 \times 0.49} \approx 31$ according to the results of Aldyhim & Khalil (1993), and by a factor $e^{7 \times 3.8} \approx 14$, according to our results. At 30 °C, the multiplication figures after one week according to the three sources would be 3, 5 and 12. This simple calculation illustrates the major differences in response of population growth capacity to temperature among the three sources. At 25 °C, our source of *A. gossypii* showed intermediate population growth capacity, compared to the other two studies, whereas at 30 °C, our source showed the largest propensity to population increase. Such differences affect the potential of natural enemy populations to prevent pest population increase in different parts of the season. Results of this study provide therefore an indispensable basis for quantitative analysis of biological control of *A. gossypii* with *C. septempunctata* on cotton in North China.

Acknowledgements

The research is part of a Ph.D. thesis by the first author, and was supported by the Wageningen Agricultural University (WAU), the Netherlands, and the China Cotton Research Institute (CCRI), China. We thank Dr Kees Eveleens of the Department of Theoretical Production Ecology of WAU for his critical review of an earlier draft of the manuscript, and Mrs Y. Ma, Mr C. Y. Wang, Mr J. J. Cui and Mr J. P. Xi of CCRI for their assistance with the experiments.

References

- Akey, D. H. & G. D. Butler Jr., 1989. Developmental rates and fecundity of apterous *Aphis gossypii* on seedlings of *Gossypium hirsutum*. *Southwestern Entomologist* 14: 295–299.
- Aldyhim, Y. N. & A. F. Khalil, 1993. Influence of temperature and daylength on population development of *Aphis gossypii* on *Cucurbita pepo*. *Entomologia Experimentalis et Applicata* 67: 167–172.
- Attia, A. A. & M. A. El-Hamaky, 1987. The biology of the cotton aphid *Aphis gossypii* Glover in Egypt (Homoptera: Aphididae). *Bulletin Société Entomologique d'Égypte* 85: 359–371.
- Auclair, J. L., 1963. Aphid feeding and nutrition. *Annual Review of Entomology* 8: 439–490.
- Bieri, M., J. Baumgärtner, G. Bianchi, V. Delucchi & R. von Arx, 1983. Development and fecundity of pea aphid (*Acyrtosiphon pisum* Harris) as affected by constant temperatures and by pea varieties. *Mitteilungen Schweizerische Entomologische Gesellschaft* 56: 163–171.
- Birch, L. C., 1948. The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* 17: 15–26.
- DeLoach, C. L., 1974. Rate of increase of populations of cabbage, green peach, and turnip aphids at constant temperatures. *Annals Entomological Society of America* 67: 332–340.
- Fang, C. Y., Y. X. Zhang, S. Q. Wen, Y. W. Yao & X. Q. Ji, 1992. A Handbook on Cotton Pest Control. Chinese Agricultural Science & Technology Press, Beijing, China (in Chinese).
- Komazaki, S., 1982. Effect of constant temperature on population growth of three aphid species, *Toxoptera citricidus* (Kirkaldy), *Aphis citricola* van der Goot and *Aphis gossypii* Glover (Homoptera: Aphididae) on citrus. *Applied Entomology and Zoology* 17:75–81.
- Liu, Y. C. & J. J. Peng, 1987. Population growth and temperature-dependent effect of cotton aphid, *Aphis gossypii* Glover, on a bottle gourd cucurbit. *Chinese Journal of Entomology* 7: 75–112 (in Chinese, English summary).
- Logan, J. A., D. J. Wollkind, S. C. Hoyt & L. K. Tanigoshi, 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology* 5: 1133–1140.
- Luo, Z. Y. & G. P. Gao, 1986. Population dynamics of cotton aphid on cotton during the square-boll stage and the relation between population age structure and parasitism. *Acta Entomologica Sinica* 29: 56–61 (in Chinese, English summary).
- Messenger, P. S., 1964. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Therioaphis maculata*. *Journal of Economic Entomology* 57: 71–76.
- Nowierski, R. M., A. P. Gutierrez & J. S. Yaninek, 1983. Estimation of thermal thresholds and age-specific life table parameters for the walnut aphid (Homoptera: Aphididae) under field conditions. *Environmental Entomology* 12: 680–686.
- Pan, Q. M., T. S. Wu & L. S. Zhang, 1986. Influence of temperature on reproduction of the cotton aphid. *Acta Entomologica Sinica* 29: 367–370 (in Chinese, English summary).
- Rabbinge, R., 1976. Biological Control of Fruit-tree Red Spider Mite. Simulation Monographs, Pudoc, Wageningen, the Netherlands, 420 pp.
- SAS Institute, 1993–1995. SAS User's Guide. SAS institute, Cary, NC, USA.
- Siddiqui, W. H., C. A. Barlow & P. A. Randolph, 1973. Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae). *Canadian Entomologist* 105: 145–156.
- Slide Write Plus for Windows, 1983–1993. User's Manual. Advanced Graphics Software, Inc., Carlsbad, CA, USA.
- Weibull, W., 1951. A statistical distribution of wide applicability. *Journal of Applied Mechanics* 18: 293–297.
- Wyatt, I. J. & P. F. White, 1977. Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *Journal of Applied Ecology* 14: 757–766.
- Xia, J. Y., 1992. New development of integrated cotton pest management systems in China. *China Cottons* 19(1): 2–6 (in Chinese).
- Xie, X. Y. & W. L. Sterling, 1987. Computer simulation of cotton aphid population dynamics. *Acta Phytophylacica Sinica* 14: 151–156 (in Chinese, English summary).

Appendix

Table A1. Relationship between temperature and the relative mortality rate of different age classes of *A. gossypii* adults on cotton, based on Equation (5) where c_1 , c_2 and c_3 are coefficients

Age class	c_1	c_2	c_3	RMSE	r^2
1	0.042	-0.0043	0.00014	0.0010	0.97
2	0.059	-0.0065	0.00021	0.0012	0.98
3	0.083	-0.0088	0.00028	0.0018	0.99
4	0.117	-0.0126	0.00040	0.0036	0.98
5	0.156	-0.0163	0.00052	0.0053	0.98
6	0.165	-0.0167	0.00054	0.0068	0.98
7	0.231	-0.0240	0.00076	0.0091	0.98
8	0.310	-0.0331	0.00104	0.0115	0.99
9	0.273	-0.0274	0.00092	0.0108	0.99
10	0.396	-0.0403	0.00127	0.0183	0.99
11	0.462	-0.0472	0.00148	0.0255	0.98
12	0.590	-0.0616	0.00188	0.0303	0.98
13	0.568	-0.0584	0.00185	0.0354	0.98
14	0.705	-0.0733	0.00227	0.0410	0.97
15	0.756	-0.0769	0.00239	0.0523	0.98
16	0.678	-0.0672	0.00218	0.0421	0.99
17	0.830	-0.0840	0.00266	0.0617	0.98
18	0.934	-0.0930	0.00292	0.0810	0.98
19	0.905	-0.0871	0.00281	0.0793	0.98
20	1.007	-0.0989	0.00318	0.1026	0.97

Table A2. Relationship between temperature and the mean reproductive rate of each age class of *A. gossypii* adults on cotton, based on Equation (6) where T_l is the lower threshold temperature (7.9 °C, Table 2), and d_1 , d_2 and d_3 are coefficients

Age class ^a	d_1	d_2	d_3	RMSE	r^2
1	20.3	2.89	52.7	0.45	0.94
2	20.3	2.96	57.6	0.51	0.94
3	20.1	3.14	59.0	0.43	0.97
4	19.7	3.06	52.3	0.33	0.97
5	19.4	3.24	47.5	0.27	0.98
6	19.4	3.43	42.3	0.13	0.99
7	19.2	3.69	33.3	0.15	0.99
8	19.1	3.92	29.7	0.11	0.99
9	19.1	3.82	25.7	0.04	0.99
10	19.1	4.24	21.2	0.03	0.99
11	19.9	4.90	15.0	0.09	0.98
12	20.1	5.30	12.7	0.07	0.98
13	20.4	5.06	9.3	0.09	0.94
14	20.1	8.97	4.3	0.01	0.99
15	20.0	9.98	3.0	0.01	0.99

^aNo nymphs were produced in age classes 16–20.