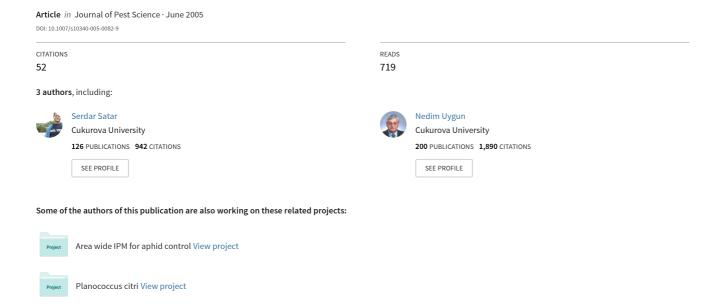
Effect of temperature on development and fecundity of Aphis gossypii Glover (Homoptera: Aphididae) on cucumber



ORIGINAL ARTICLE

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Effect of temperature on development and fecundity of *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber

Received: 22 October 2004 / Published online: 22 February 2005 © Springer-Verlag 2005

Abstract The developmental time, survivorship and reproduction of Aphis gossypii Glover was evaluated on detached cucumber leaves at nine constant temperatures ranging from 15 ± 1 °C to 35 ± 1 °C in 2.5 °C increments in the laboratory. Developmental periods of immature stages ranged from 10.8 days at 15°C to 4.1 days at 30°C and 32.5°C. Constant 35°C was lethal to immature stages of A. gossypii. The lower developmental threshold for the cotton aphid was estimated at 6.0°C and it required 92.6 degree-day development for a first instar to become adult. The average reproduction rate was 82.1 nymphs female⁻¹ at 25°C and 2.3 nymphs female⁻¹ at 32.5°C. The mean generation time of the population ranged from 6.8 days at 32.5°C to 22.8 days at 15°C. The highest per capita growth rate $(r_{\rm m} = 0.526)$ occurred at 25°C and the lowest at 15°C ($r_{\rm m}$ = 0.208) and 32.5°C ($r_{\rm m}$ = 0.132). It was evident that temperatures over 30°C prolonged development, increased mortality of immature stages, shortened adult longevity and reduced fecundity. The optimal range of temperature for population growth of A. gossypii on cucumber was very broad and ranged between 22.5°C and 30°C.

Keywords Aphis gossypii · Intrinsic rate of increase · Life table · Survival

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Introduction

Aphis gossypii Glover (Homoptera: Aphididae) has long been regarded as a cosmopolitan, highly polyphagous species, widely distributed in tropical, subtropical and temperate regions. This cotton or melon aphid is present in all cotton-growing areas of the world and is, principally in temperate zones, a pest of vegetables and ornamentals in field and greenhouse (Leclant and Deguine 1994). A. gossypii causes direct damage, resulting from searching for food, by inducing plant deformation and it causes indirect damage either by honeydew or by the transmission of viruses. This aphid is the vector of 76 viral diseases across a very large range of plants (Chan et al. 1991).

More recent findings provided strong evidence that A. gossypii is comprised of various genetically different host races that vary with respect to host alteration and host preference. Guldemond et al. (1994) showed that cotton aphids living on cucumber and chrysanthemum behave as genetically distinct host races. Similar, Kersting et al. (1998) reported that A. gossypii from cotton and cucumber consists of two genetically distinct host races, with the cotton strain of A. gossypii not being able to propagate on cucumber. Cluster analysis based on genetic distances clearly separated 18 A. gossypii populations (collected in southern France, Corsica, La Réunion, Portugal, Laos) into two groups regardless of their geographical origin: those collected on cucurbits and those collected on noncurcubits (VanLerberghe-Masutti and Chavigny 1998).

The existence of specific host races in aphids, in particular in A. gossypii, may explain the significant differences reported in the literature on temperaturedependent development and fecundity of the cotton aphid with regard to host plant and geographical region (Komazaki 1982; Liu and Perng 1987; Akey and Butler 1989; Aldyhim and Khalil 1993; Kocourek et al. 1994; van Steenis and El-Khawass 1995; Satar et al. 1998, 1999; Perng 2002). Thus, developmental 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).

The present study was designed to provide data on the developmental rate and fecundity of *A. gossypii* at different constant temperatures that might be used for developing control models of cucumber pests in the east Mediterranean region of Turkey.

Materials and methods

A. gossypii were obtained from greenhouse-grown cucumber near Adana in the east Mediterranean region of Turkey and colonized on *Cucumis sativus* cv. Beit Alpha at 26 ± 2 °C, 65 ± 10 % relative humidity and 16 h of artificial light (about 10,000 Lux) in a climatic room. Aphids were reared in the laboratory for about ten generations before individuals were used in the experiments (Kindlmann and Dixon 1989).

Experimental design

Randomly selected apterous females from the stock culture were transferred onto excised cucumber leaf disks placed upside-down on wet cotton wool in Petri dishes (5 cm diam.). Offspring born within 24 h was confined individually on cucumber leaf disks in Petri dishes. All replications in which nymphs died within 24 h after transfer were omitted. The cotton wool in the Petri dishes was wetted daily and aphids were transferred every 3–5 days to new cucumber leaf disks. Leaves used in the experiments were obtained from greenhouse-grown cucumber (cv. Beit Alpha) that was between 4 weeks and 6 weeks of age.

Experiments were conducted at nine constant temperatures ranging from $15\pm1^{\circ}\text{C}$ to $35\pm1^{\circ}\text{C}$ in 2.5°C increments, $60\pm5\%$ relative humidity and 16 h of artificial light (5,000 Lux) in temperature cabinets. Immature stages and adults were observed daily at all temperature regimes and their survivorship recorded. The exuviae were used to determine molting time; and newborn larvae were removed after counting.

Data analysis

Differences in developmental time, longevity and reproduction were tested by analysis of variance. If significant differences were detected, multiple comparisons were made using Tukey's HSD multiple range test (P=5%). A linear technique was employed to compute the lower development threshold of the nymph stages, using growth rate data as a dependent variable and temperature treatments as an independent variable. The lower developmental threshold was determined as the *x*-intercept of the linear equation and the degree—day requirements were determined as the value of the inverse of the linear equation slope.

Population growth rates were calculated from the equation of Lotka (Birch 1948):

$$1 = \sum e^{-rX} l_X m_X \tag{1}$$

in which: x = age in days (including immature stages), r = intrinsic rate of increase, $l_x =$ age-specific survival (including immature mortality) and $m_x =$ age-specific number of female offspring.

After r was computed for the original data $(r_{\rm all})$, differences in $r_{\rm m}$ values were tested for significance by estimating variances through the jack-knife method (Meyer et al. 1986). The jack-knife pseudo-value r_j was calculated for n samples using the following equation:

$$r_i = n \times r_{\text{all}} - (n-1) \times r_i \tag{2}$$

Tukey's HSD multiple range test was used to compare mean growth rates at different temperatures (P=1%). Because low probability levels were used, there was no concern over inflation of experiment-wise error rates (Jones 1984). The above-mentioned analyses were conducted using a Statgraphics software package (Statistical Graphics Corporation 1988).

Results

The developmental time of *A. gossypii* significantly decreased with increasing constant temperature, ranging from 10.8 days at 15°C to 4.1 days at 30°C and 32.5°C (Table 1). The constant temperature of 35°C was lethal to early instars of the cotton aphid. A considerably higher mortality occurred during developmental time at 15°C and 17.5°C, 18.4% and 13.6% respectively, while little mortality was observed between 25°C and 32.5°C. The average number of offspring per reproduction day was highest between 20°C and 25°C (6.1–6.9 nymphs day⁻¹) and lowest at 15°C and 32.5°C (3.1 nymphs day⁻¹, 2.4 nymphs day⁻¹, respectively; Table 1).

A linear regression analysis was applied to the developmental points within the 15–30°C range. Development at > 30°C was outside the linear segment of the growth curve and therefore excluded from the linear regression. Within the chosen temperature range, the developmental rates (r_T) of A. gossypii increased linearly with increasing temperature $(r_T = 0.0108T - 0.0644, R^2 = 0.9798, F = 242.5, P \le 0.001$; Fig. 1). The theoretical development threshold was estimated as 6°C. It required 92.6 degree—day for a first instar to become adult, based on the developmental threshold for overall immature stages.

Survival rates of *A. gossypii* adults sharply decreased right after the peak of nymph production at higher temperatures, while a relatively long post-reproductive period was observed at 15°C and 17.5°C (Fig. 2). The highest age-specific number of nymphs per female per day (m_x) ranged between 0.9 nymphs female⁻¹ day⁻¹ at 32.5°C and 9.3 nymphs female⁻¹ day⁻¹ at 25°C.

Table 1 Developmental time, longevity, mortality and fecundity rate of *A. gossypii* on excised cucumber leaf disks at nine constant temperatures. Within the same column, means followed by the same letter are not significantly different (Tukey's HSD multiple range test, $\alpha = 0.05$)

Temperature $(\pm 1^{\circ}C)$	n	Developmental time (days; mean \pm SEM)	Total nymphal mortality rate (%)	Offspring per reproduction day (mean ± SEM)
15	49	$10.8 \pm 0.16^{\mathrm{f}}$	18.4	3.1 ± 0.14^{a}
17.5	48	$8.1 \pm 0.06^{\rm e}$	13.6	$4.5 \pm 0.09^{\mathrm{b}}$
20	46	$6.7 \pm 0.09^{\rm d}$	8.7	6.5 ± 0.11^{c}
22.5	47	5.4 ± 0.12^{c}	4.3	6.1 ± 0.22^{c}
25	44	$4.6 \pm 0.08^{\mathrm{b}}$	2.3	6.9 ± 0.18^{c}
27.5	44	4.3 ± 0.07^{ab}	2.3	4.5 ± 0.22^{b}
30	46	4.1 ± 0.05^{a}	2.2	$4.2 \pm 0.25^{\text{b}}$
32.5	44	4.1 ± 0.05^{a}	2.2	2.4 ± 0.38^{a}
35	48	_	100.0	

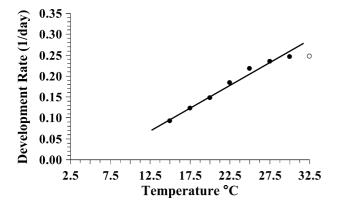


Fig. 1 Developmental rate (*r*) of *A. gossypii* at seven constant temperatures. The *line* indicates the linear regression analysis of developmental rate and temperature within the range 15–30°C

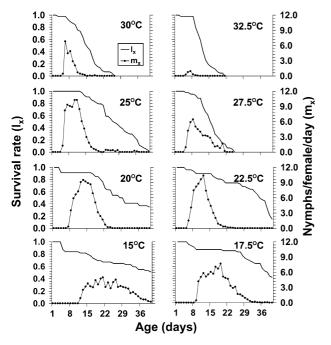


Fig. 2 Age-specific survival rate (l_x) and age-specific fecundity (m_x) of A. gossypii on excised cucumber leaf disks at eight temperatures

Increasing temperatures resulted in shorter generation times (T_0) of A. gossypii, with 22.8 days at 15°C and 6.8 days at 32.5°C (Table 2). The net reproductive rate (R_0) was highest at 25°C (82.1 aphids aphid⁻¹) and lowest at 32.5°C (2.3 aphids aphid⁻¹). A. gossypii populations kept at warmer temperatures showed a higher per capita rate of population growth, although the intrinsic rate of increase at 25°C (0.526 aphids aphid⁻¹ day⁻¹) was statistically not different from that at 27.5°C (0.384 aphids aphid⁻¹ day⁻¹). The 32.5°C treatment resulted in a sharp reduction in the per capita growth rate of the cotton aphid (r_m =0.123 aphids aphid⁻¹ day⁻¹), which was not significantly different from that at 15°C.

Discussion

Although insects are not subjected to constant temperatures in nature, controlled laboratory studies can provide a valuable insight into the population dynamics of aphids. Our results reported here clearly show the effects of temperature on the developmental time, nymphal mortality rate, longevity and fecundity of *A. gossypii* on cucumber. It is noteworthy that *A. gossypii* "cucumber" displayed quite different population parameters from an *A. gossypii* "cotton" population collected from the same area near Adana (Kersting et al. 1999). In particular, the optimum range of the cucumber population development was considerably broader (20–30°C) than that of the cotton population, which showed a much narrower range of only 27.5–30°C.

The optimum temperature for development of the cotton aphid on cucumber ranged between 27.5°C and 32.5°C, comparable with the 30°C reported by Kocourek et al. (1994) for the same aphid on the same host plant. There are small differences among the optimum temperature ranges for the developmental time of *A. gossypii* on cucumber and cotton (Akey and Butler 1989; Kersting et al. 1999; Xia et al. 1999), citrus (Komazaki 1982; Satar et al. 1998) and squash (Aldyhim and Khalil 1993). Insects reared at temperatures above the upper threshold develop slower than those reared under more

Table 2 Generation time (T_0) , net reproductive rate (R_0) and rate of population growth (r_m) of A. gossypii on excised cucumber leaf disks at eight temperatures. Increase rate means followed by the same letter were not significantly different (Tukey's HSD multiple range test, $\alpha = 0.01$)

Temperature (±1°C)	Generation time $(T_0, days)$	Reproduction rate (R_0) (aphids aphid ⁻¹)	Intrinsic rate of increase (r_m) (aphids aphid ⁻¹ day ⁻¹)
15	22.8	55.0	$\begin{array}{c} 0.208 \pm 0.0056^{ab} \\ 0.291 \pm 0.0051^{bc} \\ 0.358 \pm 0.0051^{cd} \\ 0.424 \pm 0.0082^{d} \\ 0.526 \pm 0.0068^{e} \\ 0.436 \pm 0.0127^{de} \\ 0.431 \pm 0.0137^{d} \\ 0.132 \pm 0.0489^{a} \end{array}$
17.5	17.7	77.8	
20	13.8	79.8	
22.5	11.4	66.8	
25	10.1	82.1	
27.5	9.7	38.7	
30	7.6	21.0	
32.5	6.8	2.3	

favorable conditions (Stinner et al. 1974; Curry et al. 1978; Kersting et al. 1999). This was less obvious for A. gossypii on cucumber, where the developmental time decreased to its lowest value at 30°C and 32.5°C; and with any further increase in temperature, all instars died. The theoretical development threshold of 6.0°C computed from the linear segment of the growth curve was similar to the 6.2°C on cotton reported by Kersting et al. (1999) and the 6.4°C computed from data presented by Akey and Butler (1989); but it was far higher than the -0.4°C estimate for A. gossypii on citrus (Komazaki 1982). The optimum temperature range between 20°C and 25°C for maximal production of nymphs per day in this study was considerably lower than 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) and for the bottleguard cucurbit (Liu and Perng 1987), but resembled more the 19.8°C reported by Komazaki (1982) for a Japanese cotton aphid colony obtained from citrus.

The intrinsic rate of natural increase (r_m) is a good indicator of the temperature at which the growth of a population is most favorable, because it reflects the overall effects of temperature on the development, reproduction and survival characteristics of a population. The population kept at 25°C had the highest r_m among all temperatures $(r_m = 0.526)$ aphids aphid⁻¹ day⁻¹), because of its faster development, higher survivorship of immature stages and high daily rate of progeny. However, the capita growth rate at 25°C was statistically not different from that at 27.5°C $(r_m = 0.436 \text{ aphids aphid}^{-1} \text{ day}^{-1})$. In contrast, A. gossypii "cucumber" exposed to 32.5°C had the lowest intrinsic rate of increase, due to a lower reproduction rate and a higher mortality rate of adults. A prolonged developmental time and a higher mortality rate of immature stages resulted in a similarly low intrinsic rate of increase at 15°C. The capita growth rate of A. gossypii "cucumber" at 25°C was considerably higher than that computed on cucumber ($r_m \approx 0.39$ aphids aphid⁻¹ day⁻¹) but very similar to that on squash $(r_m \approx 0.50)$ aphids aphid⁻¹ day⁻¹) (Aldyhim and Khalil 1993; Kocourek et al. 1994; van Steenis and El-Khawass 1995). Komazaki (1982) showed that the highest population

growth rate $(r_m \approx 0.32 \text{ aphids aphid}^{-1} \text{ day}^{-1})$ of a citrus population of *A. gossypii* occurred at 19.8°C, while Satar et al. (1998) reported that the highest capita growth rate of the citrus population they studied was at 25°C $(r_m \approx 0.30 \text{ aphids aphid}^{-1} \text{ day}^{-1})$.

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. Thus, it is very difficult to draw accurate conclusions from such comparisons. Kersting et al. (1999) studied a cotton population of A. gossypii on cotton collected in mid-summer near Adana. In this study, we investigated A. gossypii living on greenhouse-grown cucumber that was collected in spring near Adana. While the cotton population of the aphid appeared to be well adapted to warm summer temperatures (constant 27.5-30°C; Kersting et al. 1999), the A. gossypii "cucumber" population performed very well under much cooler conditions (20°C, 22.5°C) and at the same time showed high population growth rates at warm temperatures of 27.5°C and 30°C. These differences may be explained by the existence of two genetically distinct host races of A. gossypii on cotton and cucumber (Kersting et al. 1998). It should, however, be considered that the different times of aphid collection in the field and greenhouse (springsummer) for these two populations may have had an effect on the per capita growth rates of both populations (Owusu et al. 1994). Further studies are needed to elucidate the different effects that the specific host races, the plant hosts of the aphid and the time of collection during the year have on the population growth rates of A. gossypii on different host plants.

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