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Effect of temperature on development rate and intrinsic rate of increase of *Aphis gossypii* reared on greenhouse cucumbers

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Abstract

Thermal requirements for development and life table statistics of *Aphis gossypii* Glover (Homoptera, Aphididae) were determined over a range of constant temperatures from 10 to 30 °C. The lower development threshold and the sum of effective temperatures were 6.9 °C and 90.1 °C, respectively, for preimaginal development, and 5.8 °C and 113.6 °C from birth to the onset of reproduction. Mean total fecundity ranged from 36 larvae per female at 10 °C to 76 larvae at 30 °C. On a time scale of days, net reproductive rate (R_o) increased with increasing temperature while generation time (T) decreased causing the intrinsic rate of increase (r_m) to increase linearly from 0.115 to 0.465. On a day-degree scale r_m only varied from 0.019 to 0.028 because the growth of R_o was compensated by an increase in T with increase in temperature. The nearly constant r_m in terms of day-degrees, over a wide range of temperatures, greatly simplifies the prediction of future population numbers of *A. gossypii.*

Introduction

The cotton aphid, *Aphis gossypii,* is a polyphagous species with a world-wide distribution. It is a major pest of cultivated plants such as Cucurbitaceae (cucumbers, pumpkin and melon), Rutaceae (orange, grapefruit and lemon) and Malvaceae (cotton). Damage caused includes reduction in yield and fruit quality as well as virus transmission. The cotton aphid is not only highly efficient in transmitting the tristeza virus (TV) of Rutaceae (Roistacher *et al.*, 1984) but is also an important vector of cucumis mosaic virus (CMV) and watermelon mosaic virus 2 (WMV 2) of Cucurbitaceae (Pitrat & Lecoq, 1980; Gray *et al.*, 1986). Consequently, in many regions *A. gossypii* is one of the most important pests of greenhouse plants (Havelka, 1978).

In addition, *A. gossypii* is a polymorphic species. It is variable not only in its morphology (colour and dwarf forms) (Wall, 1933; Setokuchi, 1981) but also in its life-cycle (anholocyclic, holocyclic and mixed populations) (Takada, 1988) and in its ecological characteristics (host plant specialization, environmental requirements, fecundity, insecticide resistance etc.) (Inaizumi, 1981; Zheng *et al.*, 1989; Saito, 1990; Furk & Vedjhi, 1990; O'Brien & Graves, 1990; Grafton-Cardwell, 1991). Therefore, for each pest management programme an exact determination of the crucial population parameters is required.

In 1987, a very aggressive, pirimicarb resistant population with a mixed anholocyclic/holocyclic life cycle appeared on greenhouse cucumbers in the Czech Republic (Havelka, unpubl). In the following four years, in many places, the aphid disrupted integrated pest management systems aimed at controlling glasshouse whitefly (*Trialeurodes vaporariorum* Westwood) and two-spotted spider mite (*Tetranychus urticae* Koch), and the aphid even attacked cucumber crops in the open. The aim of this paper is to determine the thermal requirements and life table characteristics necessary for predicting its population development.

Materials and methods

Experimental design. Experiments were carried out on greenhouse cucumbers (*Cucumis sativus* L.) cv. Sandra at the three or four-leaf stage potted in standard peat soil. All aphid characteristics were determined in growth cabinets, at five constant temperatures 10 °, 17 °, 20 °, 25 ° and 30 ° ± 1.5 °C, at a L17:D7 photoperiod, light intensity 5000 lux, and r.h. of ± 80%.

The *A. gossypii* were obtained from cucumbers growing in greenhouses near Plzeň (West Bohemia, Czech Republic). The aphids were reared on cucumber seedlings for about 64 generations before adult females were transferred from the stock culture to the leaves of experimental plants and allowed to larviposit for six hours. The test aphids were randomly selected from the new-born larvae, and caged individually on marked leaves (Adams & van Emden, 1972). Three replicates of 5–33 individuals were reared at each temperature and the characteristics of the apterous virginoparous females noted.

Thermal requirements for development. The thermal requirements for larval instars (L1–L4), prereproductive period (the time from adult eclosion to onset of reproduction), total preimaginal development (the time from birth to adult eclosion), and total prereproductive development (the time from birth to onset of reproduction) were determined. The aphids were observed every 24 h at 17–25 °C, and every 12 h at 30 °C.

For each temperature, rates of developments (RD: day^{-1}) were calculated as reciprocals of the total preimaginal (RD_{pi}) and total prereproductive (RD_{pr}) development. The relationships between RD and temperature (t) were described by a linear function

$$RD = a + b.t$$

where a and b are parameters of the linear regression (Campbell *et al.*, 1974). From this, the lower development thresholds (LDT), i.e. the temperatures when development ceases, can be estimated:

$$LDT = -a/b,$$

as can the sums of effective temperatures (SET), i.e. number of day-degrees above LDT necessary for completion of development:

$$SET = 1/b.$$

Life table characteristics. Adults were observed daily at all temperatures and their age specific survivorship (l_x) and age specific fecundity (m_x) recorded. Newborn larvae were counted and removed. From this data we estimated the length of the reproductive period (in days and day-degrees), total fecundity as total mean number of progeny per female, median ($l_x = 0.5$) and maximum ($l_x = 0$) longevity (in days), and calculated R_o, net reproductive rate as expected lifetime production of female progeny for a newborn female

$$R_o = \Sigma_x l_x m_x \text{ (Birch, 1948),}$$

and T, generation time as mean lifespan to the median of R_o (in days and day-degrees). Intrinsic rate of increase (r_m) was calculated as:

$$\Sigma_x exp(-r_m x) l_x m_x = 1,$$

determining the values of r_m by an iterative computer program (Mertz, 1970). Parameter r_m was expressed both per day and in day-degrees (Graf

Table 1. The mean development time for preimaginal stages (L1, L2, L3, L4), adult prereproductive period, and total preimaginal and prereproductive development of *Aphis gossypii* reared on *Cucumis sativus* at various constant temperatures

Temperature t (°C)	Number of individuals (n)	Larval instars L1 (days)	L2	L3	L4	Total pre-imaginal development (days)	Prereproductive period (days)	Total prereproductive development (days)	(day-degrees)
10	57	-[1]–	–	–	–	–	18.5	75.9	
17[2]	93	–	–	–	–	–	–	10.0	111.0
17[2]	14	2.0	2.3	2.7	2.0	9.0	1.7	10.7	–
20	20	2.1	1.6	1.6	1.6	6.9	1.0	7.9	111.4
25	17	1.8	1.0	1.0	1.2	5.0	1.0	6.0	114.6
30	19	1.3	0.9	1.0	1.0	4.2	0.9	5.1	122.9

[1] not observed
[2] two independent experiments

et al., 1985; Elliot & Kieckhefer, 1989; Kocourek & Beránková, 1989) using the values above lower development threshold for RD_{pr}.

Results

Development times are given in Table 1. From 17 to 30 °C, the larvae on average spent 30% (larva 1), 23% (larva 2), 24% (larva 3) and 23% (larva 4) of the total preimaginal period in individual instars, and the adults started to reproduce on the 2nd day after eclosion. The relationships between the rate of total preimaginal (RD_{pi}) and total prereproductive (RD_{pr}) development and temperature were linear on the range of temperatures from 17 to 25 °C. RD_{pr} was ± 33% higher for 10 °C, and ± 26% lower for 30 °C than indicated by the linear relationships. The sum of effective temperature (SET) for the preimaginal development of *A. gossypii* was 90.1 °C, with a lower development threshold (LDT) of 6.9 °C. The SET for the prereproductive development was 113.6 °C, with a LDT of 5.8 °C.

Figures on longevity and fecundity are summarized in Table 2. There was no preimaginal mortality, and only a few prereproductive adults died at 10 °C. However, we observed two different patterns of survival during the adult reproductive and postreproductive period (Fig. 1). At 10 and 17 °C the aphids lived longer and there was a relatively high mortality during the reproductive period and a relatively long postreproductive period (representing 43 and 66% of the maximum longevity respectively) than at 20, 25 and 30 °C. At 20, 25 and 30 °C the lifespan was shorter than at the lower temperatures, with a very low mortality during reproduction and a shorter postreproductive lifespan (from 34 to 41% of maximum longevity). The maximum rate of reproduction was only four larvae per day at 10 °C compared with seven at 30 °C. Mean total fecundity ranged from 35.7 larvae per female at 10 °C to 76.1 larvae at 30 °C.

Parameters related to population growth are shown in Table 3. R_o increased with temperature. T decreased with increase in temperature when time was measured in days, but increased on a day-degree scale. Parameter r_m increased linearly from 0.115 to 0.465 on a per day scale ($r_m = -0.051 + 0.0175t$; $n = 5$, $r = 0.997$, $s.e. = 0.012$). On a day-degree scale, r_m only varied from 0.019 to 0.028. Consequently, when the aphid age distribution is stable and in an unlimited environment, one can use r_m to predict the population development of *A. gossypii* on greenhouse cucumbers using the model:

$$N_t = N_o exp(r_m t)$$

Table 2. The median ($l_x = 0.5$) and maximum ($l_x = 0$) longevity, reproductive period and mean total fecundity per female of *Aphis gossypii* reared on *Cucumis sativus* at various constant temperatures

Temperature t (°C)	Number of individuals (n)	Median longevity (l_x=0.5) (days)	Maximum longevity (l_x=0) (days)	Reproductive period (days)	Reproductive period (day-degrees)	Mean fecundity per female (number of progeny)
10	68	40.3	102.9	35.5	145.5	35.7
17	93	33.6	64.9	37.0	410.7	61.3
20	17	18.9	31.9	21.1	297.5	55.7
25	17	28.0	34.0	22.0	420.2	53.6
30	15	27.1	37.1	22.0	530.2	76.1

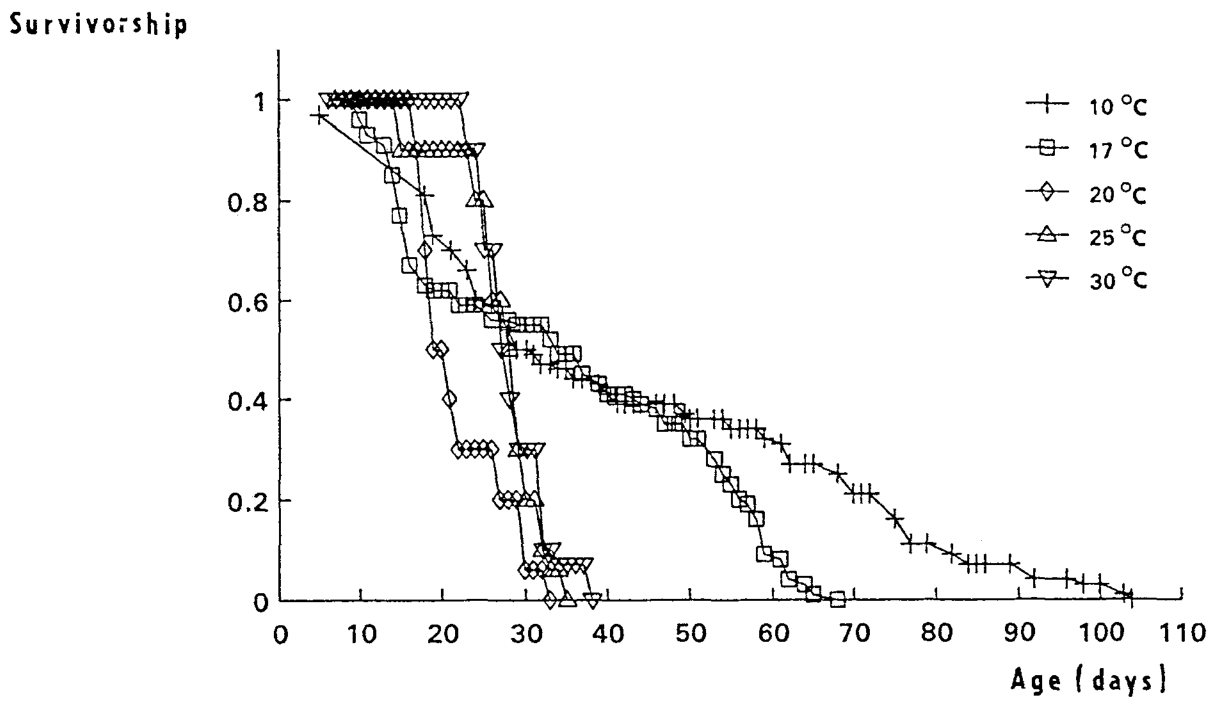

Fig. 1. Age-specific survivorship of adult *Aphis gossypii* on *Cucumis sativus* at five different constant temperatures.

where N_t is the predicted aphid density at time t, N_o is the initial population density, r_m is the intrinsic rate of increase in day-degrees, and t is time expressed in day-degrees above LDT. The average day-degree value of r_m obtained in this study was 0.022.

Discussion

The SET and LDT obtained for the preimaginal development of *A. gossypii* are similar to the values cited by Akey & Butler (1989) for this aphid reared on cotton (SET = 98.0 °C, LDT = 7.9 °C). However the SET and LDT for total prereproductive development differed slightly more from Wyatt & Brown (1977) results for cucumber leaf discs (SET = 105.6 °C, LDT = 4.8 °C), and even more so from those of Komazaki (1982) for citrus plants (SET = 181.8 °C, LDT = - 0.4 °C). That the maximum longevity was recorded at low temperature is unusual, and differs from that observed in another population of *A. gossypii* reared

Table 3. The net reproductive rate (R_0), generation time (T) and intrinsic rate of increase (r_m) of *Aphis gossypii* reared on *Cucumis sativus* at various constant temperatures

Temperature t (°C)	Number of individuals (n)	Net reproductive rate R_0 (expected lifetime progeny production per female)	Generation time T (days)	Generation time T (day-degrees)	Intrinsic rate of increase r_m (day^{-1})	Intrinsic rate of increase r_m (day-degrees^{-1})
10	68	19.6	25.0	102.5	0.115	0.0280
17	93	41.9	16.6	184.3	0.247	0.0223
20	17	47.0	12.5	176.3	0.316	0.0225
25	17	51.6	10.9	208.2	0.386	0.0200
30	15	76.1	10.7	257.9	0.465	0.0192

on cucumbers (Wyatt & Brown, 1977). This trait may enable some females to survive over winter in unheated greenhouses. On the other hand, the maximum r_m (day^{-1}) is typical for aphid species with a high reproductive potential developing on an optimal host plant (Barlow, 1962; Siddiqui *et al.*, 1973; Komazaki, 1982).

The high optimal temperatures for development, fecundity and growth suggest a subtropical origin of the population we studied. The minimum prereproductive period was achieved at 30 °C compared with 29.7 °C on citrus (Komazaki, 1982), 28 °C on cotton (Isely, 1946), and 27 °C on bottle gourd cucurbit (Liu & Perng, 1987). Maximum fecundity and R_o were also attained at 30 °C compared with maxima at 25 °C (Akey & Butler, 1989), 20 °C (Isely, 1946) and 19.8 °C (Komazaki, 1982) for other populations and on other host plants. In contrast, on cucumbers, Wyatt & Brown (1977) found a striking difference in population growth with their population having a higher R_o at 18 then at 24 °C.

Probably for the first time we record an interesting phenomenon, the intrinsic rate of increase (r_m) expressed in day-degrees is nearly constant over a range of temperature. Parameter r_m is inversely proportional to T and directly to the logarithm of R_o, which is not affected by the time scale because it is calculated on a per generation basis. Therefore, when m_x and l_x are expressed in terms of days, increase in r_m with increasing temperature can be attributed both to an increase in R_o and decline in T (Table 3). T decreased due to a reduction in the prereproductive (Table 1) and a larger reduction in the reproductive period (Table 2). However, on a day-degree scale the increase in R_o was compensated by an increase in T, and r_m declined with increase in temperature (Table 3). T in term D^o increased with increase in temperature because both the prereproductive (Table 1) and reproductive periods (Table 2) increased. On the other hand, in less thermophilous populations or species T in degree-days does not increase with increase in temperature, and R_o declines at high temperatures. The russian wheat aphid, *Diuraphis noxia* (Mordvilko) in terms of day-degrees, at fluctuating temperatures, shows a clear decrease in r_m with increase in temperature due to a decline in R_o and an unchanged T (Kieckhefer & Elliot, 1989).

However, for the population of *A. gossypii* used in this study the nearly constant r_m in terms of day-degrees simplifies the prediction of the population development of this pest under greenhouse conditions, as only two parameters: initial population density of the aphid and rate of accumulation of day-degrees, are needed for prediction.

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