

Reproduction and fertility life table of three aphid species (Macrosiphini) at different temperatures

Bruno F. De Conti¹, Vanda Helena P. Bueno¹, Marcus V. Sampaio² & Livia A. Sidney¹

¹Departamento de Entomologia, Universidade Federal de Lavras, Caixa Postal 3037, 37200-000 Lavras-MG, Brasil. bfdeconti@yahoo.com.br; vhpbueno@den.ufla.br; liviasidney@yahoo.com.br

²Instituto de Ciências Agrárias, Universidade Federal de Uberlândia, Caixa Postal 593, 38400-902 Uberlândia-MG, Brazil. mvsampaio@iciag.ufu.br

ABSTRACT. Reproduction and fertility life table of three aphid species (Macrosiphini) at different temperatures. Temperature is a key abiotic factor influencing the development and reproduction of aphids. The effect of temperature on the reproduction of three aphid species *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas) and *Uroleucon ambrosiae* (Thomas) (Aphididae, Macrosiphini) has been investigated and fertility life tables were determined. Nymphs were reared in climatic chambers at temperatures of 16, 19, 22, 25, and 28 ± 1°C, RH 70 ± 10% and 12 h photophase. Female adult aphids developed at these temperatures were then used in experiments in which pre-reproductive and reproductive periods were evaluated every 24 h. In addition, the number of nymphs produced and longevity were determined at each temperature. The reproduction period of *A. solani* and *M. euphorbiae* decreased with increasing temperature, whereas that of *U. ambrosiae* was maintained between 19 and 25°C. The total number of nymphs produced by the aphids decreased as the temperature increased. The longevities of *A. solani* and *M. euphorbiae* decreased with increasing temperature but remained stable for *U. ambrosiae* between 19 and 25°C. The largest survival rate (l_x) and specific fertility (m_x) values were found at 16 and 22°C for all three species. The most favourable temperature for reproduction of *A. solani*, *M. euphorbiae* and *U. ambrosiae* was 22°C, as demonstrated by the l_x and m_x profiles, the high values of net reproductive rates and intrinsic rates of increase, and the short intervals between generation and doubling times.

KEYWORDS. Aphids; growing parameters; intrinsic rate of increase; lettuce; longevity.

RESUMO. Reprodução e tabela de vida de fertilidade de três espécies de afídeos (Macrosiphini) em diferentes temperaturas. A temperatura é o fator abiótico chave influenciando o desenvolvimento e a reprodução dos afídeos. O objetivo desse trabalho foi avaliar o efeito de diferentes temperaturas na reprodução, assim como determinar a tabela de vida de fertilidade de *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas) e *Uroleucon ambrosiae* (Thomas) (Aphididae, Macrosiphini). Ninfas foram mantidas em placas de Petri (15 cm de diâmetro), sobre disco foliar de alface, suportado por uma camada de solução ágar/água a 1%, em câmaras climatizadas nas temperaturas de 16, 19, 22, 25 e 28±1°C; UR de 70±10% e fotofase de 12 h, até atingirem o estágio adulto. Esses adultos foram avaliados nas mesmas temperaturas a cada 24 h sob microscópio estereoscópico quanto aos parâmetros reprodutivos e longevidade. O período reprodutivo de *A. solani* e *M. euphorbiae* foi decrescente com o aumento da temperatura. *U. ambrosiae* apresentou período reprodutivo estável de 19 a 25°C. A produção total de ninfas das três espécies de pulgões foi decrescente com o aumento da temperatura. A longevidade de *A. solani* e *M. euphorbiae* foi decrescente com o aumento da temperatura. As maiores taxas de sobrevivência (l_x) e fertilidade específica (m_x) foram observadas entre 16 e 22°C para as três espécies de pulgões. A temperatura mais favorável para a reprodução e crescimento populacional de *A. solani*, *M. euphorbiae* e *U. ambrosiae* foi 22°C, como demonstrado pelo conjunto dos valores de l_x e m_x , altos valores da taxa reprodutiva e taxa intrínseca de aumento, e curtos intervalos entre gerações e tempo de duplicação da população.

PALAVRAS-CHAVE. Afídeos; alface; longevidade; parâmetros de crescimento; taxa intrínseca de aumento.

Aphids are “r-strategists”, i.e., a simple body structure allows the insect to feed and reproduce efficiently, with most of the nutrient intake being directed towards the production of nymphs (Rabasse & Steenis 1999). Temperature is one of the most important abiotic factor influencing the biology, individual behavior, and population dynamics of these insects (Campbell & Mackauer 1975; Eastop 1977). Temperatures above or below the optimum for reproduction result in deleterious effects on various biological parameters. Thus, excessively high temperatures reduce the reproductive period, the production of nymphs, longevity and population growth (Kuo *et al.* 2006; Mehrparvar & Hatami 2007).

Uroleucon Mordvilko, 1914 is one of the few genera of aphids with species native from South America, including Brazil. *Uroleucon ambrosiae* (Thomas, 1878) represents the main pest of lettuce (*Lactuca sativa* L.) cropped in greenhouses

(Starý *et al.* 2007). The aphid species *Aulacorthum solani* (Kaltenbach, 1843) and *Macrosiphum euphorbiae* (Thomas, 1878) constitute significant pests of various crops grown in protected systems (Bueno 2005), and may also attack lettuce plants cultivated hydroponically (Auaud *et al.* 2002; Starý *et al.* 2007). Dense populations of these insect species have been observed on other crops in the field, but mainly during mild seasons. In hot seasons, populations of aphids decrease dramatically and may not even be detected in agroecosystems (Sanchez *et al.* 2007; Starý *et al.* 2007).

The aim of the present study was to determine the influence of temperature on the reproduction, fertility and longevity of *A. solani*, *M. euphorbiae* and *U. ambrosiae* in order to enhance our understanding of the population dynamics of these aphid pests and to assist in the planning of strategies for their management in aphid susceptible crops.

MATERIAL AND METHODS

Insects. All experiments were conducted at the Laboratory of Biological Control of the Department of Entomology, Federal University of Lavras, in climatic chambers operating under controlled conditions. Aphid colonies were collected from hydroponically-grown lettuce plants (cultivar Verônica) that were infested with *A. solani*, *M. euphorbiae* or *U. ambrosiae*. Following identification of the species (Peña-Martines 1992), the aphids were transferred to Petri dishes (15 cm diameter) containing lettuce leaf discs (14 cm diameter) and 1% agar solution. The leaf discs originated from pesticide-free plants that had been cultivated hydroponically. Prior to experimentation, leaf material was disinfected with 1% sodium hypochlorite solution for 5 min, washed with tap water and finally rinsed with distilled water for 10 min. This procedure aimed to guarantee the quality of the lettuce leaves, which are very sensitive to water loss. The aphids were reared at $22 \pm 1^\circ\text{C}$ and $70 \pm 10\%$ relative humidity under a 12 h photophase. As soon as the leaf discs presented signs of chlorosis or dehydration, the insect colonies were transferred with the aid of a paintbrush to new leaf discs and incubation continued as described.

Generation of pre-adapted adult female aphids. Individual females of each aphid species were transferred to separate Petri dishes (10 cm diameter) containing a lettuce leaf disc and 1% agar solution. The dishes were kept at $22 \pm 1^\circ\text{C}$ and $70 \pm 10\%$ relative humidity for 6 h, after that the females and all the nymphs, except for one per dish, were removed. The dishes were then incubated in climatic chambers at 16, 19, 22, 25, and $28 \pm 1^\circ\text{C}$ at $70 \pm 10\%$ relative humidity and 12 h photophase until they developed into adult aphids, the females of which were then used in the fertility study described below.

Temperature trials. A simple random sampling design was used, which included five temperature variables (16, 19,

22, 25, and 28°C) and, respectively, 54, 56, 54, 37, and 33 repetitions for *A. solani*, 50, 50, 51, 43, and 37 repetitions for *M. euphorbiae*, and 52, 57, 47, 39, and 22 repetitions for *U. ambrosiae*. Female adult aphids were incubated at the appropriate temperature in dishes containing leaf discs, maintained under a 12 h photophase, and were transferred to new dishes when necessary. The pre-reproductive and reproductive periods were evaluated under a stereomicroscope every 24 h, and the number of nymphs produced and their longevities were determined at each temperature.

Statistical analysis. The reproductive parameters for each species were evaluated by analysis of variance using SAS software. When parameters determined at different temperatures were statistically significantly different ($p < 0.05$), the data were compared using regression analysis. Population growth was estimated from the fertility life table using the parameters net reproductive rate (R_0), intrinsic rate of increase (r_m), mean generation (T), doubling time (DT) and finite rate of increase (λ). The Jackknife technique was used to calculate the variance of these parameters (Maia *et al.* 2000).

RESULTS AND DISCUSSION

Pre-reproductive period. The relationship between temperature and the duration of the pre-reproductive period of *A. solani*, *M. euphorbiae* and *U. ambrosiae* was polynomial (Fig. 1). The estimated values of the pre-reproductive period determined at 16°C were 3 days for *A. solani*, 2.8 days for *M. euphorbiae* and 1.8 days for *U. ambrosiae*. The duration of these period decreased to estimated minima of 1.8 days at 20.9°C for *A. solani*, 2.0 days at 20.7°C for *M. euphorbiae* and 1.6 days at 18.9°C for *U. ambrosiae*, and then increased to 4.5, 3.8 and 5.9 days at 28°C . A similar study for *M. rosae* showed that the duration of the pre-reproductive period increased

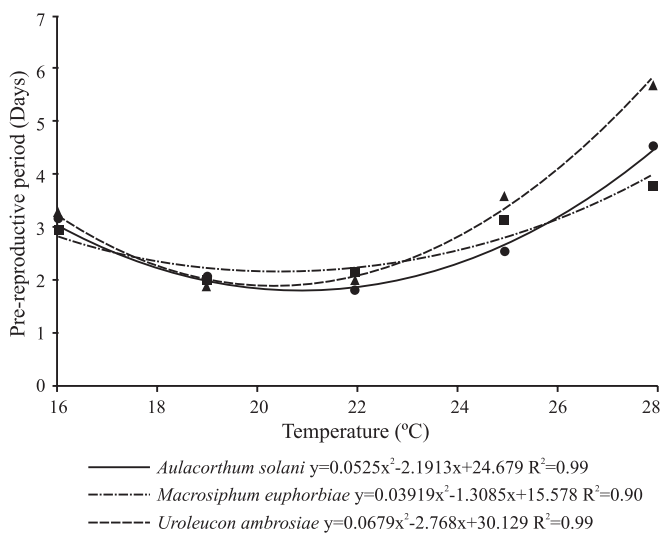


Fig. 1. Duration of the pre-reproductive periods of *Aulacorthum solani*, *Macrosiphum euphorbiae* and *Uroleucon ambrosiae* as a function of temperature.

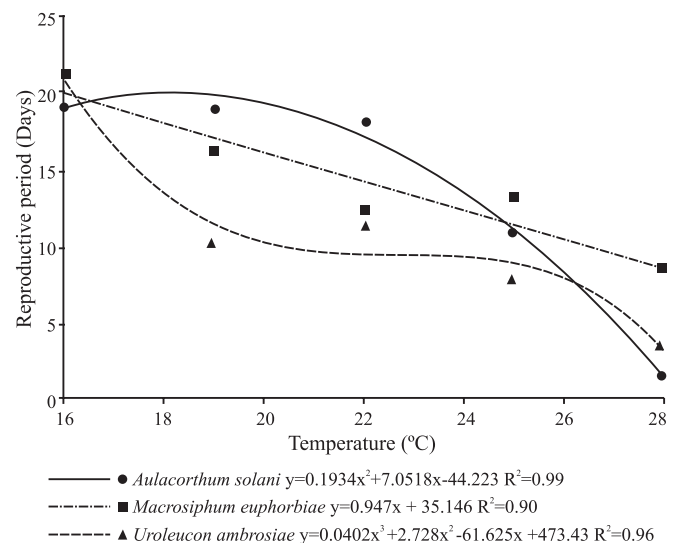


Fig. 2. Duration of the reproductive periods of *Aulacorthum solani*, *Macrosiphum euphorbiae* and *Uroleucon ambrosiae* as a function of temperature

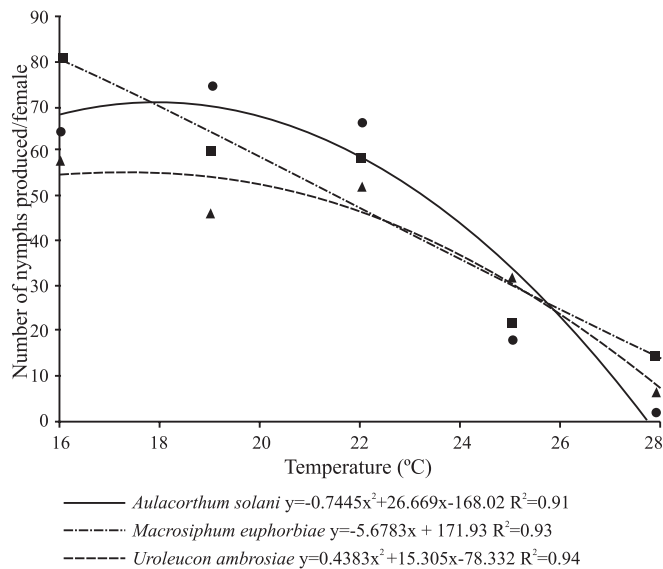


Fig. 3. Number of nymphs produced by *Aulacorthum solani*, *Macrosiphum euphorbiae* and *Uroleucon ambrosiae* as a function of temperature.

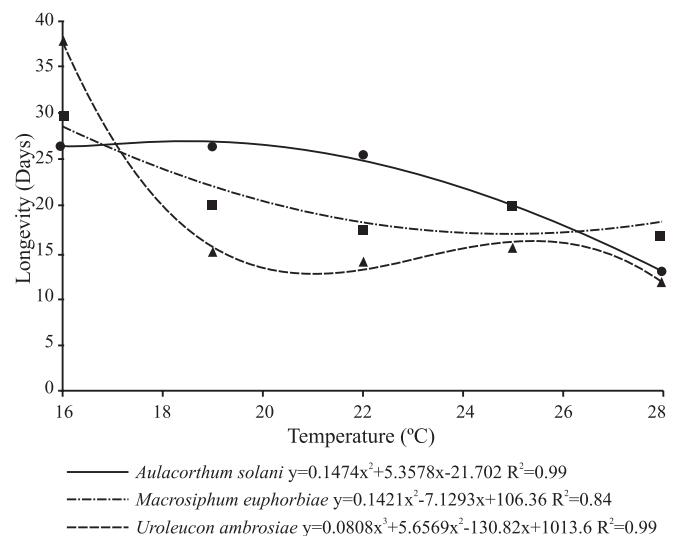


Fig. 4. Longevity of *Aulacorthum solani*, *Macrosiphum euphorbiae* and *Uroleucon ambrosiae* as a function of temperature.

at temperatures higher than 22°C (Mehrparvar & Hatami 2007). According to Auad *et al.* (2002), the duration of the pre-reproductive period of *U. ambrosiae* were 3.90, 1.77 and 2.16 days when the female aphids were reared, respectively, at 15, 20 and 25°C. In this regard, the present findings corroborate those of previous studies by demonstrating that at temperatures of approximately 20°C the duration of the pre-reproductive period of aphids is shorter than at higher temperatures (> 25°C).

Reproductive period. Figure 2 shows a polynomial relationship between temperature and the duration of the reproductive period of *A. solani*. The maximum number of reproductive days was estimated to be 20.0 at 17.8°C, but as the temperature increased, the duration of this period decreased to an observed 1.6 days at 28°C. Vasicek *et al.* (2002) previously reported that at 10°C the reproductive period of this aphid varied between 20.41 and 27.76 days.

For *M. euphorbiae*, the relationship between the duration of the reproductive period and temperature was linear, with the length of the period decreasing as the temperature increased (Fig. 2). The maximum estimated number of reproductive days was 20.0 at 16°C, and the minimum was 8.6 days at 28°C. A similar pattern has been reported for *M. rosae* at temperatures between 15 and 25°C (Mehrparvar & Hatami 2007).

The reproductive period of *U. ambrosiae* plotted as a function of temperature is described by a third order polynomial as shown on Fig. 2. At temperatures between 16 and 19°C, the estimated duration of the period decreased from 19.9 to 11.2 days, respectively, but then remained relatively stable until 25°C (estimated length 8.7 days), and finally decreased to 3.0 days at 28°C. Auad & Moraes (2003) reported that the reproductive period of *U. ambrosiae* lasted 15.57 days at 15°C, 12.23 days at 20°C and 8.47 days at 25°C, values that were similar to those reported here.

Nymph production. Polynomial relationships were established between temperature and the nymph production by *A. solani* and *U. ambrosiae* (Fig. 3). As the temperature increased above 16°C, the nymph production by *A. solani* increased from an observed value of 67.9 to an estimated maximum of 71.3 per female at 18.1°C, whereas by *U. ambrosiae* increased from 54.5 to an estimated maximum of 55.4 nymphs per female at 17.4°C. Further increase in temperature led to sharp declines in nymph production for both species. Auad & Moraes (2003) reported that the highest production of nymphs of *U. ambrosiae* occurred at 20°C when adults were feeding on lettuce. Vasicek *et al.* (2002) confirmed that at low temperature (10°C), *A. solani* produced

Table I. Growth rate of aphid populations reared at different temperatures.

Conditions T (°C)	<i>Aulacorthum solani</i>					<i>Macrosiphum euphorbiae</i>					<i>Uroleucon ambrosiae</i>				
	R_0^1	r_m^2	T ³	DT ⁴	λ^5	R_0^1	r_m^2	T ³	DT ⁴	λ^5	R_0^1	r_m^2	T ³	DT ⁴	λ^5
16	53.45 ^a	0.179 ^c	22.21 ^a	3.87 ^a	1.20 ^c	66.91 ^a	0.189 ^c	22.20 ^a	3.66 ^b	1.21 ^c	44.20 ^a	0.170 ^c	22.26 ^a	4.07 ^a	1.19 ^c
19	61.96 ^a	0.232 ^b	17.82 ^b	2.99 ^b	1.26 ^b	50.11 ^b	0.213 ^b	18.38 ^b	3.25 ^c	1.24 ^b	37.50 ^a	0.231 ^b	15.71 ^b	3.00 ^b	1.26 ^a
22	62.93 ^a	0.270 ^a	15.36 ^c	2.57 ^c	1.31 ^a	50.23 ^b	0.282 ^a	13.91 ^d	2.46 ^d	1.33 ^a	42.66 ^a	0.244 ^a	15.38 ^c	2.84 ^c	1.28 ^a
25	23.42 ^b	0.185 ^c	13.58 ^c	3.74 ^a	1.20 ^c	15.83 ^c	0.186 ^d	14.85 ^a	3.73 ^a	1.21 ^d	14.62 ^b	0.205 ^b	13.11 ^d	3.38 ^b	1.22 ^b

Mean values followed by different lower case superscript letters are significantly different at $p \leq 0.05$

¹ Net reproductive rate; ² Intrinsic rate of increase; ³ Interval between each generation; ⁴ Doubling time; ⁵ Finite rate of increase.

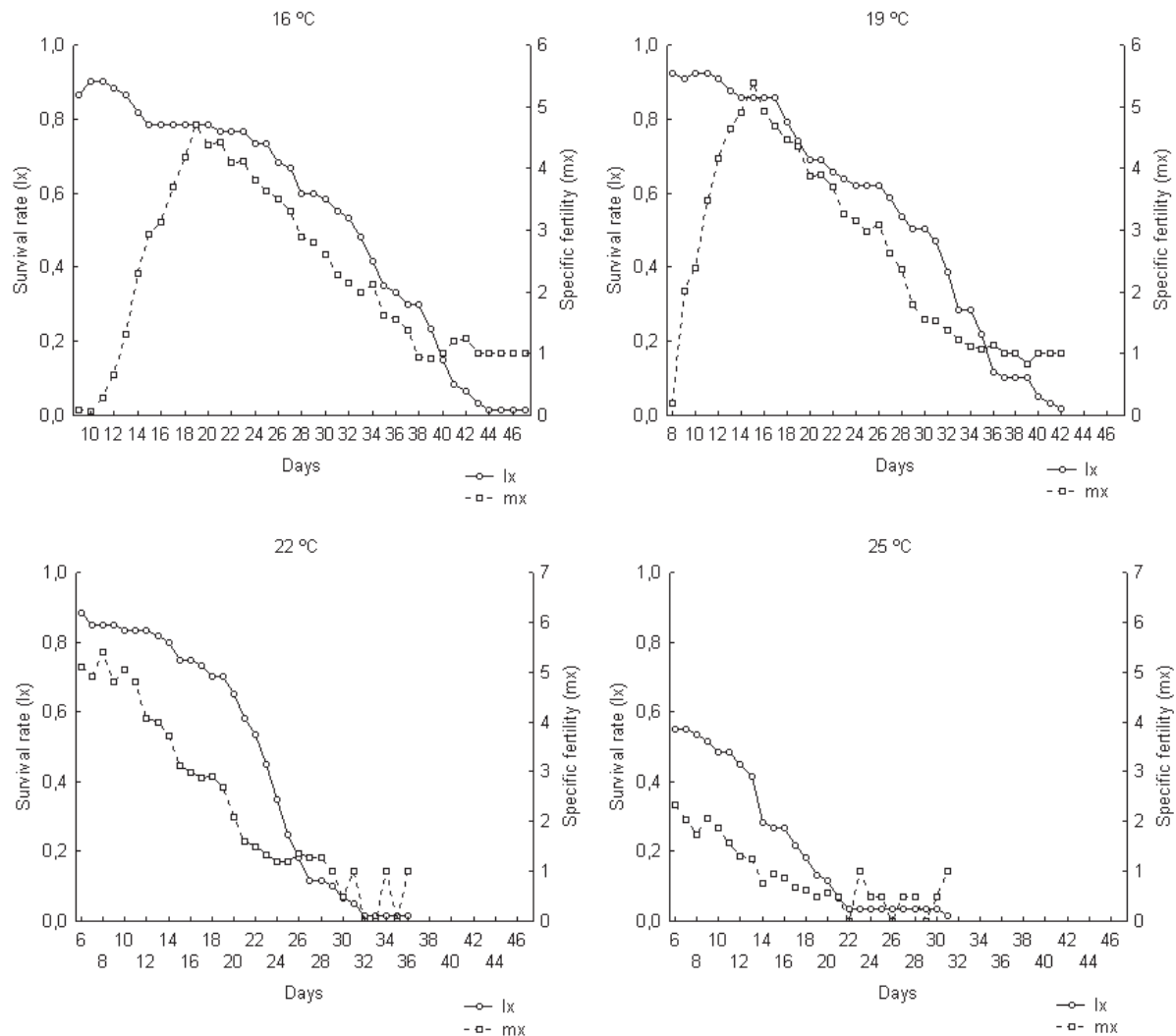


Fig. 5. Survival rate (l_x) and specific fertility (m_x) of *Aulacorthum solani* at different temperatures.

a number of nymphs that varied between 8.44 and 37.85 per insect depending on the cultivar of the lettuce host.

For *M. euphorbiae*, the relationship between temperature and nymph production was linear, with production decreasing as the temperature increased (Fig. 3). Maximum production was observed at 16°C (80.3 nymphs per female) whilst minimum production occurred at 28°C (14.4 nymphs per female). Mehrparvar & Hatami (2007) previously reported that *M. rosae* produces larger numbers of nymphs at 22°C than at 25°C.

Longevity. Figure 4 shows polynomial relationships between temperature and the longevity of *A. solani* and *M. euphorbiae*. The longevity of *A. solani* increased from an observed 26 days at 16°C to an estimated maximum of 27 days at 18.4°C, after which longevity decreased with increasing temperatures. In *M. euphorbiae* longevity decreased between 16°C (29 days) and an estimated 25.1°C (17 days), and subsequently increased as the temperature approached 28°C (18 days). It is important to emphasize that the increase in one day of life of *M. euphorbiae* between 25.1 and 28 °C is

related to the values estimated by regression, thus reflecting the behavior of the polynomial curve. In *U. ambrosiae*, the relationship between temperature and longevity followed a third order polynomial (Fig.4): life time decreased between 16°C (34 days) and 19°C (15 days), remained stable up to 25°C (14.5 days), and subsequently decreased to 7.5 days at 28°C (8 days). Previous studies of aphids of the genera *Macrosiphum* and *Uroleucon* conducted under similar conditions demonstrated that longevity decreased with increasing temperatures (Audad & Moraes 2003; Mehrparvar & Hatami 2007).

U. ambrosiae was the most sensitive to high temperatures among the three aphid species studied, since the reproductive period and longevity decreased remarkably at temperatures higher than 16°C and both were much shorter than those of *A. solani* and *M. euphorbiae* (Figs. 2 and 4).

Survival rate (l_x) and specific fertility (m_x) of aphids. It was not possible to analyse the data obtained at 28°C due to high mortality and low fertility rates at this temperature and the fact that most adult aphids did not reproduce. Therefore,

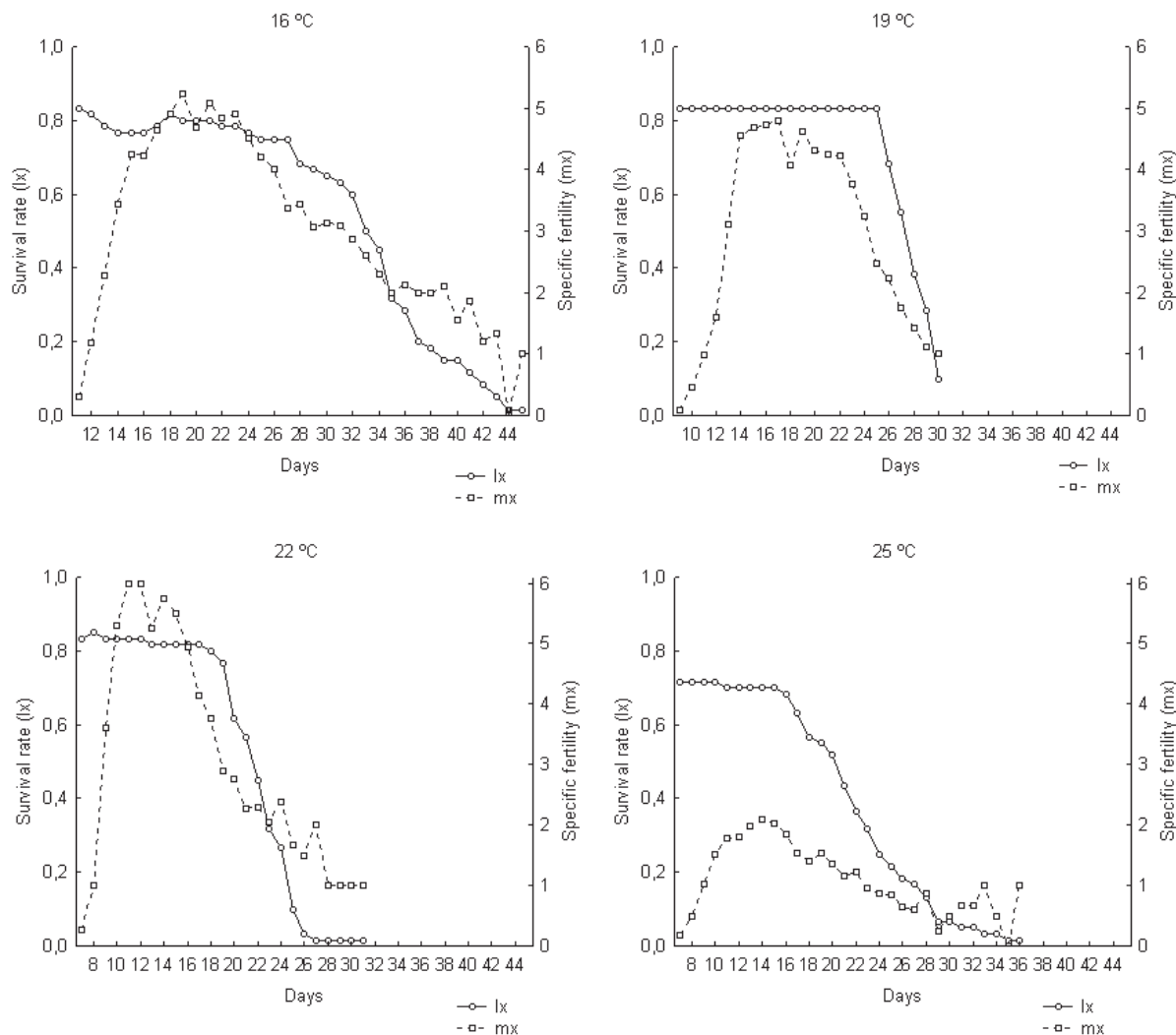


Fig. 6. Survival rate (l_x) and specific fertility (m_x) of *Macrosiphum euphorbiae* at different temperatures.

the l_x and m_x graphs, as well as the values corresponding to the fertility life table, are presented for temperatures of 16, 19, 22, and 25°C. At higher temperatures ($\geq 25^\circ\text{C}$) there was a remarkable reduction in the l_x value of *A. solani*, indicating the deleterious effect of temperature on the reproduction (Fig. 5). Based on principles established by Silveira Neto (1976), the profiles of the l_x curves at temperatures of 16, 19 and 22°C were type I, indicating a greater mortality amongst older individuals. At 25°C, the l_x curve profile was of type II, representing a continuous reduction in the survival rate of insects throughout the life cycle. Vasicek *et al.* (2003) reported that the survival of *A. solani* at 10°C followed a type I profile when pea (*Pisum sativum*) and fennel (*Foeniculum vulgare*) provided the food source, and a type II profile when lettuce (*L. sativa*) and aubergine (*Solanum melongena*) were the hosts. The m_x values during the reproductive period of *A. solani* were also negatively influenced by high temperatures, and especially above 25°C (Fig. 5). At 22°C, the m_x values suggested that the largest production of nymphs occurred at the start of the reproductive period, a situation that is

considered beneficial since aphids exhibit high mortality rates occasioned by environmental factors (Hayakawa *et al.* 1990).

In *M. euphorbiae*, the l_x curves presented type I profiles at all temperatures tested (Fig. 6), in that there was a period of stability in the l_x value at the beginning of the reproductive period, followed by a reduction towards the end of this period. The m_x values indicated that there were intense reproductive activities between days 10 and 24 of the life cycle at 16°C, between days 13 and 24 at 19°C, and between days 7 and 24 at 22°C. The lowest m_x values were observed at 25°C. A temperature of 22°C was considered most favourable for *M. euphorbiae* since the production of nymphs was highest as indicated by the m_x and l_x values.

The species *U. ambrosiae* presented l_x curves of type I at 16°C and of type II at 19, 22 and 25°C (Fig. 7), although in the latter case the survival rates at 25°C were much smaller than at 22°C. Auad & Moraes (2003) reported survival rates of > 80% at 15°C for aphids up to 22 days old, whilst for older insects the l_x values gradually declined. Additionally, these authors

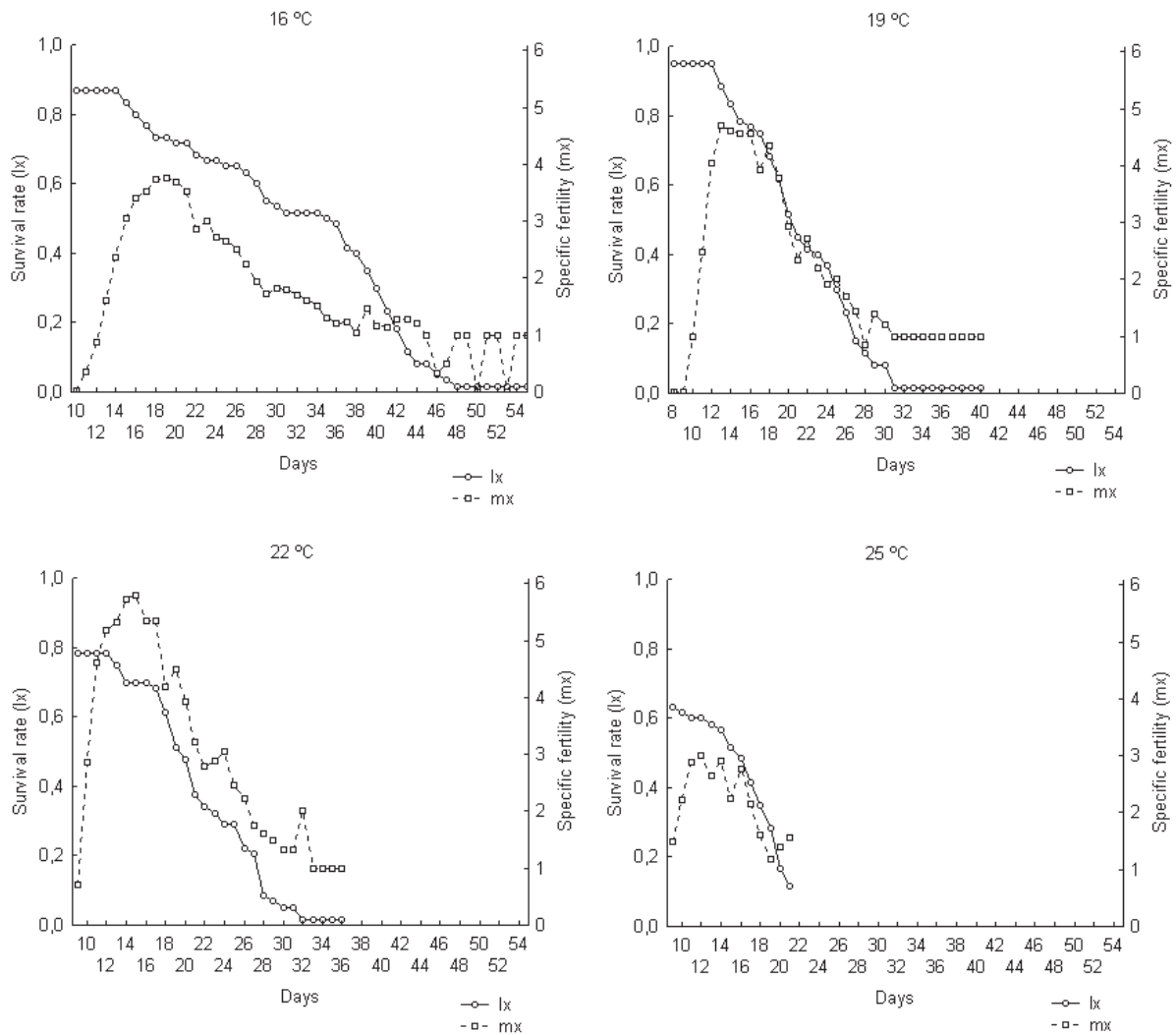


Fig. 7. Survival rate (l_x) and specific fertility (m_x) of *Uroleucon ambrosiae* at different temperatures.

observed that at 20 and 25°C the survival rates of this species fell away much more rapidly than at lower temperatures. During the reproductive period of *U. ambrosiae*, the largest m_x values were observed between days 10 and 20 at 22°C. In data reported by Auad & Moraes (2003), the largest m_x among 15, 20 and 25°C was observed at 20°C.

Fertility life table. Aphid population growth was estimated on the basis of the fertility life table parameters (Table I). In the case of *A. solani*, there were no significant differences between net reproductive rates (R_0) determined at temperatures 16, 19 and 22°C, although a significant reduction in this parameter was recorded at 25°C. The largest intrinsic rate of increase (r_m) was observed at 22°C. The pattern of variation in the finite rate of increase (λ) with temperature was analogous to that presented by the r_m values. The interval between each generation (T) decreased with increasing temperatures, the longest being observed at 16°C and the shortest at 22 and 25°C, whilst the shortest doubling time (DT) was recorded at 22°C and the longest at 16 and 25°C. Previously, Vasicek *et al.* (2002; 2003) reported that at 10°C the growth rate

of *A. solani* varied depending on the host plant, with the smallest R_0 and r_m values being observed, respectively, for pea (9.35 and 0.075) and lettuce (25.7 and 0.077), and the largest for aubergine (43.95 and 0.089, respectively). The best reproductive performance of *A. solani* is predicted to be attained at a temperature of 22°C on the basis of the recorded l_x and m_x values, together with high values of R_0 , r_m and λ and short T and DT times.

For *M. euphorbiae*, the largest R_0 value was observed at 16°C and the smallest at 25°C (Table I). The values of r_m and λ increased between 16 and 22°C and decreased between 22 and 25°C, with the smallest values being recorded at 25°C. The T values decreased between 16 and 22°C and increased between 22 and 25°C with the largest value being measured at 16°C and the smallest at 22°C. In a similar fashion, DT values decreased between 16 and 22°C and increased between 22 and 25°C, with the largest value being recorded at 25°C and the smallest at 22°C. The best reproductive performance of *M. euphorbiae* is expected to be attained at a temperature of 22°C on the basis of high values of r_m and λ with short T and

DT times.

In the case of *U. ambrosiae*, the R_0 values were not statistically different ($p \leq 0.05$) at 16, 19 and 22°C, although all were significantly larger than the value measured at 25°C. The values of r_m and λ increased up to 22°C and decreased between 22 and 25°C, with the smallest value being recorded at 16°C. T values decreased with increasing temperatures with the largest T value measured at 16°C and the smallest at 25°C. The largest DT value for *U. ambrosiae* was obtained at 16°C and the smallest at 22°C. Although the R_0 value was high at 16°C, at this temperature the m_x values were more uniformly distributed throughout the reproductive period, resulting in a reduction in growth of the aphid population and a consequent increase in T value. Thus, a temperature of 16°C was the most unfavourable condition for the reproduction of *U. ambrosiae*, whilst 22°C was the most favourable. In a previous study (Auaad & Moraes 2003), the largest fertility and life expectancy parameters reported were: $R_0 = 70.02$ (at 20°C) and $r_m = 0.25$ and $\lambda = 1.28$ (at 20 and 25°C). According to those authors, the T values of *U. ambrosiae* decreased between 15 and 25°C.

The most favourable temperature for the reproduction of *A. solani*, *M. euphorbiae* and *U. ambrosiae* was 22°C, as demonstrated by the I_x and m_x profiles, the relatively large values of R_0 , r_m and λ and the small T and DT times recorded in the present study. At higher temperatures (25 and 28°C) the reproductive capacity of these species was drastically reduced. Thus, the selection of natural enemies of these pests should consider its performance in these conditions.

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