

Thermal requirements, life expectancy and fertility tables of *Aphis craccivora* (Hemiptera: Aphididae) in *Vigna unguiculata* (Fabales: Fabaceae) under laboratory conditions

Exigências térmicas e tabelas de esperança de vida e fertilidade de Aphis craccivora (Hemiptera: Aphididae) em Vigna unguiculata (Fabales: Fabaceae) sob condições de laboratório

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ABSTRACT: The objective of this research was to determine the thermal requirements and develop life expectancy and fertility tables of *Aphis craccivora* (L.) in *Vigna unguiculata* (Walp.). The insects were kept in Petri dishes and fed *V. unguiculata* leaf discs (cultivar BRS-Tumucumaque) under five constant temperatures (18, 22, 25, 28 and 31°C). Live and dead insects and stages of development; the onset and duration of the pre-reproductive, reproductive and post-reproductive periods; the number of nymphs per female; and the longevity of the adults were quantified daily. Based on these observations, fertility life expectancy tables were developed, and the thermal requirements of the cowpea black-aphid were determined. Increased temperature influenced all stages of insect development, as well as the pre-reproductive and post-reproductive periods and the total number of nymphs per female. The base temperature for development was 9.13°C with thermal development constant of 99.0 GD. The highest net reproduction rate (R_0) was at 25°C. At 28°C, the greatest capacity to increase in number (r_m) was observed, as well as the highest finite rate of increase (λ) and the shortest time to double in number (TD). The thermal range between 22 and 28°C can be considered most favourable to the development of *A. craccivora* in *V. unguiculata*. Temperatures below 22 and above 28°C affect the fertility and survival of cowpea black-aphids. Increased temperature induces reproduction and reduces the longevity and life expectancy of *A. craccivora* in cowpeas.

KEYWORDS: insect ecology, integrated pest management, base temperature, thermal constant, black-aphid.

RESUMO: Objetivou-se com esta pesquisa determinar as exigências térmicas e elaborar as tabelas de esperança de vida e de fertilidade de *Aphis craccivora* (L.) em *Vigna unguiculata* (Walp.). Os insetos foram mantidos em placas de Petri, alimentados com discos foliares de *V. unguiculata*, cultivar BRS-Tumucumaque, sob 5 temperaturas constantes: 18, 22, 25, 28 e 31°C. Diariamente, foram quantificados os insetos vivos e mortos, o estágio de desenvolvimento, bem como o início e a duração dos períodos pré-reprodutivo, reprodutivo e pós-reprodutivo, o número de ninfas por fêmea e a longevidade de adultos. Com base nessas observações, elaboraram-se as tabelas de esperança de vida de fertilidade e determinaram-se as exigências térmicas do pulgão-preto do caupi. O aumento da temperatura influenciou todos os estágios de desenvolvimento do inseto, bem como os períodos pré-reprodutivo e pós-reprodutivo e o número total de ninfas por fêmea. A temperatura base de desenvolvimento foi de 9,13°C, e a constante térmica de desenvolvimento, de 99,0 GD. A maior taxa líquida de reprodução (R_0) foi a 25°C. A 28°C, constatou-se a maior capacidade de aumentar em número (r_m), bem como a maior razão finita de aumento (λ) e menor tempo para duplicar em número (TD). Pode-se considerar que a faixa térmica mais favorável ao desenvolvimento de *A. craccivora* em *V. unguiculata* está entre 22 e 28°C. Temperaturas abaixo de 22 e acima de 28°C prejudicam a fertilidade e a sobrevivência do pulgão-preto do caupi. O aumento da temperatura antecipa a reprodução e reduz a longevidade e esperança de vida de *A. craccivora* em feijão-caupi.

PALAVRAS-CHAVE: ecologia de insetos; manejo integrado de pragas; temperatura base; constante térmica; pulgão-preto.

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INTRODUCTION

Cowpea (*Vigna unguiculata* (L.) Walp.) is widely cultivated in northern and north-eastern Brazil and is traditionally planted by family farmers in small areas with low technology and low productivity. However, the cultivation of this bean has been expanding to the areas of the Brazilian cerrado, where it is planted as “safrinha” or main crop (FREIRE FILHO, 2011), and, according to CONAB (2017), with an estimated gross revenue of 4.7 billion reais in the 2016/2017 harvest.

The change in cowpea cultivation, from small (family farming) to large areas (modern agriculture), can lead to serious phytosanitary problems. According to SILVEIRA NETO et al. (1976), the main factors that regulate insect abundance are the availability of food and climate factors, especially temperature, which influences behaviour and the speed of development. Temperature is able to accelerate the population increase of a species, which can result in surpassing the level of insect damage in a smaller space of time.

Aphis craccivora (Koch, 1854) (Hemiptera: Aphididae) is one of the main phytosanitary problems encountered by cowpea producers in Africa, Asia and Latin America (SINGH; JACKAL, 1985; PETTERSSON et al., 1998).

A black-aphid infestation begins in the seedlings, and, as they develop, the insects colonize the shoots, branches, flowers and pods (BERBERET et al., 2009). In addition to the direct damage caused by the insects sucking elaborated sap, the black aphid is the main transmitter of the *cucumber mosaic virus* (CMV) and *cucumber aphid-borne mosaic virus* (CABMV), viruses that can infect cowpeas through simple or mixed infection (OLIVEIRA, 2011). Viral infection has the possibility to reduce cowpea production by 87%, depending on the susceptibility of the cultivar, the virus strain and the environmental conditions (BASHIR et al., 2002).

According to CALORE et al. (2013), the success of integrated pest management implementation is dependent on basic studies of insect population dynamics, especially the identification and mode of action of the factors that regulate the growth of these populations.

One of the ways to understand the population dynamics of an insect is to determine its population parameters based on life tables, as well as determining its thermal requirements by means of the thermal constant K of development and the lowest base temperature of development T_b . These parameters can be used to predict population peaks in the field, which help to identify the best season for applying a pest control technique (CIVIDANES, 2003; CIVIDANES; SOUZA, 2003).

Studies involving life tables of *A. craccivora* with different hosts are common in the literature (BERBERET et al., 2009; OBOPILE; OSITILE, 2010; ZHAOZHI et al., 2016). However, there are only two reports of their thermal requirements. One of these reports is about the alfalfa, *Medicago sativa* L. (Fabales: Fabaceae), performed

in Oklahoma (BERBERET et al., 2009), and the other one is in Australia (BERG, 1984).

Considering that the latitude (ADDO-BEDIAKO et al., 2000), the association with endosymbiotic bacteria (BRADY et al., 2014) and the host (ZHAOZHI et al., 2016) influence the ecological parameters of black aphids, it is necessary that ecological studies be performed regionally in order to obtain more accurate data.

Thus, the objectives of this research were to determine the thermal requirements and to develop the tables of life expectancy and fertility of *A. craccivora* in cowpea (*V. unguiculata*) in a laboratory under five constant temperatures.

MATERIALS AND METHODS

Cowpea-black picking and raising of cowpea

Aphids were collected from cowpea plants on the campus of the Universidade Federal of Piau , Teresina, Piau , Brazil, and then transferred to plants susceptible to cowpea (cultivar BR 17 — Gurgueia), kept in an air conditioned room (25°C), under a light bench consisting of eight T10 40 W daylight fluorescent lamps and eight 40 W incandescent lamps, with the aim of maintaining a predator-free population of aphids.

Bioassay

After stabilization of the stock population, an assay was conducted under five constant temperatures in biochemical oxygen demand (BOD) chambers with temperature and photoperiod control. The temperatures used were 18, 22, 25, 28 and 31°C, in a 12-hour photophase, in which 40 nymphs of 0 to 12 hours of life were maintained in Petri dishes until their death.

To obtain nymphs with a known age, 5-cm-long Petri dishes with perforated lids were used and closed with voile fabric. Each dish contained a 0.5-cm-thick sponge and a paper filter disc, both of which were within the internal diameter of the plate and moistened with water daily — methodology adapted from VALENTE et al. (2014). In these plates, eight per temperature, a cowpea leaf disc of 3 cm in diameter was washed in running water, dried with paper towels, and added to each plate (eight plates per temperature). A total of five *A. craccivora* adults were conditioned from stock creation and placed onto each cowpea leaf. After 12 hours, these insects were removed, and the nymphs produced from 0 to 12 hours were placed individually into new Petri dishes, as already described. A total of 40 repetitions per temperature were included.

The plaques containing the nymphs were observed daily, and the live and dead insects, the stages of development and

the number of exuviae were quantified, as well as the beginning and duration of the pre-reproductive, reproductive and post-reproductive periods, the number of nymphs per female per day, and adult longevity. The nymphs produced were quantified and removed from the plates. The leaf discs were changed at the first sign of wilt or yellowing.

Cultivation of cowpea plants for leaf supply

For the supply of leaf discs, cowpea plants, cultivar BRS-Tumucumaque, were sown in 2.8 L pots containing a mixture of sandy soil and 5:1 vegetable soil, fertilized with 5 g of NPK 5-30-15 and maintained in natural conditions with daily irrigation when necessary. The leaves collected from the upper third of the plants were taken to the laboratory and washed in running water, and the leaf discs were later removed to replace the leaf discs in Petri dishes.

Thermal requirements and life expectancy and fertility tables

The hyperbola method and its reciprocal development were used to calculate the lower base development temperature (Tb) and the thermal development constant K (CIVIDANES, 2000).

The beginning of the adult phase was considered to be the day in which the fourth exuvia was observed. The pre-reproductive period occurred from the fourth exuvia to the first nymph, the reproductive period included the days of parturition, and the post-reproductive period consisted of the days without parturition until the death of the adult insect.

The elaboration of the tables of life expectancy and fertility was based on the methodology of SILVEIRA NETO et al. (1976), which determined the following values: the number or rate of survivors at the beginning of age x (L_x); the number of individuals killed during the age range x (d_x); age structure (E_x), which corresponds to the number of individuals living between one day and another; survival rate (T_x), which represents the number of live insects beyond a given age; the life expectancy for individuals of age x (e_x); and the probability of death at age x ($100 q_x$), which indicates the probability of death occurring before the time established in E_x , according to Equations 1, 2 and 3:

$$E_x = [L_x + (l_x + 1)] / 2 \quad (1)$$

$$e_x = T_x / L_x \quad (2)$$

$$100 q_x = (d_x / L_x) * 100 \quad (3)$$

The values of the net reproduction rate (R_0), the time interval between each generation (T), the innate ability to increase in number (r_m), the ratio (λ), defined as the

number of times the population multiplies in a unit of time, and the necessary time for the population to double in number of individuals (TD) were calculated as Equations 4, 5 and 6:

$$R_0 = \sum (m_x (\sum m_x * l_x)), r_m = \log R_0 / T * 0.4343 \quad (4)$$

$$\lambda = \text{anti log} (r_m * 0.4343) \quad (5)$$

$$TD = \text{Ln} (2) / r_m \quad (6)$$

In which:

m_x = number of females produced per female at age x;

l_x = survival rate at age x, and m_x ;

* l_x = total number of females produced per female during the time interval.

The survival curves obtained at the temperatures tested were statistically analysed using the G-test ($p < 0.1$), and the population parameters obtained in the fertility life tables were analysed using the jack-knifed method (MAIA et al., 2000).

The experimental design was completely randomized, with treatments consisting of five treatments and 40 repetitions, considering each nymph as a repetition. The computer system TabVida, by PENTEADO (2007), and the software Assistat were used for the analysis of the data.

RESULTS AND DISCUSSION

Nymphal stages, nymphal period, longevity and biological cycle

The temperature increase from 18 to 31°C inversely influenced the developmental period of all nymphal stages, the nymphal period, longevity and the biological cycle of cowpea black-aphids, reducing the nymphal period by 63%, the longevity of adults by 44% and the biological cycle by 54.5% (Table 1). This inversely proportional relationship was observed by other authors and it is because insects are poikilothermic animals that maintain their body temperature close to the temperature of their environment (CIVIDANES, 2003; BARBOSA et al., 2011).

The data obtained from the literature regarding the development time of *A. craccivora* are quite variable, suggesting that the development time of *A. craccivora* in cowpea is influenced by the degree of resistance of the cultivar used and possible genetic differences in the population of black-aphids, highlighting the importance of regional studies.

The effect of three cultivars of cowpea on black aphid development was evaluated by VALENTE et al. (2014) and ranged from 1.12 to 1.96 days for the first nymphal stage,

1.12 to 1.24 days for the second stage, 0.64 to 0.92 days for the third stage, and 0.28 to 0.56 days for the fourth instar, and a nymphal period ranging from 3.16 to 4.68 days at 25°C in susceptible and resistant cultivars. HAFIZ (2006) tested nine cowpea cultivars for black aphid infestation and obtained values ranging from 1.6 to 2.2, 1.5 to 2.0, 1.5 to 1.7 and 1.1 to 1.7 days, respectively, for the first, second, third and fourth instars at 25°C.

Regarding the effect of temperature on the longevity of the black aphid, the same inversely proportional pattern was reported by BERBERET et al. (2009), varying from 14.7 to 32.2 days at 29.4 and 18.3°C, respectively, in alfalfa (*Medicago sativa* L.).

In relation to the biological cycle of the cowpea black-aphid, JALALIPOUR et al. (2017) observed a cycle of 24.2 days at 25°C in false acacia (*Robinia pseudoacacia*). BERBERET et al. (2009) recorded the times of 32.2 days at 18°C, 19.3 days at 23.9°C and 14.7 days at 29.4°C in alfalfa. DE LA PAVA; SEPÚLVEDA-CANO (2015) recorded the time of 16.5 days at 28°C in cowpea, which was a higher value than the one verified in this research and that can be explained, in part, by the different hosts used (ZHAOZHI et al., 2016) and the different levels of and origin of the aphid population used (BRADY et al., 2014).

Pre-reproductive, reproductive, post-reproductive and fertility period

The increased temperature statistically influenced the pre-reproductive and post-reproductive periods, the number of nymphs per female and the number of nymphs per female per day (Table 2).

Reproduction of the aphids began within the first 24 hours after the fourth ecdysis at all tested temperatures, except for 18°C, which started one day later. The post-reproductive period was only observed at 18 days and 31°C, also for approximately one day (Table 2).

BARBOSA et al. (2011) found that the reproductive period of *Myzus persicae* (Sulzer, 1776) (Homoptera: Aphididae) in peppers at temperatures of 20 and 25°C began on the same day that the aphid became an adult. At 15 and 30°C, reproduction started one day after the emergence of adults, corroborating the results presented. From the ecological point of view, this characteristic is important for species with short longevity that are susceptible to temporal changes, as that is the case with aphids (ILHARCO, 1992).

Although the reproductive period was statistically the same at all temperatures, there was 43% reduction in the

Table 1. Mean development time (days \pm SE) of *Aphis craccivora* in *Vigna unguiculata* at different constant temperatures and a 12-hour photophase.

Biological parameters	Temperature (°C)				
	18	22	25	28	31
1° instar	3.7 \pm 0.18a	2.1 \pm 0.05b	1.6 \pm 0.09c	1.1 \pm 0.06d	1.1 \pm 0.05d
2° instar	3.0 \pm 0.20a	1.6 \pm 0.09b	1.3 \pm 0.08bc	1.5 \pm 0.07c	1.1 \pm 0.05c
3° instar	3.3 \pm 0.21a	1.7 \pm 0.10b	1.2 \pm 0.07c	1.1 \pm 0.06c	1.2 \pm 0.08c
4° instar	3.3 \pm 0.20a	2.0 \pm 0.11b	1.7 \pm 0.08bc	1.5 \pm 0.1c	1.6 \pm 0.11bc
Nymphal period	13.4 \pm 0.32a	7.4 \pm 0.11b	5.8 \pm 0.12c	4.9 \pm 0.12d	4.9 \pm 0.11d
Longevity	11.5 \pm 1.97a	11.5 \pm 1.68a	10.1 \pm 1.42a	6.8 \pm 0.44a	6.4 \pm 0.4a
Biological cycle	24.9 \pm 1.9a	18.9 \pm 1.67b	15.9 \pm 1.42bc	11.8 \pm 0.4cd	11.3 \pm 0.40d

Means on the same line followed by the same letter do not differ statistically from each other, as determined by the Tukey test ($p < 0.01$). SE: standard error.

Table 2. Mean time of pre-breeding, reproduction, and post-reproduction periods, and the mean number of nymphs per female (days \pm SE) of *Aphis craccivora* at different constant temperatures and a 12-hour photophase in cowpeas.

Biological parameters	Temperature °C				
	18	22	25	28	31
Pre-reproductive period	1.0 \pm 0.2a	0.1 \pm 0.1b	0.1 \pm 0.0b	0.04 \pm 0.0b	0.1 \pm 0.1b
Reproductive period	9.7 \pm 1.8a	10.9 \pm 1.5a	9.2 \pm 1.3a	6.3 \pm 0.7a	4.7 \pm 0.5a
Post-reproductive period	1.2 \pm 0.4ab	0.8 \pm 0.3ab	0.8 \pm 0.3ab	0.2 \pm 0.1b	1.6 \pm 0.5a
Nymphs per female	26.2 \pm 5.9bc	54.4 \pm 8.4ab	60.5 \pm 7.4a	47.5 \pm 5.1ab	16.0 \pm 3.5c
Nymphs per female per day	2.7 \pm 0.6c	4.99 \pm 0.7b	7.2 \pm 0.8a	7.5 \pm 0.8a	3.4 \pm 0.7bc

Means followed by the same letter on the same line were not significantly different from each other as determined the Tukey test ($p < 0.05$). SE: standard error.

number of reproductive days at 31°C compared to that for aphids kept at 22°C. However, the number of nymphs per female was highly influenced by temperature, increasing linearly from 18 to 25°C and decreasing from 25 to 31°C. It was observed that at 18 and 31°C there was reduction of 56.7 and 73.5%, respectively, in the production of nymphs per female relative to 25°C. BERBERET et al. (2009) also observed increase in the reproductive period and decrease in the number of nymphs per female with decreased temperature for *A. craccivora* raised in alfalfa. However, BERBERET et al. (2009) found variation of 25.1 days at 18.3°C and 12.4 days at 29°C, values which were higher than those ones found in this study and by VALENTE et al. (2014) at 25°C, who observed 4- and 7-day reproductive period in cowpeas.

Although there are differences between the results presented in this research with those of BERBERET et al. (2009) and VALENTE et al. (2014) in relation to the reproductive period, when comparing the number of nymphs per female, we observed similarities. BERBERET et al. (2009) noticed the production of nymphs per female ranging from 20 to 82, with 0.6 to 5.9 nymphs per female per day. VALENTE et al. (2014) recorded the production of nymphs per female ranging from 15.4 in a resistant cultivar to 85.8 nymphs per female in susceptible cultivars, with 1.72 to 5.73 daily production of nymphs, corroborating the presented values in Table 2.

In general, it was observed that there is an inversely proportional relationship between reproductive period and nymphs produced per female per day in the thermal range of 22 to 28°C, corroborating the data presented by BERBERET et al. (2009). These results suggest that there are probably adaptive differences among the studied aphid populations.

Thermal requirements

The linear portion of the development curve *versus* temperature (Fig. 1), obtained at constant temperatures, allowed for the calculation of the lower base temperature (T_b) and the thermal constant (K) for all stages of development of *A. craccivora* (Table 3).

BERBERET et al. (2009) in Oklahoma found that *A. craccivora* failed to reach reproductive status when raised in alfalfa at 7.2°C and calculated a lower development temperature of 7.1°C with a thermal constant K of 100 GD for the nymphal development period. This result was consistent with the thermal constant presented in this work (99 GD). BERG (1984) studied the thermal requirements of cowpea black-aphid in different hosts in Australia and obtained the base temperature of 8.1°C.

The differences observed in the thermal development constant and the base temperature of the black-aphid boar of the cowpea can be explained in part by the theory of functional prediction, which postulates that a high value for the development threshold and a small value for the thermal sum are expected for species more adapted to hot (tropical) areas than for those adapted to cold (temperate) areas (TRUDGILL; PERRY, 1994; TRUDGILL, 1995).

In this study, it was verified that the development time of *A. craccivora* decreased linearly up to 25°C. From this temperature, there was tendency for stabilization, with decrease in the development velocity between 28 and 31°C, which is similar to what was reported by CIVIDANES (2003) and ZHAOZHI et al. (2016). According to WILSON; BARNETT (1983), this stabilization, and even a slight increase in the development time with increased temperature, may be related to the proximity of the upper base temperature of development T_s . According to CHEN et al. (2013), at the constant temperature of 35°C, only 16% of

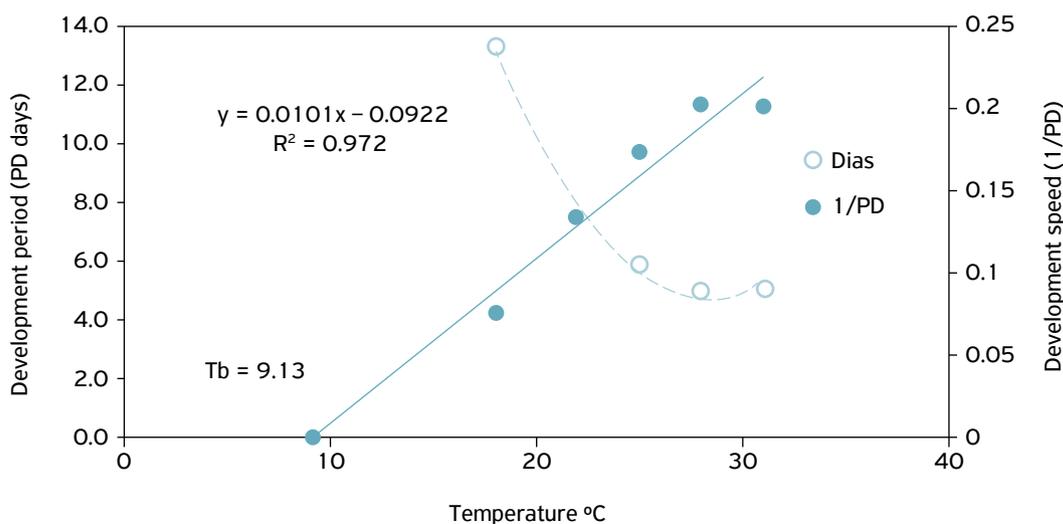


Figure 1. Relationship between temperature, time (days) and developmental speed of the *Aphis craccivora* nymphal period in cowpeas kept at the constant temperatures of 18, 22, 25, 28 and 32°C with a photophase of 12 hours.

the black-aphid nymphs of cowpea reached adulthood when kept in *Vigna unguiculata sesquipedalis* (L.), and they did not reproduce, corroborating the hypothesis that this temperature is near or above the T_s .

It can be considered in general that temperatures above 22 and below 28°C are within the thermal range that is most favourable to the development of *A. craccivora*, because the insects presented the highest fertility rates and a shorter time period, and 18 and 31°C as sub-optimal temperatures, causing reduction in the development speed and birth rate (Tables 2 and 4). These results differ from those observed by BERBERET et al. (2009), which stated that the optimum temperature range of *A. craccivora* development is between 18 and 24°C. However, it is possible that these biological differences may be due to the different biotypes of *A. craccivora* analysed, as well as the differences between endosymbiont organisms, which may interfere with insect biological rates (BRADY et al., 2014).

Life table and fertility demographic parameters

The net reproduction rate, the number of times the population increases in each generation (R_0), increased linearly up to 25°C. From this temperature, a slight decrease was observed at 28°C and an abrupt drop at 31°C, with reduction of 80.6% over 25°C (Table 4). These results corroborate those presented by BARBOSA et al. (2011), who observed reduction in the

net reproductive rate of *M. persicae* at extreme temperatures of 15 and 30°C.

The temperature negatively influenced the time interval between the generations in a linear fashion, being that at 18°C this period was 59.63% sooner compared to at 28°C. This fact is directly related to the lower base temperature (T_b), the upper base temperature (T_s), and the thermal constant (K) (Table 3), considering that poikilothermic animals need to accumulate an amount of energy, x (degree-day), to complete or reach a stage of development. Thus, the greater the difference within the optimum thermal range, between T_b and the temperature at which the insect is, the more energy is accumulated and the faster the development occurs (CIVIDANES, 2000).

CHEN et al. (2013) found the opposite of T when the aphids were confined to 28.6, 30.0, or 32.5°C in *Vigna sesquipedalis*. This difference can be explained by the mean of the T_s of development, in which WILSON; BARNETT (1983) could slow the rate of development when the ambient temperature approached the upper development threshold. In addition, according to ZHAOZHI et al. (2016), the host also has an influence. FERREIRA (2015) observed a T ranging from 5.3 to 8.0 days for *A. craccivora* that were kept in cultivars of cowpeas (temperatures ranging from 28.7 to 35°C in the greenhouse) and were susceptible and resistant at the values within the ranges presented in this research. Thus, the relationship between temperature and cultivar is an important component that must be considered in phytosanitary management programmes of cowpea black-aphids.

Table 3. Base temperature (T_b), thermal constant (K), determination coefficient and equation of the development rate of *Aphis craccivora* in cowpeas kept at the constant temperatures of 18, 22, 25, 28 and 32°C with a photophase of 12 hours.

Stage of development	T_b °C	K GD	R^2	Equation
I stadium	12.8	18.58	0.99	$y = 0.054x - 0.67$
II stadium	9.3	21.88	0.94	$y = 0.048x - 0.42$
III stadium	9.0	23.31	0.81	$y = 0.043x - 0.39$
IV stadium	3.5	40.00	0.82	$y = 0.025x - 0.087$
Nymphal period	9.1	99.00	0.97	$y = 0.0101x - 0.0922$
Biological cycle	9.0	243.9	0.98	$y = 0.0041x - 0.037$

Table 4. Population and biological parameters (\pm SE) of *Aphis craccivora* in cowpeas under constant temperatures.

Biological parameters	Temperature °C				
	18 (n = 21)	22 (n = 27)	25 (n = 30)	28 (n = 25)	31 (n = 18)
R_0	12.4 \pm 0.6a	32.6 \pm 1.2b	39.13 \pm 1.3c	29.4 \pm 1.2b	7.59 \pm 0.1e
T	19.0 \pm 0.9a	12.6 \pm 0.5b	9.77 \pm 0.5c	7.67 \pm 0.3d	6.73 \pm 0.0d
r_m	0.13 \pm 0.0a	0.28 \pm 0.0ab	0.38 \pm 0.0ab	0.44 \pm 0.0ab	0.30 \pm 0.0b
λ	1.14 \pm 0.1a	1.32 \pm 0.0a	1.46 \pm 0.0a	1.55 \pm 0.1a	1.35 \pm 0.0a
TD	5.23 \pm 0.3a	2.50 \pm 0.1b	1.85 \pm 0.1bc	1.57 \pm 0.1c	2.3 \pm 0.0bc

Means followed by the same letter in the same row were not significantly different as determined by the Student's t test ($p < 0.05$).

R_0 : net reproduction rate; T: time between generations; r_m : innate ability to increase in number; λ : finite rate of increase; TD: time for population to double; n: number of insects analysed; SE: standard error.

The innate ability to increase in number (r_m), as well as the finite ratio (λ), increased linearly with increasing temperatures up to 28°C. At 31°C, there was decrease in these values, indicating that above this temperature the speed of population growth decreases, as well as the number of females added to the population, demonstrating the effect of thermal stress and corroborating the results presented by CHEN et al. (2013).

A. craccivora is considered a cosmopolitan insect, which is therefore adapted to the most diverse thermal conditions. However, while temperatures below 22 and above 28°C decrease its net reproduction rate, they do not impede population growth, considering the positive values of r_m .

Survival and specific fertility

The life expectancy (e_x) of *A. craccivora* linearly decreased with increased temperature, with values of 21, 18, 15, 9 and 8 days at temperatures of 18, 22, 25, 28 and 31°C, respectively (Fig. 2),

which corroborated the results from BARBOSA et al. (2011). At 28 and 31°C, it was observed that mortality affected the population as a whole, including nymphs and adults, which could be characterized as a type II pattern curve. At temperatures of 18, 22 and 25°C, there was increase in mortality in adults after the fifth day, which could be characterized as a type I pattern curve (Fig. 2). The same survival curve pattern was observed by CHEN et al. (2013), who reported type II patterns at the highest temperature tested, 35°C.

Statistically, the survival curves of the aphids created at 28 and 31°C were the same ($p = 0.006$), as determined by the G-test (chi-square 0.1%), and all the other temperature combinations were different. A mortality rate of 50% was observed between days 20.5 and 21.5 at 18°C, between days 16.5 and 17.5 at 22°C, between days 13.5 and 14.5 at 25°C, between days 11.5 and 12.5 at 28°C and at 8.5 days at 31°C (Fig. 2). CHEN et al. (2013) observed this same pattern for *A. craccivora* reared on *V. unguiculata sesquipedalis*, submitted

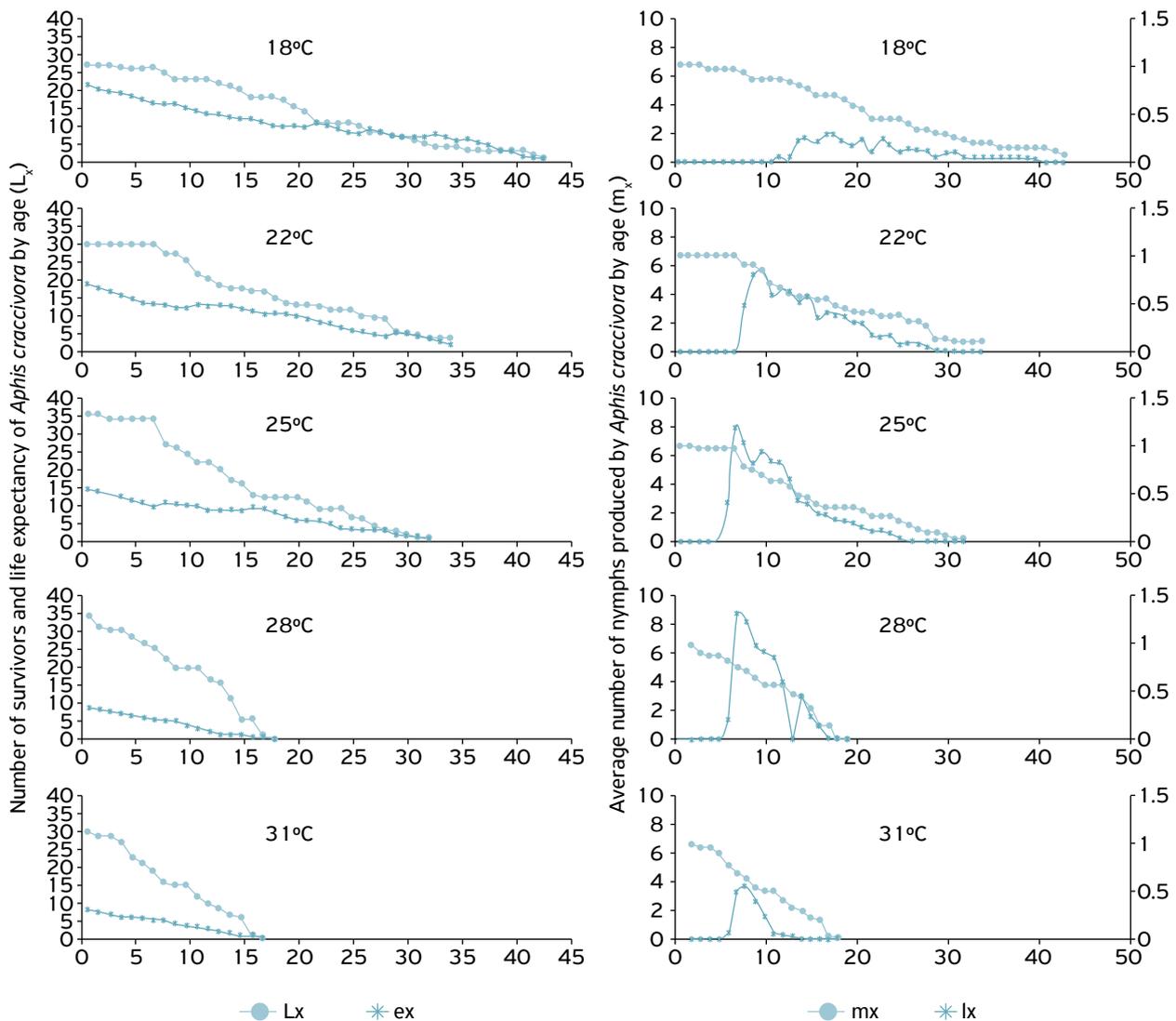


Figure 2. Survival curves (L_x), life expectancy (e_x) and specific fertility (m_x) of *Aphis craccivora* in cowpeas under constant temperatures.

to constant temperatures and oscillating; at constant temperatures, a 50% mortality was observed on the 16th day at 28.6°C and on the 7th day at 35°C.

The influence of temperature on the reproduction of *A. craccivora* can also be observed in Figure 2, in which the relationship between the average number of nymphs produced per female (m_x) per age range is shown. It was observed that the aphids kept at 18°C began to reproduce between day (x) 10.5 and 11.5, with a mean of 0.3 nymphs per female, reaching their breeding peak between 16.5 and 17.5 days, with the average daily production of two nymphs per female. At 22°C, the insects began breeding in the range of 6.5 to 7.5 days, with production of 3.1 nymphs per female. The breeding peak at this temperature was reached in the range of 8.5 to 9.5 days, with the average yield of 5.9 nymphs per female. When kept at 25°C, the start of reproduction was observed at 4.5 days, with the peak at 6.5 days, with mean yields of 0.1 and 7.8 nymphs per female, respectively. At 28°C, 1.5 nymph per female was produced between 3.5 and 4.5 days, with the peak at 5.5 days with rate of 8.8 nymphs per female. Finally, it was observed that at 31°C the insects started reproduction in the age range of 3.5 to 4.5 days, with m_x of 0.4 and the highest m_x rate between 5.5 and 6.5 days, with a mean of 3.6 nymphs per female (Fig. 2). In general, a decrease in the time to the beginning of reproduction, as well as the time to reach the reproductive peak, was observed with increased temperature: at 28°C the highest m_x rate was obtained in a smaller amount of time. According to SILVEIRA NETO et al. (1976), the optimal temperature is one in which the

insects produce a greater number of descendants in a shorter time. However, this high production of nymphs at 28°C is balanced by higher mortality and lower life expectancy of the individuals (Fig. 2).

CONCLUSIONS

Aphis craccivora completes its development accumulating 99.0 GD, with a lower base temperature of 9.13°C.

Temperatures above 22 and below 28°C are more favourable to population growth and development of *A. craccivora* in cowpeas.

Temperatures below 22 and above 28°C reduce the biotic potential of *A. craccivora*.

An increase in temperature, within the most favourable range, anticipates reproduction and reduces the longevity and life expectancy of *A. craccivora* in cowpeas.

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