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THE IMPACT OF TEMPERATURE ON BIOLOGICAL ASPECTS
AND LIFE TABLE OF *RHOPALOSIPHUM PADI*
(HEMIPTERA: APHIDIDAE) FED WITH SIGNAL GRASS

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ABSTRACT

The impact of temperature was evaluated on *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae). Nymphs, 12-h-old, were placed individually in cylindrical plastic dishes (2.5 × 2.5 cm), with a layer of 1% agar in which leaf disks of signal grass had been placed. The nymphs were reared at 12, 16, 20, 24, 28, and 32°C ± 1°C, RH of 70 ± 10% and 12-h photophase. We evaluated number of instars, duration of each instar and the nymphal period, survival of instars, duration of the reproductive period, daily and total production of nymphs, and longevity of the nymphal and adult phases. To construct the life expectancy table and fecundity, daily observations were made of 70 nymphs at each temperature, from birth to death. Development of *R. padi* was faster with increased temperature, but they did not complete the last nymphal instar at 32°C. The same pattern occurred for the pre-reproductive, reproductive, and post-reproductive periods. The highest fecundity rates were between 16°C and 24°C. The highest fertility (4 nymphs/female/day) was recorded at 12°C and 20°C. The highest net reproduction rates were at 24°C and 28°C, and the time interval between each generation (T) and the population doubling time (DT) diminished as temperature increased. The finite rate of increase ($\lambda = 1.9$ nymphs/female/day) and the intrinsic rate of increase ($r_m = 0.64$) were greatest at 24°C and 28°C, respectively. There was a negative impact on the biology and life table of *R. padi* at 32°C, but the range of 12°C to 28°C, despite some fluctuations, was favorable for survival and reproduction.

Key Words: ecology, aphid, signal grass, pest

RESUMO

Objetivou-se avaliar o impacto da temperatura nos aspectos biológicos e na tabela de vida de *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae). Ninfas com até 12 horas de idade, foram individualizadas em placas cilíndricas de plástico (2,5 × 2,5 cm). No interior destas, foi depositada uma camada de ágar sobre a qual foram dispostos discos foliares de braquiária que receberam as ninfas, as quais foram submetidas a 12, 16, 20, 24, 28, e 32°C ± 1°C, UR 70 ± 10% e fotofase de 12 horas. Avaliou-se o número de instares, a duração de cada instar e do período ninfal, a sobrevivência nos diferentes instares, a duração do período reprodutivo, capacidade diária e total de produção de ninfas, longevidade da fase ninfal e adulta. Para a tabela de esperança de vida e de fecundidade efetuaram-se observações diárias de 70 ninfas, para cada temperatura, do nascimento até a morte. Verificou-se que a velocidade de desenvolvimento de *R. padi* aumentou à medida que a condição térmica era mais elevada; no entanto, não completaram os dois últimos estádios ninfais à 32°C. A mesma tendência foi constatada para os períodos pré-reprodutivo, reprodutivo e pós-reprodutivo. As maiores taxas de fecundidade estiveram entre 16 e 24°C. A maior fertilidade específica foi registrada a 12 e 20°C, sendo de 4 ninfas/fêmea/dia. As maiores taxas líquidas de reprodução, foram a 24 e 28°C e o intervalo de tempo entre cada geração (T) e o tempo necessário para a população duplicar em número de indivíduos (TD) diminuíram com o aumento da temperatura. A razão finita de aumento ($\lambda = 1,9$ ninfas/fêmea/dia) e a capacidade inata de aumentar em número ($r_m = 0,64$) foram superiores à 24 e 28°C, respectivamente. Constatou-se impacto negativo na a biologia e tabela de vida de *R. padi* a 32°C, porém, na faixa de 12 a 28°C, apesar das oscilações, constata-se que o inseto encontra condições favoráveis para sobrevivência e reprodução.

Translation by the authors.

The quality of forage plants is one of the most important factors for reducing milk production costs. Signal grass (*Brachiaria* sp.), a perennial with large production of leaf mass, is widely

grown in pastures in Brazil (Botrel et al. 1987). Various aphids in Brazil, including *Rhopalosiphum padi* (L.) vector viruses to grasses (Hutchinson & Bale 1994), and although *R. padi* is con-

sidered only an occasional pest on signal grass, at high population levels it can considerably reduce the quantity and quality of forage. Aphids in the genus *Rhopalosiphum* Koch, are widely distributed in tropical and subtropical regions (Blackman & Eastop 2000) and affect various crops of economic importance, such as sorghum, corn, sugarcane, oats, rye and barley (Robison 1992; Jauset et al. 1998). Hence, strategies to manage *R. padi* should be defined.

The effect of temperature on the biological aspects of *R. padi* on various host plants has been studied by Leather & Dixon (1984), Elliott & Kieckhefer (1989), De Barro et al. (1992), Hutchinson & Bale (1994), and Asin & Pons (2001), but there are no published studies of *R. padi* on signal grass. Knowledge in this respect will make it possible to predict the intensity of occurrence, to serve as a base for developing control strategies, and consequent improvement in management programs. In the present study we examined the effect of temperature on biology and development of *R. padi* and constructed a life table for *R. padi* fed with signal grass.

MATERIALS AND METHODS

Biological Aspects of *R. padi* on Signal Grass

Adults of *R. padi* were collected on signal grass, *Brachiaria ruziziensis* (Germain & Everard), grown in greenhouses at the Embrapa Dairy Cattle Research Center in Juiz de Fora, Minas Gerais, Brazil. The aphids were multiplied in the laboratory in Petri dishes kept in climate controlled chambers at a temperature of $24 \pm 1^\circ\text{C}$, RH of $70 \pm 10\%$ and 12-h photophase. Nymphs up to 12-h age were collected with tweezers and placed individually in cylindrical plastic dishes (2.5 cm diameter and 2.5 cm height). Each dish was first filled with a solution of 1% agar in water to a height of 1.0 cm, in which leaf disks of signal grass were placed in order to keep the leaves turgid. The dishes were covered with fabric and secured with rubber bands.

The aphids were reared at temperatures of 12, 16, 20, 24, 28, and $32^\circ\text{C} \pm 1^\circ\text{C}$, RH of $70 \pm 10\%$ and photophase of 12 h. Each treatment contained 150 nymphs in a fully randomized setup. The following parameters were evaluated: number of instars; duration of each instar and nymphal period; survival of the different instars; duration of the reproductive period; daily and total capacity to produce nymphs; and longevity of the nymphal and adult phases.

The data were submitted to variance analysis and the means were compared by the Scott Knott (1974) test at 5% significance. Data were submitted to regression analysis and the lower threshold temperatures (LTT) and development time in de-

gree-days (DD) were estimated based on a hyperbolic relation, according to the method proposed by Bean (1961).

Life Table of *R. padi* on *B. ruziziensis*

Newly emerged *R. padi* nymphs were maintained individually in plastic dishes containing a layer of agar solution and leaf disk of signal grass, as described above. Nymphs were kept at temperatures of 12, 16, 20, 24, 28, and 32°C , with 70 insects at each temperature. The insects were observed daily from birth to death to record the viability throughout their life cycle and to enable calculating the life tables at each temperature.

The life expectancy tables were based on the number of survivors at the start of age $\times (l_x)$, number of individuals that died during interval $\times (d_x)$, age structure (E_x), corresponding to the number of live individuals between one day and the next, life expectancy for individuals of age $\times (e_x)$ and probability of death at age $\times (100q_x)$, which indicates the probability of dying before the time established in e_x . The following equations were used, as proposed by Silveira Neto et al. (1976): $E_x = [L_x + (L_{x+1})] / 2$; $e_x = T_x / L_x$ and $100 q_x = (d_x / l_x) \cdot 100$.

For the fertility tables, the reproduction rates (Ro), time interval between generations (T), intrinsic rate of increase (r_m), finite rate of increase (λ), time necessary for the population to double (DT), means of the age interval (\bar{x}), specific fertility (m_x) and probability of survival (l_x) were calculated, according to the following equations: $Ro = \sum(m_x l_x)$; $T = \sum(m_x l_x \bar{x}) / \sum(m_x l_x)$; $r_m = \log_e Ro / T = \ln Ro / T$; $\lambda = e^{r_m}$ and $DT = \ln(2) / r_m$.

RESULTS AND DISCUSSION

Temperature influenced the duration of the instars and the nymphal cycle of *R. padi*, with increased rate of development as the temperature increased (Table 1, Fig. 1). These results agree with those reported by Elliott & Kieckhefer (1989) and Asin & Pons (2001) for the same aphid species. The last 2 instars at the highest temperature, 32°C , did not survive (Table 1). Asin & Pons (2001) found average survival of 55% of immatures of *R. padi* fed on corn at 30°C . According to Campbell et al. (1974), higher temperatures lead to greater mortality due to the denaturing of proteins or metabolic disturbances from the accumulation of toxic products, and these harmful effects mainly occur if the temperature is held constant.

The period in which *R. padi* remained in the immature phase was shortest at 28°C . This agrees with the findings of Asin & Pons (2001). However, Elliot & Kieckhefer (1989) and Dean (1974), using barley as food for *R. padi*, found that the maximum development rate occurred at 25°C . At 16 and 20°C , the insects remained in the nymphal stage longer than found by Segonca et

TABLE 1. MEAN DURATION IN DAYS, FOR 1ST, 2ND, 3TH AND 4TH INSTAR TO DEVELOP, PRE-REPRODUCTIVE, REPRODUCTIVE AND POST-REPRODUCTIVE PERIODS, DAILY AND TOTAL FERTILITY, AND LONGEVITY OF NYMPHS AND ADULTS OF *RHOHALOSIPHUM PADI* AS A FUNCTION OF TEMPERATURE.

	Nymphal stage					
	Temperatures (°C)					
	12	16	20	24	28	32
1 st instar	3.42 ± 0.16 e (n = 112)	2.87 ± 0.06 d (n = 150)	2.01 ± 0.06 c (n = 141)	1.73 ± 0.04 b (n = 150)	1.64 ± 0.07 b (n = 75)	1.33 ± 0.07 a (n = 54)
2 nd instar	2.93 ± 0.16 c (n = 84)	3.10 ± 0.08 c (n = 135)	2.01 ± 0.06 b (n = 126)	1.79 ± 0.04 b (n = 150)	1.47 ± 0.08 a (n = 63)	1.88 ± 0.21 b (n = 18)
3 rd instar	4.35 ± 0.25 d (n = 57)	3.40 ± 0.07 c (n = 99)	2.22 ± 0.04 b (n = 113)	1.71 ± 0.05 a (n = 136)	1.48 ± 0.07 a (n = 52)	—
4 th instar	6.84 ± 0.49 d (n = 43)	3.83 ± 0.11 c (n = 69)	2.33 ± 0.09 b (n = 57)	1.94 ± 0.06 a (n = 95)	1.64 ± 0.09 a (n = 44)	—
Nymphal stage	17.3 ± 0.53 e (n = 43)	12.93 ± 0.17 d (n = 69)	8.37 ± 0.13 c (n = 57)	7.13 ± 0.11 b (n = 95)	6.24 ± 0.15 a (n = 44)	—
	Adult stage					
Pre-reproductive	3.00 ± 0.43 c (n = 12)	2.42 ± 0.26 b (n = 19)	1.88 ± 0.12 a (n = 35)	1.86 ± 0.08 a (n = 77)	1.92 ± 0.09 a (n = 36)	—
Reproductive	7.91 ± 1.48 b (n = 12)	11.31 ± 1.67 c (n = 19)	4.63 ± 0.45 a (n = 35)	6.75 ± 0.44 b (n = 77)	4.08 ± 0.42 a (n = 36)	—
Post-reproductive	2.67 ± 0.48 c (n = 12)	1.84 ± 0.33 b (n = 19)	1.22 ± 0.08 a (n = 35)	1.40 ± 0.08 a (n = 77)	1.30 ± 0.09 a (n = 36)	—
Longevity	13.58 ± 1.59 c (n = 12)	15.58 ± 1.77 c (n = 19)	7.74 ± 0.45 a (n = 35)	10.00 ± 0.40 b (n = 77)	7.30 ± 0.44 a (n = 36)	—
	Fertility (Number of nymphs produced)					
Daily	1.54 ± 0.14 a (n = 12)	1.81 ± 0.14 a (n = 19)	2.68 ± 0.18 b (n = 35)	2.73 ± 0.14 b (n = 77)	1.83 ± 0.09 a (n = 36)	—
Total	13.00 ± 3.18 a (n = 12)	21.21 ± 3.98 b (n = 19)	12.88 ± 1.55 a (n = 35)	19.97 ± 1.83 b (n = 77)	7.75 ± 0.94 a (n = 36)	—

Means followed by the same letter in the rows did not differ by Scott Knott (1974) at 5%. A dash, —, indicates absence of data due mortality.

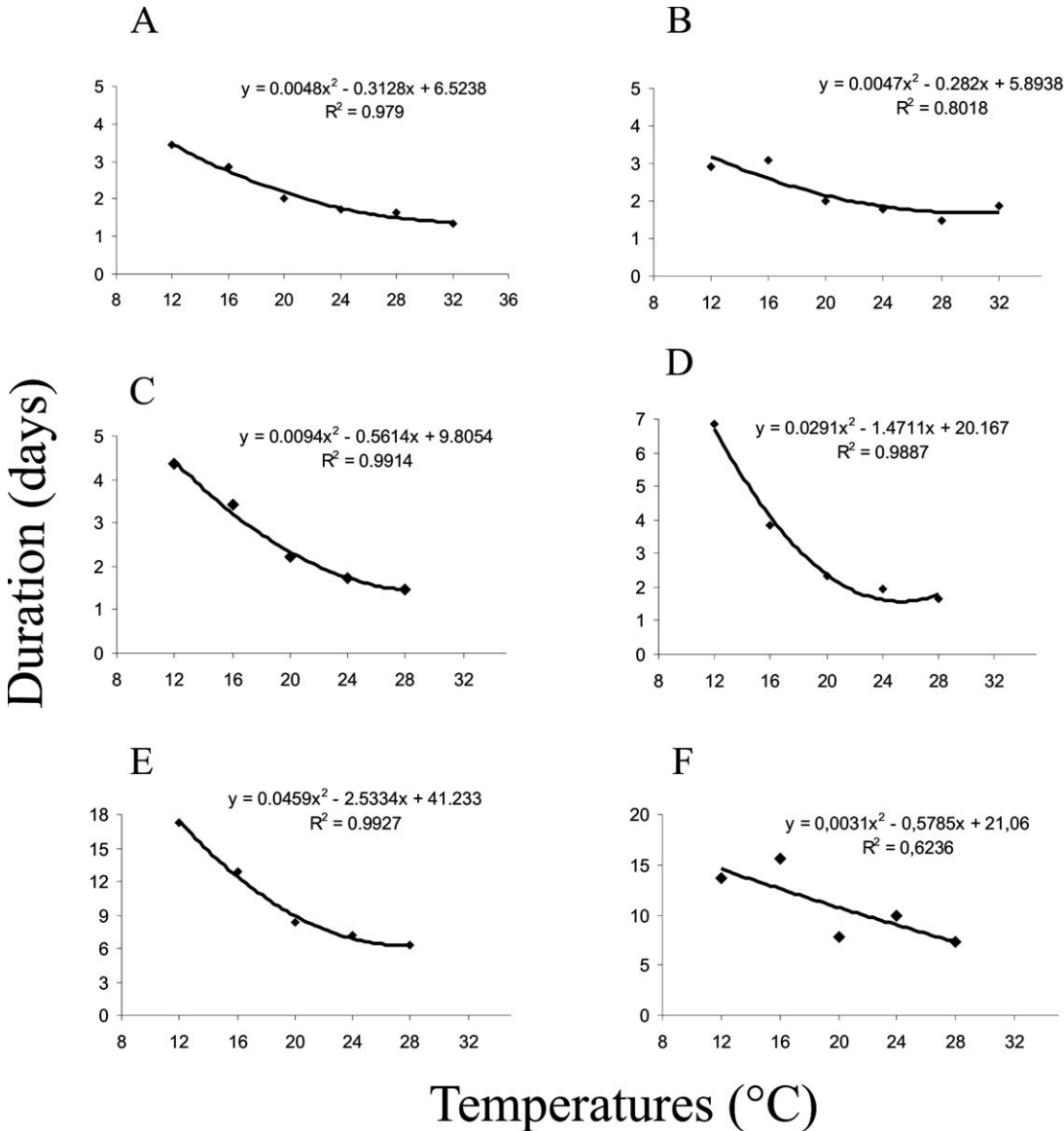


Fig. 1. Fitted regression curves for the duration of the first (A), second (B), third (C), fourth (D) instars, nymphal (E), and adult (F) phases of *Rhopalosiphum padi*, as a function of temperature.

al. (1994) at the same temperatures. Elliott & Kieckhefer (1989) also found a shorter nymphal cycle at similar temperatures to those studied here. These results suggest that the type of host plant offered as well as the geographic origin of the aphid can affect its development, even when kept under similar heat conditions. This is in line with the observations of Smith (1922).

The nymphal period of *R. padi* was on average 3 times longer at the lowest temperature (12°C) compared with the upper limit for survival (28°C). The effects of low temperature on the duration of *R. padi* were described by Hutchinson & Bale (1994), show-

ing that sublethal stress affects the development process and longevity, which can exercise a dominant influence on the aphid's population dynamic. Asin & Pons (2001) also found that development increased with rising temperature. They reported complete development of the immature phase at 30°C, with a period significantly equal to that of the insects maintained at 27.5°C. These results also agree with the findings of Campbell & Mackauer (1975) that the average development time of aphids declines as temperature increases.

The lower threshold temperatures (LTT) for nymphs of *R. padi* are shown in Table 2. The in-

TABLE 2. REGRESSION EQUATIONS, DETERMINATION COEFFICIENTS (R²), THE LOWER THRESHOLD TEMPERATURES (LTT), AND DEVELOPMENT TIME IN DEGREE-DAYS (DD) OF IMMATURES OF *RHOPALOSIPHUM PADI* FED WITH SIGNAL GRASS.

Nymphal stage	Equation	R ²	LTT (°C)	DD
1 st instar	-0.0229 + 0.0251x	0.97	0.91°C	39.84
2 nd instar	-0.1069 + 0.0282x	0.97	3.79°C	35.46
3 rd instar	-0.1439 + 0.0295x	0.98	4.87°C	33.89
4 th instar	-0.1996 + 0.0296x	0.99	6.74°C	33.78
Nymphal stage	-0.0227 + 0.0067x	0.98	3.38°C	149.2

sects were tolerant up to the limit of 28°C and the LTT increased as the insects reached the adult phase. Higher values were found by Elliott & Kieckhefer (1989) for the different instars (5.73 to 6.10 d) and nymphal phase (5.76 d), except for the fourth instar, when the temperature was the same as that found here. The numbers of degree-days (DD) required for the development of the different instars and the nymphal cycle were higher than those reported by Elliott & Kieckhefer (1989) for *R. padi* kept at temperatures from 11 to 29°C. With 3.38 as the lower temperature limit for development of the nymphal phase, 149.2 degree-days are required for this aphid species to reach the adult phase. These results are important to predict the number of annual generations of this insect.

The longest pre-reproductive and post-reproductive periods for *R. padi* maintained on *B. ruziziensis* were at the lowest temperature (12°C) and no significant differences were found in the range from 20°C to 28°C (Table 1). In this interval the adults began laying nymphs more quickly than at the other temperatures (Table 1 and Fig. 2). Elliott and Kieckhefer (1989) reported a shorter pre-reproductive period in the range from 15 to 26°C in relation to the extreme conditions of 11 and 29°C. Segonca et al. (1994) did not find any significant differences in the pre-reproductive period of *R. padi* in the range from 4 to 20°C. The values found by these authors were lower than those found in the present study.

The aphid's reproductive period was longest at 16°C, and there was no reduction in this biological parameter with increasing temperature (Table 1). Likewise, Segonca et al. (1994) did not find significant reductions in the duration of the reproductive period of *R. padi* submitted to temperatures from 8 to 20°C.

The highest fecundity rates occurred at 16 and 24°C, with 21.2 and 20.0 nymphs/female, respectively. Higher rates were found by Asin & Pons (2001) in the range from 18 to 27.5°C, varying from 35.2 to 45.0 nymphs/female, and a similar number of nymphs/female was found by Dean (1974) at 25°C. At 16 and 20°C, the average number of nymphs produced was 21.2 and 12.9, respectively. In contrast, Segonca et al. (1994) found

twice as many nymphs produced when the aphids were reared at the same temperatures, indicating that the same aphid species, under the same climate conditions, can have different reproductive potentials, which are possibly influenced by other biotic or abiotic factors.

Hesler et al. (2005a) found production of 7.5 to 11.4 *R. padi* nymphs in a 24-h period when 3 winged females were reared at temperature of 20°C on transgenic wheat plants. The effect of the host plant on nymph production was also reported by Hesler (2005b), in which the same aphid species, during 7 d of observation, produced between 23.6 and 43.3 nymphs/female, according to the type of host grass. Nutritional factors are also responsible for variation in fecundity, as mentioned in the study by Adams (2007), in which an increase in nitrogen content was responsible for higher fecundity of *R. padi*.

The daily and total nymph production was lower at the extreme temperatures (12 and 28°C), as shown in Table 1. Asin & Pons (2001) also found a low reproductive capacity of *R. padi* when the females were reared at 30°C. According to Tang et al. (1999), aphids respond in different ways to adapt to different geographic regions and climate conditions. Nava-Camberos et al. (2001) added that besides temperature, the host plant also influences the aphid's physiological response. Therefore, the number of nymphs found in other studies possibly was higher than our findings because the *R. padi* aphids originated from other populations and were provided with host plants that permitted better development. However, Loeck et al. (2006) did not find significant differences in the reproduction of *R. padi* when testing different oat cultivars.

The survival of the various instars was above 70%, from 12 to 28°C, except at 20°C for the fourth instar (51%), indicating that in this temperature range the nymphs reach the adult phase. Third and fourth instars did not survive at the highest temperature (32°C), corroborating the results of Dean (1974), according to which 30°C was lethal to *R. padi* nymphs. However, Asin & Pons (2001) reported survival of 55% of this aphid species at this temperature. Tolerance of this aphid species to high temperatures was reported

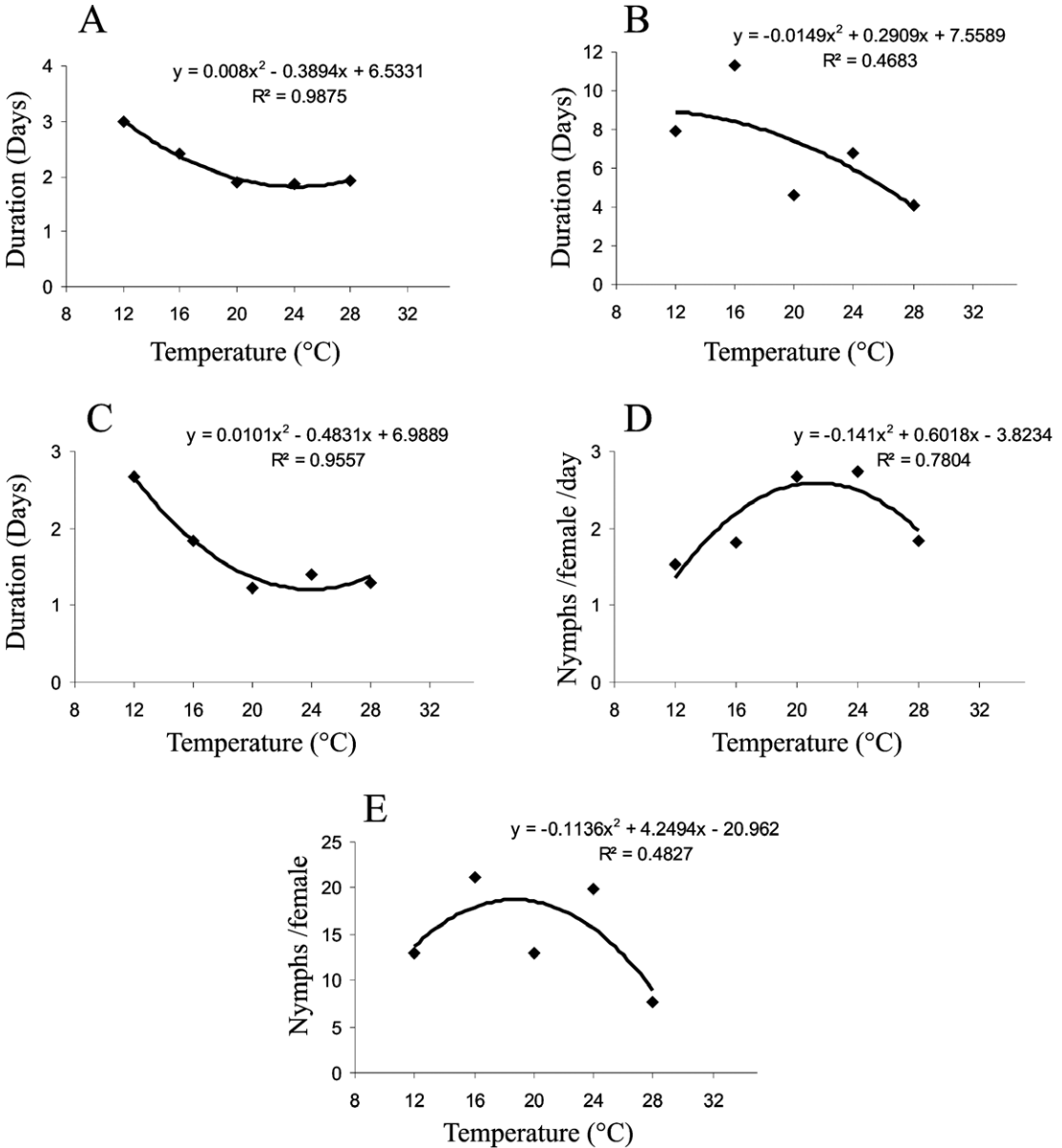


Fig. 2. Fitted regression curves for the duration of pre-reproductive (A), reproductive (B), post-reproductive (C), and daily (D) and total (E) fertility of *Rhopalosiphum padi*, as a function of temperature.

by De Barro et al. (1992), who mentioned that the initial mortality of this aphid was 32°C, and that above 39°C mortality was greater than 90%.

Table of Life Expectancy and Fecundity of *R. padi* on Signal Grass

The survival (lx) started to diminish after the first day at a temperature of 12°C, as of 3.5 d at 16°C and from 1.5 d at the other temperatures (Fig. 3). These figures to not agree with those re-

ported in the literature for other aphid species, probably because the insect's life expectancy is associated with the particular species (Tamaki et al. 1982) or host plant (Wale et al. 2000) being studied.

The highest life expectancies (ex) were 14.9, 14.3, 9.7, 10.3, 7.5 and 2.5 d in the nymph phase at 12, 16, 20, 24, 28, and 32°C, respectively. In the adult phase, the longest life expectancies were 6.7, 10.8, 5.2, 6.2, and 4.7 days at 12, 16, 20, 24, and 28°C, respectively. At the highest tempera-

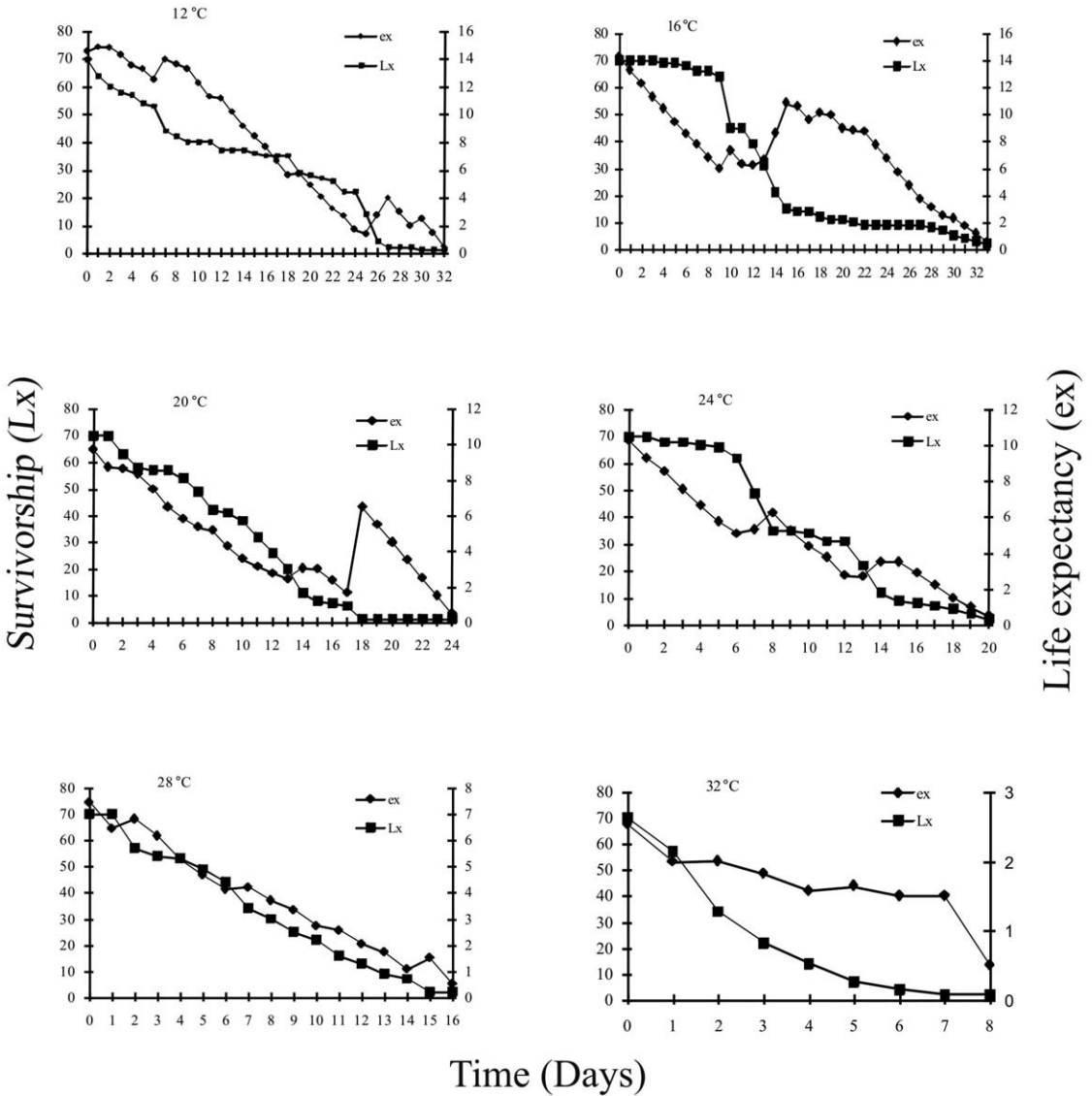


Fig. 3. Survivorship (Lx) and life expectancy (ex) of *Rhopalosiphum padi* as a function of temperature.

ture (32°C), life expectancy of nymphs was lowest, and the individuals died before reaching the adult phase.

The probability of death before the period established (100 q_x) occurred during the entire nymph and adult phase, with the majority of nil values for this parameter occurring at 16°C. The highest mortality rates (d_x) were 10, 19, 9, 14, 13, and 23 dead individuals, and the probability of death (100 q_x) on these occasions was 71.4, 29.7, 45.0, 28.6, 18.6, and 40.4% at 12, 16, 20, 24, 28, and 32°C, respectively.

The highest specific fecundity ($m_x = 4$ nymphs/female/day) was recorded at 12 and

20°C. The aphids did not reach the adult phase at 32°C, which prevented calculating the fecundity table figures at this temperature. Likewise, Asin & Pons (2001) found a significant decline in the reproductive capacity of *R. padi* maintained at 30°C. The highest net reproduction rates (R_0) occurred at 24 and 28°C (Table 3). At 16 and 20°C, the R_0 values were 9.92 and 9.85, respectively. Segonca et al. (1994), studying the same temperature conditions, found respective values of 46.6 and 38.0, indicating that the number of times *R. padi* increases in population from 1 generation to the next was nearly 5 times higher.

TABLE 3. FERTILITY TABLE FOR *RHOPALOSIPHUM PADI* AS A FUNCTION OF TEMPERATURE

Temperatures (°C)	Parameter				
	T	R ₀	r _m	λ	DT
12	21.90	6.59	0.086	1.09	8.06
16	17.80	9.92	0.128	1.14	5.42
20	11.32	9.85	0.202	1.22	3.43
24	9.43	13.42	0.280	1.32	2.47
28	4.08	13.88	0.640	1.89	1.08

T = time interval between each generation; R₀ = Net reproductive rate; r_m = intrinsic rate of population increase; λ = finite rate of increase and DT = time necessary for the population to double (days).

The time interval between each generation (T) diminished with increasing temperature (Table 3). A significant reduction in this interval was also found by Segonca et al. (1994) studying *R. padi* kept at 8 to 20°C.

The intrinsic rate of increase (r_m) was higher at 28°C (0.64), indicating that at this temperature the population increases faster, while aphids kept at 12°C had a lower r_m (0.09). These results corroborate those of Asin & Pons (2001) for *R. padi*, according to which the highest rate occurred at 27°C, considered to be the most suitable temperature for the species to develop. Segonca et al. (1994) found a gradual increase in r_m from 8 to 20°C, and when compared to the results of the present study (16 and 20°C), the authors observed higher r_m values. The same results occurred when *R. padi* individuals were exposed to temperatures fluctuating between 12.8 to 26.6°C or 20 to 33.4°C.

We found that r_m was 4 times higher when the temperature increased from 16 to 28°C. Asin & Pons (2001) found that in the range of 18 to 27°C, r_m of this aphid doubled at the highest temperature, suggesting the ability of this species to adapt to higher temperatures. The finite rate of increase was higher at 28°C, at 1.9 nymphs/female/day. The population doubling times (DT) were 8.06 and 1.08 days at 12 and 28°C, respectively.

The results show that with higher temperatures, up to a limit of 28°C, although the life expectancy of *R. padi* fed with signal grass is lower, the aphid's fecundity is higher when compared to lower temperatures, explaining population spikes at certain times of the year. These findings can assist in planning control measures. In conclusion, in the range of 12 to 28 °C, nymphs reached the adult phase, and 16 to 24°C was the most favorable temperature range for reproduction of *R. padi* on *B. ruziziensis*. The life expectancy of *R. padi* decreased with increasing temperature, but fecundity was best at 28°C.

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