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Impact of fluctuating and constant temperatures on key life history parameters of *Sipha flava* (Hemiptera: Aphididae)

Alexander M. Auad, Sandra E. B. Silva, Juliana C. Santos, and Tamiris M. Vieira

Abstract

This study aimed to evaluate the impact of constant and fluctuating temperatures on the biology of *Sipha flava* (Forbes) (Hemiptera: Aphididae) in order to determine whether the results of laboratory studies can be extrapolated to those performed in natural conditions. We compared the biological parameters of *S. flava* kept in an uncontrolled greenhouse in which temperatures fluctuated (treatment 1) with those kept in a phytotron-type climate chamber that simulated the mean hourly average temperatures of the greenhouse (treatment 2). In addition, we compared the effects of treatment 2 versus the effects of having a set temperature during photophase and another set temperature during scotophase versus a constant daily average temperature. The experimental design was completely random, and 150 nymphs were used per treatment at the outset of the bioassays. However, the number of repetitions was altered in relation to survival of the aphids in the different instars and treatments. By daily use of a stereoscopic microscope, we evaluated the following parameters: the duration (days) and survival (%) of each instar and stage as well as the reproductive capacity (offspring per female per day) and the longevity (days) of adults. The simulation of mean hourly temperatures of an uncontrolled greenhouse favored the survival, reproductive capacity, and longevity of adults — which are factors of great importance in the insect population growth — compared with those insects kept at 27 °C (photophase) and 18 °C (scotophase) or kept at the constant daily average temperature. The results showed that much caution must be exercised in extrapolating results obtained in the laboratory under constant temperatures to predict the population dynamics of field populations of *S. flava*.

Key Words: insect; forage; aphid

Resumo

Objetivou-se avaliar o impacto de temperaturas constantes e flutuantes sobre a biologia de *Sipha flava* (Forbes) (Hemiptera: Aphididae), visando verificar se resultados dos estudos de laboratório podem ser extrapolados para aqueles realizados em condições naturais. Foi comparado os parâmetros biológicos de *S. flava* mantidos em uma casa de vegetação onde as temperaturas flutuavam em decorrência de ser um ambiente não controlado (tratamento # 1) com daqueles mantidos em uma câmara climática tipo fitotron, que simulavam as temperaturas médias a cada hora na casa de vegetação (tratamento # 2). Além disso, foi comparado os parâmetros biológicos dos afídeos mantidos no tratamento # 2 com daqueles mantidos em temperaturas que flutuavam em função do fotoperíodo e, com temperatura constante. Em um delineamento inteiramente casualizado, foram utilizados um total de 150 ninfas por tratamento no início dos bioensaios, sendo esse número alterado em função da sobrevivência dos afídeos em diferentes estádios e tratamentos. Diariamente, com um microscópio estereoscópico, foram avaliados os seguintes parâmetros: a duração (dias) e sobrevivência (%) de cada estágio e fase ninfal, bem como a capacidade reprodutiva (número de ninfas por fêmea por dia) e longevidade (dias) dos adultos de *S. flava*. A simulação das temperaturas média a cada hora da casa de vegetação favoreceu a sobrevivência, capacidade reprodutiva e longevidade dos adultos, que são fatores de grande importância no crescimento da população de insetos, comparado com aqueles insetos mantidos a 27 °C (fotofase) e 18 °C (escotofase) ou mantidos em temperatura média diária constante. Dessa forma, deve-se ter cautela em extrapolar os resultados obtidos em laboratório sob temperaturas constantes para prever a dinâmica populacional de *S. flava*.

Palavras Chave: inseto; forrageiras; pulgões

Sipha flava (Forbes, 1884) (Hemiptera: Aphididae) is widely distributed throughout the Americas (Blackman & Eastop 2000) and causes damage directly to elephant or Napier grass, *Pennisetum purpureum* Schumacher, forage sorghum, *Sorghum bicolor* (L.) Moench, and sugarcane, *Saccharum officinarum* L. (Poales: Poaceae) (Medina-Gaud et al. 1965; Kindler & Dalrymple 1999) by feeding, which induces plant deformation (Breen & Teets 1990; Webster 1990), indirectly by “honeydew” excretion (Nuessly 2005), or by transmitting sugarcane mosaic potyvirus (Blackman & Eastop 2000).

Under laboratory conditions, a constant temperature in the range of 20–24 °C enables *S. flava* to reach “pest status” on elephant grass, *P. purpureum* (Oliveira et al. 2009). However, the influence of temperature on insect development is related not only to the daily average temperature corresponding to conditions in the field but also to the levels of the temperature peaks. Similarly, one should take into account periods when the temperature is unfavorable.

Typically, insects develop faster, have greater fertility, and show increased survival when kept under fluctuating temperatures in natu-

ral conditions, with the maximum and minimum thermal conditions within the optimal range for the organism's development (Müller & Obermaier 2012). Thus, care should be taken when extrapolating the measurements of biological patterns of insects maintained at a constant temperature to those kept under field or uncontrolled greenhouse conditions in which temperatures are fluctuating (Barbosa et al. 2006, 2011). Usually insects are adapted to fluctuating temperatures.

Most studies investigating the influence of temperature on the development of insects use constant temperatures and/or fluctuating temperatures depending on the photoperiod (Bosch & Kemp 2000; Auaud et al. 2009; Oliveira et al. 2010; Radmacher & Strohm 2011; Kjaersgaard et al. 2013; Warren & Anderson 2013; Tochen et al. 2014). In comparison with the effect of a constant temperature on the development of insects, the effects of fluctuating temperatures have been found to accelerate the development of many species (Beck 1983; Ratte 1985), to decelerate the development of a few other species (Messenger 1969; Hagstrum & Leach 1973), or to have no differential effect as in the case of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) (Butler & Lopez 1980).

The influence of temperature on the development of insects is not only related to the daily average temperature, but also to the rate of temperature variation (Hagstrum & Hagstrum 1970; Mironidis & Savopoulou-Soultani 2008), although the magnitude of this influence has not been defined in the literature. This study was designed to evaluate the impact of constant and fluctuating temperatures on key life history parameters of *S. flava*. The purpose of this investigation was to determine if measurements of this aphid's life history parameters made in the laboratory can be extrapolated to estimate these parameters in the field.

Materials and Methods

Sipha flava aphids used in the experiments were obtained from populations maintained in a greenhouse at the Research Station of Embrapa Dairy Cattle in Juiz de Fora, Minas Gerais, Brazil. Approximately 50 adults, collected in the greenhouse, were transferred to Petri dishes (8.5 cm × 2 cm) each containing a leaf disc of *P. purpureum* (8.5 cm diameter) placed on a 1 cm thick layer of 1% agar to maintain the turgidity of the

leaf disc. These Petri dishes were covered with fabric and secured with rubber bands, and kept in climate-controlled chambers (BOD) (Eletrólabs, São Paulo, São Paulo State, Brazil) at $25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH, and a 12:12 h L:D photoperiod.

Nymphs up to 18 h old were taken from the above-mentioned Petri dishes and placed individually in cylindrical plastic dishes (2.5 cm diameter × 2.5 cm height), containing a leaf disc of *P. purpureum* placed on a 1% agar layer. Each cylindrical plastic dish was covered with fabric and secured with a rubber band. The leaf disc was changed every 48 h to prevent food-resource degradation.

In treatment 1 (Trt. #1), the first bioassay, individual nymphs each held in a cylindrical plastic dish were kept in an uncontrolled greenhouse with fluctuating temperatures. To record temperature data, a Data Logger U12-012 (Onset Co., Pocasset, Massachusetts, USA) was placed inside this greenhouse. This device recorded the temperature every 2 min throughout the first bioassay (53 d). After this period, the hourly mean temperatures were calculated (Fig. 1) together with the overall daily mean temperature for the 53 d period of the first bioassay.

In treatment 2 (Trt. #2), the mean hourly temperatures in the greenhouse were reproduced in a phytotron-type climate chamber (Fig. 1). In treatment 3 (Trt. #3), a phytotron-type climate chamber simulated the mean temperature of the greenhouse during the photophase (27°C) and the scotophase (18°C). In treatment 4 (Trt. #4), a phytotron-type climate chamber held the temperature constant at 22.5°C , which was the overall mean temperature in the greenhouse bioassay, as recorded in Trt. #1. The phytotron-type climate chambers ($2.5 \times 2.20 \times 2.80$ m) (Eletrólabs, São Paulo, São Paulo State, Brazil) used in all the experiments were maintained at $70 \pm 10\%$ RH and a photoperiod of 12:12 h L:D.

Using a completely random design, 150 nymphs were used per treatment at the start of each bioassay, and the number of repetitions was altered to compensate for mortality of the aphids in the different instars and treatments (see values of *n* in Tables 1 and 2). By daily use of a stereoscopic microscope, we evaluated the following parameters: the duration (days) and survival (%) of each instar, and the reproductive capacity (offspring per female per day) and longevity (days) of the adults.

We compared the percentage survival, reproductive capacity, and longevity of adults kept in the uncontrolled greenhouse with fluctuating temperatures with those kept in the climatic chamber that simulated

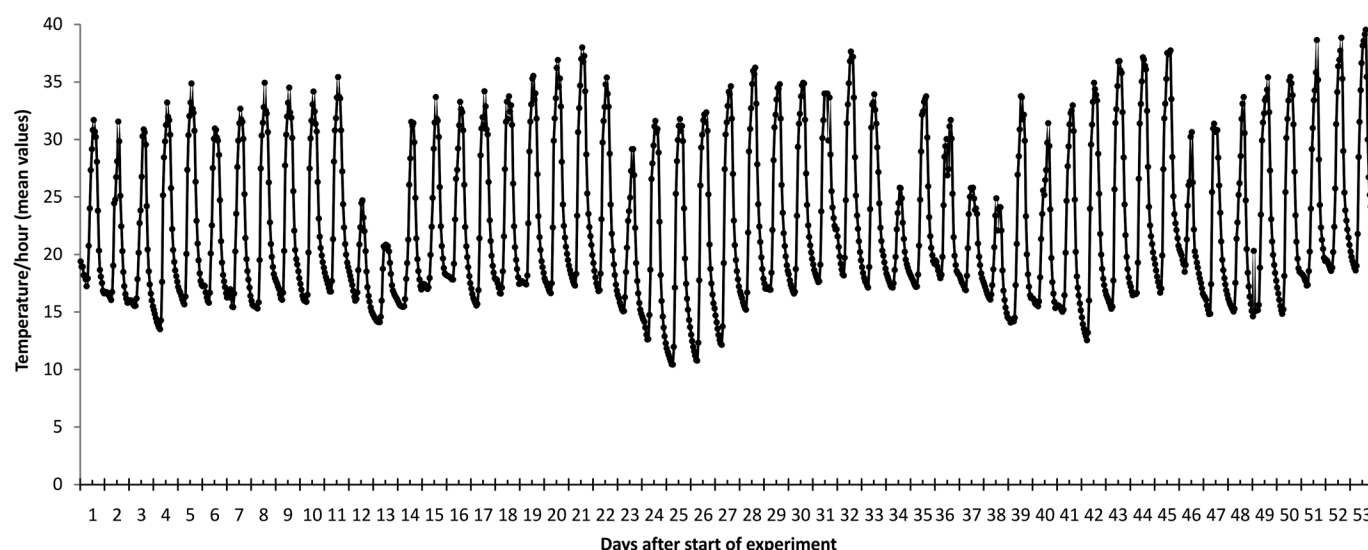


Fig. 1. Simulated hourly mean temperatures in the uncontrolled greenhouse every day during the 53 d period when the effects of various temperatures on the longevity and reproductive capacity of *Sipha flava* were determined.

the mean hourly temperatures of the greenhouse. We made the same comparisons for the *S. flava* maintained in the climatic chamber simulating mean hourly temperatures of the uncontrolled greenhouse with those kept with a simulated greenhouse mean photophase temperature of 27 °C and a mean scotophase temperature of 18 °C and those kept at the constant mean greenhouse temperature of 22.5 °C.

The parameter measurements were subjected to analysis of variance (ANOVA), and means were separated Tukey's HSD test at 5% significance using the Sisvar 5.1 software (Lavras, Minas Gerais, Brazil).

Results

LIFE HISTORY PARAMETERS OF *SIPHA FLAVA* IN AN UNCONTROLLED GREENHOUSE WITH FLUCTUATING TEMPERATURES (TRT. #1), OR IN A CLIMATE CHAMBER THAT SIMULATED THE MEAN HOURLY TEMPERATURES OF THE GREENHOUSE (TRT. #2)

Sipha flava nymphs kept in the uncontrolled greenhouse with fluctuating temperatures (Trt. #1) showed significantly longer developmental periods than those maintained in the climate chamber that simulated the mean hourly temperatures of the uncontrolled greenhouse (Trt. #2) in the 1st ($F_{(1,256)} = 24.01, P = 0.0001$), 2nd ($F_{(1,245)} = 5.41, P = 0.0208$), and 3rd instars ($F_{(1,239)} = 122.32, P = 0.0001$) and the overall nymphal period ($F_{(1,231)} = 95.71, P = 0.0001$). Such a difference did not occur in the 4th instar ($F_{(1,231)} = 3.21, P = 0.0743$) (Table 1).

Percentage survival of the nymphs maintained in the uncontrolled greenhouse with fluctuating temperatures was significantly less than that of the nymphs kept in the climate chamber that simulated the mean hourly temperatures of the uncontrolled greenhouse for the 1st instar ($F_{(1,28)} = 10.64, P = 0.0029$) and consequently the total nymphal period ($F_{(1,28)} = 13.81, P = 0.0009$). The measured survival was not significantly different in the 2nd ($F_{(1,28)} = 0.52, P = 0.4788$), 3rd ($F_{(1,28)} = 3.64, P = 0.0667$), and 4th instars ($F_{(1,28)} = 0.05, P = 0.8312$) between the 2 treatments (Table 1).

The longevity of adults differed significantly between the 2 fluctuating temperature regimes ($F_{(1,228)} = 23.51, P = 0.0001$): the adults kept in the greenhouse were longer-lived (23 d) than those maintained in the climate chamber that simulated the mean hourly temperature in the greenhouse (16 d) (Fig. 2A). The reproductive capacity of *S. flava* was not significantly affected ($F_{(1,228)} = 1.13, P = 0.2894$) when *S. flava* were maintained under the fluctuating conditions of the uncontrolled greenhouse compared with when maintained under the fluctuating hourly

mean temperatures of the climate chamber, and the average numbers of nymphs produced were 37.56 and 34.80, respectively (Fig. 2B).

LIFE HISTORY PARAMETERS OF *SIPHA FLAVA* IN CLIMATIC CHAMBERS SIMULATING MEAN HOURLY GREENHOUSE TEMPERATURES (TRT. #2), OR THE GREENHOUSE MEAN PHOTOPHASE TEMPERATURE (27 °C) AND MEAN SCOTOPHASE TEMPERATURE (18 °C) (TRT. #3), OR THE CONSTANT MEAN OF THE GREENHOUSE TEMPERATURE (22.5 °C) (TRT. #4)

With regard to aphids kept in the climatic chamber simulating the mean hourly temperatures in the greenhouse (Trt. #2), kept at 27 °C (photophase) and 18 °C (scotophase) (Trt. #3), or kept at the constant daily average temperature of the greenhouse (22.5 °C) (Trt. #4), there were no significant differences in the durations of the 1st ($F_{(2,344)} = 2.66, P = 0.0716$), 2nd ($F_{(2,248)} = 1.84, P = 0.1609$), and 4th instars ($F_{(2,196)} = 1.68, P = 0.1895$) and in the total nymphal period ($F_{(2,196)} = 2.54, P = 0.0817$) (Table 2). The duration of the 3rd instar in Trt #2 was significantly reduced ($F_{(2,210)} = 6.84, P = 0.0013$) (Table 2).

Major differences were observed in survival depending on the temperature regime to which the nymphs were subjected. Nymphs kept in the climatic chamber simulating mean hourly temperatures of the uncontrolled greenhouse had significantly greater percentage survival than those kept either at the constant mean greenhouse temperature of 22.5 °C (Trt. #4), or those exposed to the simulated greenhouse mean photophase temperature of 27 °C and mean scotophase temperature of 18 °C (Trt. #3). This was true for 1st instars ($F_{(2,42)} = 14.32, P = 0.0001$), 2nd instars ($F_{(2,42)} = 40.90, P = 0.0001$), and the overall nymphal period ($F_{(2,42)} = 110.34, P = 0.0001$), with lower nymphal survival in the thermal conditions of Trt. #3 (Table 2). In the 3rd instar, there were also significant differences among the treatments ($F_{(2,42)} = 10.93, P = 0.0002$), with the highest survival under fluctuating temperatures in the climate chamber simulating the mean hourly temperatures in the greenhouse compared with the other treatments (Table 2). Only in the 4th instar was no significant difference ($F_{(2,38)} = 1.33, P = 0.2773$) observed between the treatments with constant and fluctuating temperatures (Table 2).

The aphids kept at the constant temperatures (22.5 °C; and 27 °C [photophase]: 18 °C [scotophase]) had significantly reduced longevity ($F_{(2,187)} = 34.80, P = 0.0001$) (Fig. 2C) and reproductive capacity ($F_{(2,187)} = 32.79, P = 0.0001$) (Fig. 2D) compared with those kept in the climatic chamber simulating the mean hourly temperatures in the greenhouse.

Table 1. Duration and survival of *Sipha flava* nymphs subjected to different temperatures in an uncontrolled greenhouse with fluctuating temperatures (Trt. #1) and in a phytotron climate chamber simulating the mean hourly temperatures of the uncontrolled greenhouse (Trt. #2).

Instar	Duration (d)		Survival (%)	
	Trt. #1	Trt. #2	Trt. #1	Trt. #2
1st	3.26 ± 0.06 a n = 120	2.86 ± 0.04 b n = 138	80.00 ± 3.08 b n = 150	92.00 ± 2.00 a n = 150
2nd	2.58 ± 0.005 a n = 114	2.40 ± 0.05 b n = 133	94.68 ± 2.18 a n = 120	96.51 ± 1.31 a n = 138
3rd	2.81 ± 0.04 a n = 109	2.12 ± 0.04 b n = 132	96.09 ± 1.48 a n = 114	99.25 ± 0.74 a n = 133
4th	2.90 ± 0.06 a n = 105	2.74 ± 0.05 a n = 128	96.40 ± 2.12 a n = 109	96.94 ± 1.35 a n = 132
Total nymphal stage	11.51 ± 0.11 a n = 105	10.14 ± 0.09 b n = 128	70.00 ± 3.38 b n = 105	85.33 ± 2.36 a n = 128

Means in compared between Trt. #1 and Trt. #2 followed by the same letter are not significantly different by Tukey's test ($P > 0.05$).

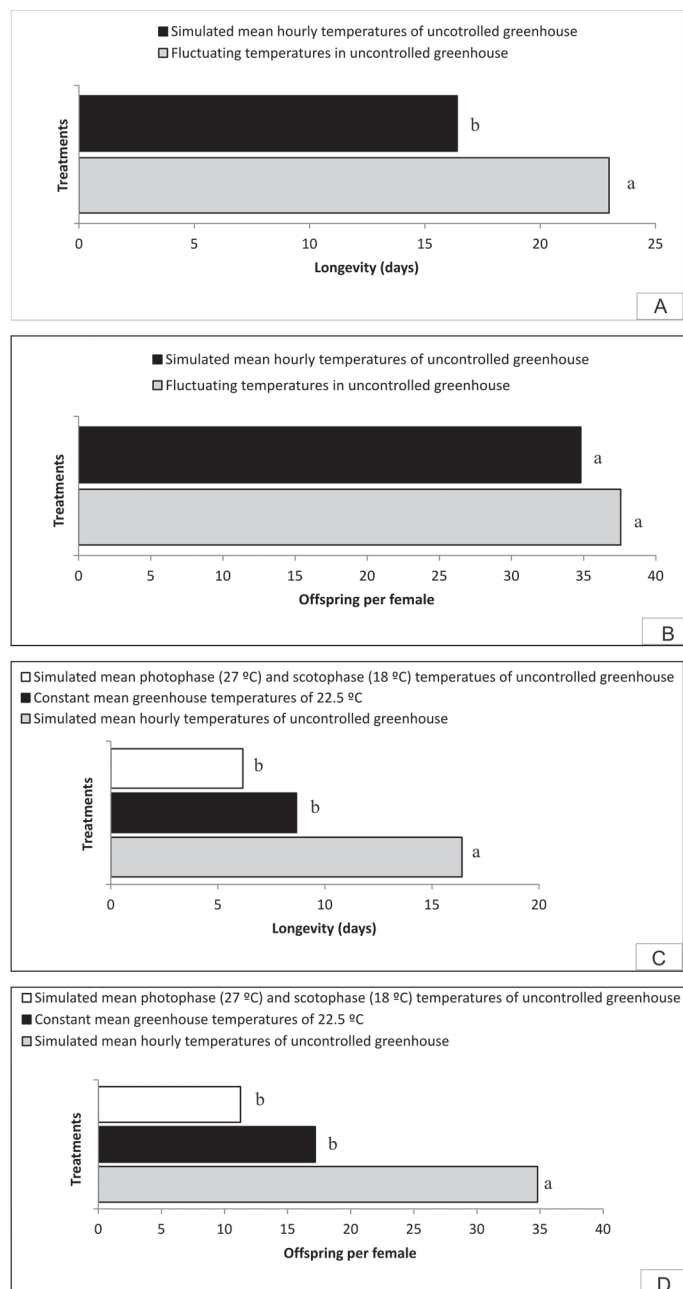


Fig. 2. Effects of either fluctuating or constant temperatures on the longevity (days) and the reproductive capacity (offspring per female) of *Sipha flava*, i.e., **Panel A**, effect on the longevity of *Sipha flava* subjected to Trt. #1 (uncontrolled greenhouse with a fluctuating temperature regime) and Trt #2 (simulated mean hourly temperatures of the greenhouse with a fluctuating temperature regime); **Panel B**, effect on fecundity of *Sipha flava* subjected to the same treatments as in Panel A; **Panel C**, effect on the longevity of *Sipha flava* subjected to Trt #2 (simulated mean hourly temperatures of the greenhouse with a fluctuating temperature regime), Trt #4 (a constant mean temperature of 22.5 °C), Trt #3 (simulated mean temperatures of 27 °C during photophase and 18 °C during scotophase); **Panel D**, effect on fecundity of *Sipha flava* subjected to the same treatments as in Panel C. Mean longevity and fecundity values followed by different lowercase letters are significantly different based on ANOVA followed by the Tukey test.

The average reproductive capacity and average longevity of the insects kept at temperatures depending on the photoperiod (27 °C day/18 °C night) were reduced by approximately 3.1-fold and 2.7-fold, respectively, compared with aphids kept at the simulated mean hourly temperatures of the greenhouse (Figs. 2C and 2D).

Discussion

Understanding the relationship between temperature regimes and life-history parameters of insects is essential for formulating models and for studies of population dynamics. Under natural conditions, insects are exposed to fluctuating cycles of temperature, and the development of such insects can be different from that of insects maintained at constant temperatures (Beck 1983). Some insect species were shown to develop more rapidly under fluctuating temperatures than under constant temperatures when the maximum and minimum values of the fluctuating temperatures were within the optimal range for the development of the organism (Hagstrum & Hagstrum 1970). Therefore, rates of development reported in the literature that are based on one constant temperature or one constant temperature during the photophase and another during the scotophase need to be validated under fluctuating temperatures (greenhouse or field).

In the present study, the development period of *S. flava* was shorter, and conversely the rate of development was faster, when the aphids were subjected to temperatures fluctuating inside the uncontrolled greenhouse (Trt. #1) than when they were maintained in a climate chamber simulating the mean hourly temperatures inside the uncontrolled greenhouse (Trt. #2). Other abiotic factors, i.e., photoperiod and humidity that were constant in the phytotron-type climate chamber, may have affected this result; nevertheless, the observed difference can be attributed largely to the fact that the amplitude of the fluctuating temperatures reached the peak temperatures tolerated by this species only in the environment with fluctuating temperatures that occurred throughout the 24 h cycle. These observations agree with those noted by Mironidis & Savopoulou-Soultani (2008), who mentioned that the development of *Helicoverpa armigera* (Hübner, 1808) (Lepidoptera: Noctuidae) was faster under an alternating thermal regime (mean 25 °C) than in a constant temperature (25 °C). Rock (1985) explained this acceleration based on the hypothesis that alternating temperatures would meet the optimal temperatures of the various components involved (e.g., enzymes) in the physiological processes of insects, favoring insect development. Bahar et al. (2012) found a reduction in the development period of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) kept at fluctuating temperatures compared with the other tested thermal conditions, and they associated the reduction with increased regulation of several proteins that play key roles in energy metabolism and protein degradation.

Sipha flava completed the immature phase regardless of whether it was maintained in an uncontrolled greenhouse with fluctuating temperatures or under simulated mean hourly temperature fluctuations; however, nymphal survival was reduced slightly under the fluctuating temperatures in the greenhouse due to the lower survival of 1st instars. This greater sensitivity of the 1st instar under widely fluctuating temperatures can be explained by its thin soft cuticle, which makes it more vulnerable to environmental factors. The increased cuticle thickness in other stages possibly confers some protection from transient temperature extremes (Omkar & Pervez 2004). This suggests that tolerance of temperature extremes of a species varies greatly with the age of the insect (Bowler & Terblanche 2008). It is noteworthy that although the variations observed in the oscillating temperature of the greenhouse (< 10.4 °C to > 39.5 °C) provided the least survival of the nymphal stage in the present study, yet this survival is considered to be high (70%), thus demonstrating that these insects exhibit plasticity to tolerate natural temperature fluctuations. The reproductive capacity of *S. flava* was the same in the environments with fluctuating temperature in the greenhouse and with simulated mean hourly temperatures, but the adults kept in the greenhouse were longer-lived. This difference may lead to greater overlapping of generations, resulting in more damage to plants.

Table 2. Duration and survival of *Sipha flava* nymphs subjected to different temperatures in a phytotron climate chamber simulating the mean hourly temperatures of an uncontrolled greenhouse (Trt. #2), simulating the mean temperature of the greenhouse during the photophase (27 °C) and the scotophase (18 °C) (Trt. #3), and simulating the overall mean temperature in the greenhouse, which was a constant temperature of 22.5 °C (Trt. #4).

Instar	Duration (d)			Survival (%)		
	Trt. #2	Trt. #3	Trt. #4	Trt. #2	Trt. #3	Trt. #4
1st	2.86 ± 0.04 a n = 138	2.97 ± 0.08 a n = 97	2.75 ± 0.06 a n = 115	92.00 ± 2.00 a n = 150	62.66 ± 5.47 c n = 150	76.66 ± 3.33 b n = 150
2nd	2.40 ± 0.05 a n = 133	2.03 ± 0.07 a n = 44	2.25 ± 0.06 a n = 74	96.51 ± 1.31 a n = 138	46.55 ± 4.34 c n = 94	64.74 ± 5.12 b n = 115
3rd	2.12 ± 0.04 b n = 132	2.53 ± 0.15 a n = 28	2.37 ± 0.10 a n = 53	99.25 ± 0.74 a n = 133	53.33 ± 10.72 b n = 44	73.25 ± 5.48 b n = 74
4th	2.74 ± 0.05 a n = 128	2.50 ± 0.10 a n = 26	2.71 ± 0.06 a n = 45	96.94 ± 1.35 a n = 132	88.63 ± 8.10 a n = 28	86.00 ± 4.47 a n = 53
Total nymphal stage	10.14 ± 0.09 a n = 128	10.46 ± 0.23 a n = 26	9.88 ± 0.15 a n = 45	85.33 ± 2.36 a n = 128	17.33 ± 4.41 c n = 26	30.00 ± 3.23 b n = 45

Means in the rows per parameter followed by the same letter are not significantly different by Tukey's test ($P > 0.05$).

The influence of temperature on insect development is related not only to the daily mean average temperature, but also to the rate of temperature change (Müller & Obermaier 2012). Explanations for this event are related to thermoperiodic stimulation of the neuro-endocrine system, diurnal organization of behaviors and metabolic processes, circadian effects, and optimization of enzyme functioning (Beck 1983; Ratte 1985). Therefore, studies conducted under constant temperatures do not predict what normally occurs with respect to insects exposed to naturally fluctuating temperatures (Lamb 1961; Messenger 1964). When comparing the life history of *S. flava* held under fluctuating temperatures (with other abiotic factors held constant) or held under a constant temperature, we found that the total development period of *S. flava* nymphs was neither influenced by the fluctuating temperatures in an uncontrolled greenhouse, nor by the simulated greenhouse mean photophase temperature of 27 °C and the mean scotophase temperature of 18 °C, nor by the constant mean greenhouse temperature of 22.5 °C. This pattern was also observed for 2nd and 3rd instars of *Uroleucon ambrosiae* (Thomas) (Hemiptera: Aphididae), which, despite being reared in the laboratory (20 °C) or greenhouse (mean 21 °C), required the same amount of time to reach the following stage (Auaud & Moares 2003). Based on studies of 26 insect species available in the literature, Liu et al. (1995) showed that the total development period, or a partial development period (eggs, nymphs or larvae, and pupae) of insects is equal under conditions of variable and constant temperature. This phenomenon was also observed for other insect species, such as *Aglaia urticae* L., *Inachis io* L., *Polygonia c-album* L., and *Vanessa atalanta* L. (Lepidoptera: Nymphalidae) (Bryant et al. 1999). For these insects, it is possible to estimate the development time under natural conditions from the development time under constant temperatures. Likewise, Wang & Tsai (2001) assumed that models of the development period of *Toxoptera aurantii* (Boyer de Fonscolombe, 1841) (Hemiptera: Aphididae) obtained under constant temperatures (7–32 °C) can be used to estimate the development time of this species under natural conditions.

In addition to the development period, other life history parameters of *S. flava*—based on laboratory studies—should be considered in estimating parameters of insect populations in the field. The variations in fluctuating temperature in the climate chamber simulating mean hourly temperatures of an uncontrolled greenhouse increased the percentage survival of *S. flava* compared with the treatment with a simulated greenhouse mean photophase temperature of 27 °C and mean scotophase temperature of 18 °C, and compared with a constant mean greenhouse temperature of 22.5 °C. This species tolerates extremes of temperature fluctuation (Fig. 2). However, it does not tolerate a constant high temper-

ature. Aphids contain bacteria (endosymbionts) that convert sugar into amino acids that are essential for the aphids' survival (Dadd 1985), and in extreme temperatures, the endosymbionts can be eliminated, impairing the production of amino acids (Ohtaka & Ishikawa 1991) and causing aphid mortality (Davis et al. 2006). Furthermore, according to Campbell et al. (1974), high temperatures lead to increased mortality due to denaturation of proteins by metabolic or toxic accumulations, and these harmful effects occur mainly when the temperature is kept constant.

Oliveira et al. (2009) found that the nymphal survival rates of *S. flava* maintained at 28 °C and 32 °C were 22.6% and 20.6 %, respectively. Liu & Meng (2000) found that the aphid *Lipaphis erysimi* (Kaltenbach, 1843) reared at constant temperatures could not develop to adulthood at temperatures outside the interval of 8–35 °C. However, this aphid exhibits significantly different survival rates and development periods in variable temperature regimes that include temperatures <8 °C to > 35 °C for only a part of each day. Nowierski et al. (1983) observed in the field that the survival of the aphid *Chromaphis juglandicola* (Kaltenbach) can be affected by extremes of temperature, either low (spring 6.5 °C) or high (summer 40 °C). However, it is evident that the duration of the period of exposure during which an insect is subjected to extreme temperatures can affect its physiology. In addition, the thermal tolerance of a species is highly variable depending on feeding, body size, and age (Bowler & Terblanche 2008). The low survival of *S. flava* at 27 °C for 12 h suggests that the nymphs of this species are not well adapted to constant high temperatures. At this same temperature, according to Asin & Pons (2001), the aphid *Metopolophium dirhodum* (Walker) does not fully grow. However, nymphal survival rates of 66.5 % and 81.7 % were found for the aphids *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.), respectively, indicating interspecific variation regarding thermal tolerance.

We showed that fluctuating temperatures caused the fecundity of *S. flava* to increase. Davis et al. (2006) found that each female *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) maintained under fluctuating temperatures (25–35 °C, mean 27 °C) produced 12.2 nymphs at the end of a week, whereas under a constant temperature, each female produced only 5.9 nymphs. It is noteworthy that the exposure time to unfavorable temperatures is a crucial factor that affects insect reproduction. Adults of *S. flava* kept at a high constant temperature during a period of the day (27 °C day/18 °C night) showed low reproductive capacity, a phenomenon that was also observed at the constant temperature of 22.5 °C. Such thermal conditions may not be favorable to the development of embryos, and thus, population growth can be delayed in subsequent generations.

According to Ratte (1985), the neuroendocrine system of insects can be stimulated by thermoperiods, which, subsequently, change hormone concentrations that stimulate reproduction.

Considering that the simulated mean hourly temperatures of an uncontrolled greenhouse did not affect the duration of the nymphal stage, but enhanced survival, reproductive capacity, and longevity of adults—which are factors of great importance in insect population growth—one should be cautious when extrapolating results obtained in the laboratory under constant temperatures to predict the population dynamics of *S. flava* in the field.

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