Potential population growth of *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae) under six constant temperatures on grain sorghum (*Sorghum bicolor* L.)

*M. F. Souza*, and *J. A. Davis*†*,*†

---

Abstract

Sugar cane aphid, *Melanaphis sacchari* Zehntner (Hemiptera: Aphididae), is now widely established in sorghum, *Sorghum bicolor* (L.) Moench (Poaceae), production areas of the USA, and is an important economic pest. To calculate economic thresholds, population growth parameters under varied temperature conditions are needed. However, detailed laboratory studies of temperature effects on the biology and population parameters of *M. sacchari* since the sorghum outbreak in the US have not been performed previously. Therefore, this study evaluated the response of *M. sacchari* to 6 different constant temperatures (15, 20, 25, 30, 32, and 35 °C) on sorghum tissue. Aphid development, age-specific survivorship, fecundity, and longevity were compared at the mentioned temperatures. At 20 °C, the reproductive period was longest and total fecundity was greatest. Development time of *M. sacchari* was shortest at 25 and 30 °C. Intrinsic rate of increase was highest at 25 °C (*r* = 0.405 ± 0.030). Net reproductive rate (*R*) was highest at 20 °C, and age-specific survivorship decreased with increasing temperature. At 25 °C, aphid populations doubled in 1.7 d, the shortest among all temperatures tested. Using a modification of the nonlinear Logan model, the lower and upper developmental thresholds of *M. sacchari* were calculated at 8.6 and 37.8 °C, respectively, with the optimum temperature for development occurring at 28.3 °C. Population parameters, together with high minimum and maximum thermal thresholds, indicate that *M. sacchari* is an aphid species adapted to higher temperatures.

Key Words: aphid; population physiology; population dynamics; thermal threshold

---

Resumo

*Melanaphis sacchari* Zehntner (Hemiptera: Aphididae) é uma praga agrícola de importância econômica, que se encontra amplamente distribuída nas áreas produtoras de sorgo, *Sorghum bicolor* (L.) Moench (Poaceae), dos Estados Unidos. A fim de calcular os níveis de danos econômicos, é necessário o conhecimento do crescimento populacional da praga sob diferentes regimes de temperatura. Entretanto, desde a explosão populacional de *M. sacchari* em sorgo nos Estados Unidos, ainda não surgiram estudos para avaliar os efeitos da temperatura nos parâmetros biológicos e de crescimento populacional do pulgão. Assim sendo, esse estudo avaliou as variações no período de desenvolvimento, sobrevivência, fecundidade e longevidade de *M. sacchari* em sorgo sob seis temperaturas constantes (15, 20, 25, 30, 32, e 35 °C). A 20 °C, o período reprodutivo e a maior fecundidade total. O menor período de desenvolvimento de *M. sacchari* foi observado a 25 e 30 °C, e a taxa intrínseca de crescimento populacional foi maior a 25 °C (*r* = 0,405 ± 0,030). O taxa líquida de reprodução (*R*) foi maior a 20 °C e a taxa de sobrevivência por idade foi reduzida com o aumento da temperatura. A 25 °C, a populações de *M. sacchari* em sorgo dobrou em 1,7 d, e a menor entre todas as temperaturas testadas. Usando uma modificação do modelo não linear de Logan, os limiares térmicos inferior e superior de desenvolvimento de *M. sacchari* foram calculados em 8,6 e 37,8 °C, respectivamente, com a temperatura ótima para o desenvolvimento ocorrendo em 28,3 °C. Os parâmetros populacionais, juntamente com altos limiares térmicos mínimos e máximos, indicam que *M. sacchari* é uma espécie de afeito adaptada a altas temperaturas.

Palavras Chave: pulgão; fisiologia de população; dinâmica de população; limiares térmicos

---

Among environmental conditions, temperature is a major influence on insects, affecting development, sex ratio, and longevity (Harrison et al. 1985; Bleicher & Parra 1990; Davis et al. 2006; Keena 2006). Temperature also influences behavioral aspects of insects, such as mating, spatial orientation, and walking speed (Langer et al. 2004; Colinet & Hance 2009). Morphological and physiological plasticity due to temperature changes often are observed through alterations in development time, fecundity, and size. Generally, at lower temperatures, development often is extended, while at higher temperatures, the adult insect is smaller and has a faster development (Atkinson 1994; Angilletta & Dunham 2003; Angilletta et al. 2004; Pigliucci 2005; Sibly et al. 2007).

Alterations in development time and size frequently are related to changes in metabolic rates due to temperature (Kingsolver & Huey 2008; Angilletta 2009). Effects on oxygen consumption, carbon excretion, and respiration rates also can be altered (Neven 1998). Besides metabolic alterations, temperature changes also can affect the nervous and endocrine systems of insects (Neven 2000). Furthermore, temperature affects the plant host, altering food quality for herbivores, which may modify the insect’s response to temperature (Acreman & Dixon 1989).

Among hemipterans, aphids are set apart by their distinct life cycle of alternating asexual and sexual reproduction. When com-
pared to other insect groups, aphids exhibit a much greater phenotypic plasticity due to environmental effects. Temperature plays an important role in aphid life history, influencing development rate, size, fecundity, polymorphism, mating, and migration (Lees 1963; Dixon & Glen 1971; Dixon 1972; Leather & Dixon 1982; Liu 1994; Dixon 2000; Collins & Leather 2001; Müller et al. 2001). Aphids exhibit a high level of phenotypic plasticity (changes in morphology or physiology in response to an environmental condition). Consequently, analysis of growth, development rates, and fecundity of individual aphids have been reliable tools to predict aphid population dynamics under different conditions (Leather & Dixon 1984; Acreman & Dixon 1989; Dixon 1990, 2000).

The sugarcane aphid, Melanaphis sacchari Zehntner (Hemiptera: Aphididae), historically has been an important sugar cane (Saccharum officinarum L.; Poaceae) pest in the US, vectoring sugar cane yellow leaf virus (Schenck & Lehrer 2000; Singh et al. 2004). However, in 2013, outbreaks of M. sacchari on sorghum were reported in Texas, Louisiana, Oklahoma, and Mississippi (Villanueva et al. 2014; Bowling et al. 2016). In 2014, M. sacchari tripled its range, reaching 12 sorghum-producing states with infestation occurring early in the crop season. In 2015, all of the 17 states producing sorghum in the US reported major infestations of M. sacchari (Villanueva et al. 2014; Kerns et al. 2015; Bowling et al. 2016). In Louisiana and Texas, aphid populations can reach over 900 aphids per leaf with yield declines of 60 to 100%, requiring up to 4 insecticide applications to control M. sacchari infestations (Brewer et al. 2017).

By genotyping with 52 microsatellite makers, Harris-Shultz et al. (2017) showed that this outbreak is associated with 1 clonal lineage. Subsequently, Nibouche et al. (2018) confirmed that the outbreak is associated mainly with 1 M. sacchari genotype, and that this genotype was not present in the US prior to the outbreaks. During the sexual phase, aphids produce several clones that will thrive in different environments (Douglas & van Emden 2007). A superclone arises when 1 of these clones becomes widespread in different environments in a high frequency and over time (Vorburger et al. 2003; Chen et al. 2013; Harrison & Mondor 2011). Because of this sorghum-associated M. sacchari clone’s extensive distribution and high frequency in the US, it can be classified as a superclone, and it is expected to show differential fitness responses across distinct temperatures ranges (Vorburger et al. 2003; Harrison & Mondor 2011; Chen et al. 2013). Studies on the M. sacchari response to temperature changes are inconclusive. Previous work in Asia with M. sacchari indicated that temperatures over 20 °C decreased longevity and fecundity while increasing mortality (van Rensburg 1973a; Chang et al. 1982; Kawada 1995; Abe et al. 2011). However, the M. sacchari intrinsic rate of increase (rI) is known to increase with rising temperatures (Abe et al. 2011), and M. sacchari populations build up faster in summer than in winter, when an individual female can produce up to 96 nymphs (Chang et al. 1982), resulting in infestations of up to 30,000 aphids per plant (van Rensburg 1973b). In a study after the sorghum outbreaks in the USA, Michaud et al. (2017) observed that M. sacchari on sorghum plants took 5 to 6 d to develop at 23 °C.

Although it is known that temperature affects M. sacchari population growth, specific studies detailing the effect of temperature on a colony collected after the current outbreaks in the US has not been conducted. In addition, before economic thresholds can be developed, information on population growth under simulated field conditions is needed. Therefore, the objective of this study was to study development of M. sacchari population dynamics on sorghum under 6 constant temperatures to estimate upper and lower developmental thresholds and optimum developmental temperature.

### Materials and Methods

#### Aphid Colony

The sugarcane aphid colony used in these experiments was found from a single apterae collected from a sorghum field at the Louisiana State Agricultural Center Dean Lee Research Station, Alexandria, Louisiana, USA, in Jul 2014 by J. A. Davis. This colony, designated LSU-SCA14, was maintained on Pioneer 85GB58 (Pioneer Hi-Bred International, Inc., Johnston, Iowa, USA) planted in 10 cm diam plastic pots containing sterile potting mix (Sun Gro Horticulture, Elma, Manitoba, Canada) and 5 g Osmocote (14-14-14), a slow-release fertilizer (The Scotts Company, Marysville, Ohio, USA). Plants were grown in a Percival E-36L2 Plant Growth Chamber (Percival Scientific, Perry, Iowa, USA) held at 25 ± 0.2 °C, 50 ± 5% RH, and a photoperiod of 14:10 h (L:D).

#### Host Plants

Determination of thermal requirements for the sugarcane aphid was performed on Sorghum bicolor (L.) Moench (Poaceae) variety ‘Pioneer 85GBS’. Plants were planted in plastic pots (11.4 × 15.2 × 15.2 cm) (Model Plastic Nursery Pots Azalea Style, Pöppelmann TEKU®, Claremont, North Carolina, USA) using commercial organic soil for seedlings (Miracle-Gro Organic Choice Garden Soil, Marysville, Ohio, USA) supplemented with 5 g Osmocote (14-14-14). Pots were maintained in the greenhouse at 22 to 28 °C under natural lighting from May to Oct. When the plants were 4 to 6 wk old, leaves were excised and used in the experiment.

#### Life Table Experiments on Excised Leaves

The study was conducted at 6 constant temperatures (15, 20, 25, 30, 32, and 35 °C) in climate regulated chambers (Model I-41VL, Percival Scientific, Perry, Iowa, USA) using sorghum excised leaves following procedures by van Schelt (1994) outlined in van Lenteren et al. (2003) and adapted by Sampao et al. (2001). Temperature inside the chambers were monitored per hr using a miniature data logger (Model HOBO Pendant, Onset Computer Corporation, Bourne, Massachusetts, USA).

Leaf sections of approximately 2 × 3 cm were placed in 30 mL Solo cups (Dart Container Corporation, Mason, Michigan, USA) filled with 15 mL of a 0.1% agarose (w/v) (RM301-500G Agar Powder Extra Pure, HiMedia, Einhausen, Germany). In each cup, 1 leaf section was placed on the surface of the agarose with the abaxial surface upward, and was replaced every 4 d for the lower temperatures of 15 and 20 °C, every 3 d at 25 °C, and every 2 d at 30, 32, and 35 °C. This method avoided dehydration of the leaves and prevented aphids from escaping from the leaf sections. A single apterous adult was placed on the leaf section using a hair paintbrush (21 × 3 × 2 cm) (Arteza Model ARTZ-8009, Wilmington, Delaware, USA), and allowed to reproduce for 24 h. The adult aphid was then removed, leaving only 1 nymph per leaf section. Fifty single first instar nymphs were held at the same time in each temperature, constituting a cohort. The cohort for each temperature regimen was replicated in 3 separate experiments. The cohort was evaluated every 24 hr until death. Development time, survivorship, fecundity, and longevity were recorded and measured.

Age-specific survival (l') and fecundity (m') were calculated for each temperature. Net reproductive rate, R0 defined as the product of age-specific survival and age-specific fecundity, was calculated using the formula $R_0 = \Sigma l' \\times m'$, where $l'$ is the proportion of females alive on a given d, and $m'$ is the mean number of female births on that d. The intrinsic rate of increase, $r^*_e = \lim_{d \to \infty} l' \times m' = 1$, finite rate of increase ($\lambda = e^{r^*_e}$), mean
generation time \( [T_r = \ln R/r_r] \), and doubling time (DT = ln(2)/r_r) of a generation were estimated according to Birch (1948). Jackknife procedure was used to estimate \( r_r \) standard error. This procedure is based on recombining the original data and calculating pseudo-values of \( r_r \) for each recombination of the original data, and estimating the mean value and standard error of \( r_r \) from the resulting frequency distribution of pseudo-values in accordance with Meyer et al. (1986).

### Statistical Analysis

The biological variables (longevity, development time, nymphs per female, reproductive period, and nymphs per female per d) and the population estimation variables (mean generation time, net reproductive rate, doubling time, and finite rate of increase) were analyzed as randomized block design experiment. PROC MIXED procedures in SAS (SAS Version 9.4, SAS Institute, Cary, North Carolina, USA) were used for all datasets. Analysis of variance tests were used to detect presence of differences among treatments for each variable, and Tukey-Kramer analysis at 0.05% of significance allowed us to compare the least square mean of differences among treatments for each variable. Age-specific survival graphs were plotted using SigmaPlot (SigmaPlot Version 14.0, Systat Software Inc., San Jose, California, USA).

Temperature-dependent thresholds under constant temperature regimes were estimated using a Logan model (Logan et al. 1976) as modified by Lactin et al. (1995), as seen below:

\[
r(T) = e^{\rho T} \cdot e^{\lambda(T - T_{\text{max}})} + \Lambda
\]

Where \( r(T) \) is the mean developmental rate at temperature \( T \) (°C). Fitted parameters \( \rho \) (rate of increase at optimal temperature), \( T_{\text{max}} \) (upper developmental threshold), \( \Delta \) (difference between optimal and upper developmental threshold), and \( \lambda \) (which allows the curve to intercept the x-axis), were estimated using Marquardt’s method on PROC NLIN (SAS Version 9.4, SAS Institute, Cary, North Carolina, USA).

The average temperatures per mo from 2002 to 2017 for each continental location in the US were obtained upon special request from the National Oceanic and Atmospheric Administration (NOAA 2017). The average temperature per mo for 15 years was then calculated for each state.

### Results

#### Life Table Analysis

Temperature affected \( M. \ sacchari \) development time \( (F = 510.12; P < 0.0001) \). \( M. \ sacchari \) reached adulthood faster when it was reared at both 25 and 30 °C (Table 1). Development time decreased by 4.4 d when the temperature increased from 15 °C (12.2 d) to 20 °C (7.8 d) \( (F = 19.48; df = 5, 149; P < 0.0001) \), and decreased by 3.1 d when the temperature increased again from 20 °C (7.8 d) to 25 °C (4.8 d) \( (F = 28.63; P < 0.0001) \). Differences were not detected in development time when the temperature increased from 25 to 30 °C (4.8 d); however, at 32 °C (5.9 d) the development time increased by approximately 1 d \( (F = 10.15; P < 0.0001) \). The aphid was not able to complete development at a constant 35 °C.

The amount of time in which the female remained reproductively active (reproductive period) was affected by temperature \( (F = 152.15; P < 0.0001) \) (Table 1). The longest reproductive period, 18.8 and 15.3 d, occurred at 15 and 20 °C, respectively. Raising the temperature to 25 °C decreased reproductive activity to 8.9 d \( (F = 6.63; P < 0.0001) \). Females reduced their reproductive period to 1.5 d at 30 °C \( (F = 12.29; P < 0.0001) \); however, differences were not detected in the reproductive period when temperature increased from 30 to 32 °C. Likewise, temperature treatments affected fertility of \( M. \ sacchari \) females \( (F = 172.15; P < 0.0001) \) (Table 1). The greatest production of nymphs per female was at 20 °C; females produced an average of 49.8 nymphs, ranging from 4.0 to 111.0 nymphs per female. High fecundity rates also occurred at 15 and 25 °C, with 36.4 and 40.0 nymphs per female, respectively. Increasing the temperature to 30 °C caused a decrease \( (F = 13.94; P < 0.0001) \) in nymph production per female. At 30 °C and 32 °C, females had the lowest nymph production of 4.1 and 5.1 nymphs produced per female, respectively, and at these temperatures, many females reached adulthood but did not produce any nymphs.

The average lifespan from d 1 until death (longevity) was affected by temperature, and decreased with increasing temperature \( (F = 250.02; P < 0.0001) \) (Table 1). The longest \( M. \ sacchari \) longevity was achieved at 15 °C with insects living for 32.3 d on average, and the shortest longevity was observed at 35 °C with insects living only for an average of 2.8 d.

Age-specific survivorship \( (lx) \) decreased linearly with the increase in temperature (Fig. 1). At 15 °C, the greatest age-specific survivorship was observed at 75 d. Observations up to 53 d at 20 °C, and up to 31 d at 25 °C were recorded. Even at the highest constant temperatures of 30 and 32 °C, aphids could survive for approximately 20 d, but at 35 °C, only a few individuals survived until d 10. Survival started to diminish after d 7 at a temperature of 20 °C, at d 4 at 25 °C, and at d 2 at the other temperatures (Fig. 1).

The highest net reproduction rate of 50.4 occurred at 20 °C (Table 2). At 15 and 25 °C, the \( R_n \) values were 31.1 and 34.0, respectively, and the lowest \( R_n \) values of 3.6 and 4.5 were found at 30 and 32 °C, respectively. The intrinsic rate of increase was highest at 25 °C (0.405 ± 0.030), indicating that population increases fastest at this temperature, while aphids kept at the colder temperatures had lower \( r_r \) (Table 2). The finite rate of increase \( (\lambda) \) was highest at 25 °C at 1.5 nymphs per female per d. The maximum and minimum population doubling times (DT) were 5.6 at 30 °C and 1.7 d at 25 °C (Table 2).

### Table 1. Mean (± SD) development time (d), reproductive period (d), nymphs per female and longevity (d) of \( M. \ sacchari \) collected on sorghum under constant 15, 20, 25, 30, and 32 °C on grain sorghum.

| Temperature (°C) | n   | Development time (d) | Reproductive period (d) | Nymphs per female | Longevity (d) |
|------------------|-----|----------------------|-------------------------|-------------------|---------------|
| 15               | 150 | 12.2 ± 0.2 a         | 18.8 ± 1.2 a            | 36.4 ± 2.4 b      | 32.3 ± 1.5 a  |
| 20               | 150 | 7.8 ± 0.1 b          | 15.3 ± 0.9 a            | 49.8 ± 2.8 a      | 25.8 ± 1.1 b  |
| 25               | 150 | 4.8 ± 0.1 d          | 8.9 ± 0.6 b             | 40.0 ± 2.6 b      | 15.8 ± 0.7 c  |
| 30               | 150 | 4.8 ± 0.1 d          | 1.5 ± 0.4 c             | 4.0 ± 1.4 c       | 6.5 ± 0.4 d   |
| 32               | 150 | 5.9 ± 0.1 c          | 1.8 ± 0.3 c             | 5.1 ± 1.3 c       | 5.8 ± 0.5 d   |
| 35               | 150 | —                    | —                       | —                 | 2.8 ± 0.3 e   |

Means in a column followed by different lowercase letters are significantly different \( (P < 0.05; \) ANOVA and Tukey-Kramer test).
When we fitted the observed data in the Logan Lactin-modified model (Lactin et al. 1995), the lower developmental threshold for *M. sacchari* development was 8.6 °C, and the maximum developmental threshold was 37.8 °C, with an optimum development rate at 28.3 °C (Table 3, Fig. 2).

Based on *M. sacchari* lower thermal requirements, shaded areas in Table 4 represent the mo in which *M. sacchari* would be actively developing for each state. In Florida and Louisiana, *M. sacchari* populations are constantly developing over the yr, meaning that regardless of the rate, nymphs are developing to adults and reproducing. In Mississippi, Georgia, and Texas, *M. sacchari* development is ceased only in the mo of Jan when temperatures are below the 8.6 °C development thresh-old. Contrarily, in Idaho, Maine, Minnesota, Montana, New Hampshire, North Dakota, Wisconsin, and Wyoming, *M. sacchari* have only 5 mo, from May through Sep, in which the average temperature allows active development.

**Discussion**

The lower developmental threshold of 8.6 °C for *M. sacchari* and the upper developmental threshold of 37.8 °C observed in the present study are higher than the threshold for most aphid species. Even though lower developmental thresholds of different aphid species can vary from

---

**Table 2.** Intrinsic rate of increase ($r_m$), net reproductive rate ($R_0$) (nymphs per female), mean generation time (d), doubling time (d), and finite rate of increase (nymphs per female per d) of *Melanaphis sacchari* under constant temperatures on grain sorghum.

| Temperature (°C) | n  | $r_m$ ± SE   | Net reproductive rate | Mean generation time | Doubling time | Finite rate of increase |
|-----------------|----|--------------|-----------------------|----------------------|--------------|------------------------|
| 15              | 150| 0.197 ± 0.006 | 31.1 ± 0.2            | 17.4 ± 0.5           | 3.5 ± 0.1    | 1.2 ± 0.1              |
| 20              | 150| 0.274 ± 0.013 | 50.4 ± 0.7            | 14.3 ± 0.4           | 2.5 ± 0.1    | 1.3 ± 0.1              |
| 25              | 150| 0.405 ± 0.030 | 34.0 ± 0.6            | 8.7 ± 0.3            | 1.7 ± 0.1    | 1.5 ± 0.1              |
| 30              | 150| 0.124 ± 0.017 | 3.6 ± 0.7             | 10.3 ± 0.3           | 5.6 ± 0.8    | 1.1 ± 0.1              |
| 32              | 150| 0.197 ± 0.017 | 4.5 ± 0.5             | 7.6 ± 0.3            | 3.5 ± 0.3    | 1.2 ± 0.1              |
3.6 °C (Carter et al. 1982; Zhou et al. 1989) to 11.8 °C (Bayhan et al. 2005), lower developmental thresholds above 7.0 °C are not common in the literature. High lower development thresholds like our results are unusual among aphids that colonize sorghum. *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) exhibits above average thermal thresholds (Asin & Pons 2001; Ma & Ma 2007); however its lower development threshold does not reach 7.0 °C (Elliot & Kieckhefer 1989; Auad et al. 2009; Park et al. 2017) with an optimum temperature for development between 25 °C and 28 °C (Dean 1974; Asin & Pons 2001), and upper development threshold < 30 °C (Dean 1974; Elliot and Kieckhefer 1989; Asin & Pons 2001; Auad et al. 2009). Under 7 constant temperatures ranging from 10 to 33 °C, *Sipha flava* Forbes (Hemiptera: Aphididae) and *Schizaphis graminum* Rondani (Hemiptera: Aphididae) (aphids which can infest sorghum) showed lower thermal thresholds of 2.1 °C and 5.7 °C, respectively, with an optimum temperature for development between 20 °C and 26 °C (Oliveira et al. 2009; Tofangsazi et al. 2010).

In the literature, we could not find developmental thresholds for *M. sacchari* on any of its host plants to make related comparisons. Our developmental threshold data indicate a great tolerance of *M. sacchari* to elevated temperatures; however, the metabolic and morphological features that allow this species to have optimum development above 25 °C are not clear, but heat shock proteins may be an important component of this condition.

Heat shock proteins act as chaperones and prevent protein denaturation under heat stress (Okada et al. 2014; King & MacRae 2015), and species-specific production of heat shock proteins have been reported (Sharma et al. 2007; Wang et al. 2013; Li et al. 2017). For *R. padi*, heat shock proteins were induced when the aphid was exposed to temperatures ranging from 36 to 38 °C, indicating that for this species, heat shock proteins are an important component in heat tolerance (Li et al. 2017).

While most aphid species start to suffer in temperatures above 25 °C, *M. sacchari* had faster development at 25 and 30 °C and higher upper developmental thresholds. Symbionts, such as *Serratia symbiotica* Sabri et al. (Enterobacteriaceae), are thought to increase aphid heat tolerance (Montlort et al. 2002; Russell & Moran 2006; Heyworth & Ferrari 2015) through nutritional compensation when heat impairs heat tolerance (Montlort et al. 2002; Russell & Moran 2006).

**Table 3.** Estimated parameters of Lactin model for constant temperature regimes: $\rho =$ rate of increase at optimal temperature, $T_{\text{max}} =$ upper developmental threshold, $\Delta =$ difference between optimal and upper developmental threshold, and $\lambda =$ value that allows the curve to intercept x-axis.

| Model   | $\rho$     | SE        | $T_{\text{max}}$ | SE        | $\Delta$ | SE        | $\lambda$ | SE        |
|---------|------------|-----------|------------------|-----------|----------|-----------|-----------|-----------|
| Constant | 0.01081    | ± 0.00035 | 37.808           | ± 0.517   | 2.506    | ± 0.242   | −1.097    | ± 0.007   |

*Buchnera aphidicola* Munson et al. (Enterobacteriaceae) (Koga et al. 2003; Russell & Moran 2006). Secondary endosymbionts conferring heat tolerance are in aphids more frequently found in tropical areas (Henry et al. 2013). Currently, there are no reports of the secondary endosymbionts harbored by *M. sacchari*.

Development, survivorship, growth, and fecundity of individual aphids can predict population trends (Leather & Dixon 1984; Acreman & Dixon 1989; Dixon 2000), and this has been used to predict population growth in diverse environmental conditions (Zuniga et al. 1985; Sumner et al. 1986; Warrington et al. 1987; Fereres et al. 1989). The intrinsic rate of increase observed in *M. sacchari* on sorghum corroborates previous reports of a greater *M. sacchari* population increase during hotter periods (van Resburg 1973a, b; Chang et al. 1982; Kawada 1995). Lopes-da-Silva et al. (2014) found an intrinsic rate of increase of *M. sacchari* on sorghum at 24 °C of 0.30, a much smaller value than the present study found at 25 °C (0.405). We found that $r_n$ doubled when the temperature increased from 15 to 25 °C, and the same rate was observed for *M. sacchari* on sorghum by Abe et al. (2011). However, Abe et al. (2011) observed that the $r_n$ increased from 0.390 at 25 °C to 0.450 under 30 °C, whereas in the present study the $r_n$ decreased from 0.405 to 0.124 when the temperature increased from 25 to 30 °C. At 24 °C, *M. sacchari* $R$ was 27.70 (Lopes-da-Silva et al. 2014), while in the present study, *M. sacchari* population growth from 1 generation to the next was nearly 6 times higher at 25 °C. These markedly different biological responses under similar temperature conditions may be part of the explanation for the recent *M. sacchari* sorghum outbreaks in the US.

The findings of this study reveal key aspects of *M. sacchari* under different temperatures that have not been investigated before, and may shed some light on the recent outbreaks in the US. Even though this study was not designed to understand the mechanisms of *M. sacchari* responses to different temperatures, the hypotheses raised here give perspective for future studies. Although laboratory conditions of low densities and constant temperature are not consistent with field conditions, a laboratory study can provide valuable information about life history and population dynamics, because comparisons of $r_n$ are the most reliable way to predict population performance under different conditions. In addition, to estimate economic thresholds, the observations made in the present study are essential.

Therefore, these findings will assist in planning control measures. For instance, using the mo average for the past 15 yr (NOAA 2017) and *M. sacchari* lower developmental threshold, we suggest that monitoring of remnant sorghum (patches of sorghum that survived winter) in Florida, Georgia, Louisiana, Mississippi, and Texas has to start before the crop season, because *M. sacchari* population did not stop developing during winter, or stopped only for a brief period on far northern areas of states with an extensive latitude, such as Georgia and Texas. In addition, because populations have been in constant development, colonization pressure of sorghum fields is expected to be higher in these states. In the states where *M. sacchari* has a narrower window of development, monitoring frequency can be reduced, which in turn decreases production costs from scouting. Thus, the use of *M. sacchari* thermal thresholds to adjust the monitoring frequency of sorghum fields according to actual climate conditions reduces production costs and prevents unexpected outbreaks.
**Acknowledgments**

We acknowledge the financial support to Monique Ferreira de Souza from the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES). This study was also partially funded by the Louisiana Soybean and Grain Promotion Board, and the Louisiana State University Agricultural Center. This article was approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript No. 2018-234-32038.

---

**References Cited**

Abe J, Mitsunaga T, Kumakura H, Yano E. 2011. Comparative studies on development and reproduction of four cereal aphid species reared on sorghum or barley to evaluate as alternative prey for banker plant system. Japanese Journal of Applied Entomology and Zoology 55: 227–239.

Acreman SJ, Dixon AFG. 1989. The effects of temperature and host quality on the rate of increase of the grain aphid (*Sitobion avenae*) on wheat. Annals of Applied Biology 115: 3–9.

Angilletta MJ. 2009. Looking for answers to questions about heat stress: researchers are getting warmer. Functional Ecology 23: 231–232.
Angilletta MJ, Dunham AE. 2003. The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. American Naturalist 342: 332–342.

Angilletta MJ, Steury TD, Sears MW. 2004. Temperature, growth rate, and body size in ectotherms: wetting pieces of a life-history puzzle. Integrative and Comparative Biology 44: 498–509.

Asin L, Pons X. 2001. Effect of high temperature on the growth and reproduction of corn aphids (Homoptera: Aphididae) and implications for their popula- tion dynamics on the Northeastern Iberian Peninsula. Environmental Ento- mology 30: 1127–1134.

Atkinson D. 1994. Temperature and organism size: a biological law for ecto- therm? Advances in Ecological Research 25: 1–58.

Auad AM, Alves SO, Carvalho CA, Silva DM, Resende TT, Verissimo BA. 2009. The impact of temperature on biological aspects and life table of R hapalosiphum padi (Hemiptera: Aphididae) fed with signal grass. Florida Entomologist 92: 569–577.

Bayhan E, Olmez-Bayhan S, Ulusoy MR, Brown JK. 2005. Effect of temperature on the biology of Aphis punicae (Passerini) (Homoptera: Aphididae) on pomegranate. Environmental Entomology 34: 22–26.

Birch LC. 1948. The intrinsic rate of natural increase of an insect population. Journal of Animal Ecology 17: 15–20.

Bleicher E, Parra JRP. 1990. Species of Trichogramma parasitoid of Alabama ar- gilacea. iii. Determination of thermal requirement of three strains. Brazilian Agricultural Research 25: 215–219.

Bowling RD, Brewer MJ, Kerns DL, Goryd J, Seiter N, Elliott NE, Buntin GD, Way MO, Royer TA, Biles S, Maxson E. 2016. Sugarcane aphid (Hemiptera: Aphi- didae) fosters new sorghum in North America. Journal of Integrated Pest Management 12: 1–13.

Brewer MJ, Goryd JW, Kerns DL, Woolley JB, Rooney WL, Bowling RD. 2017. Sugarcane aphid population growth, plant injury, and natural enemies on selected grain sorghum hybrids in Texas and Louisiana. Journal of Economic Entomology 6: 2109–2118.

Carver N, Snen-AFG, Rabbringe R. 1982. Cereal Aphid Populations: Biology, Simula- tion and Prediction. PUDOC, Wageningen, Netherlands.

Chang CP, Fang MN, Tseng HY. 1982. Studies on the life history and varietal re- sistance in grain sorghum aphid, Melanaphis sacchari Zehntner in central Taiwan. Chinese Journal of Entomology 2: 70–81.

Chen Y, Vanlerberghe-Masutti F, Wilson LJ, Barchia I, Mcloon MO, Smith T, Her- ran GA. 2013. Evidence of superclones in Australian cotton aphis Aphis gossypii Glover (Aphididae: Hemiptera). Pest Management Science 69: 938–948.

Colinet H, Hance T. 2009. Male reproductive potential of Aphiidus colemani (Hymenoptera: Aphididae) exposed to constant or fluctuating thermal regi- mens. Environmental Entomology 1: 242–249.

Collins CM, Leather SR. 2001. Effect of temperature on fecundity and develop- ment of the giant winged aphis, Tuberculaphis salignus (Sternorrhyncha: Aphididae). European Journal of Entomology 98: 177–182.

Davis JA, Radcliffe EB, Ragsdale DW. 2006. Effects of high and fluctuating tem- peratures on immature development and age-specific life tables of R hapalosiphum padi (L.) (Homoptera: Aphididae). The Canadian Entomologist 123: 131–140.

Douglas AE, HF van Emden. 2007. Nutrition and symbiosis, pp. 115–134 in Van Emden HF, Harrington R [eds.]. Aphids as Crop Pests. CAB International, Wallingford, United Kingdom. 15–26.

Elliott NC, Kieckhefer RW. 1989. Effects of constant and fluctuating tempera- tures on immature development and age-specific life tables of R hapalosiphum padi (L.) (Homoptera: Aphididae). Molecular & Integrative Physiology 31: 48–57.

Fereres A, Lister RM, Araya JE, Foster JE. 1989. Development and reproduction of the English grain aphid (Homoptera: Aphididae) on wheat cultivars infection with barley yellow dwarf virus. Environmental Entomology 18: 288–293.

Ferreres A, Lister RM, Araya JE, Foster JE. 1989. Development and reproduction of the English grain aphid (Homoptera: Aphididae) on wheat cultivars infection with barley yellow dwarf virus. Environmental Entomology 18: 288–293.

Harrison JS, Mondor EB. 2011. Evidence for an invasive aphis "superclone": extremely low genetic diversity in oleander aphid (Aphis nerii) populations in the southern United States. PLoS ONE 6: e17524. doi: 10.1371/journal. pone.0017524

Harrison WW, King EG, Outz JD. 1985. Development of Trichogramma exiguum and T. pretiosum at five temperature regimes. Environmental Entomology 14: 118–121.

Henry LM, Peccoud J, Simon JC, Haddfeld JD, Maiden MJ, Ferrari I, Godfray HC. 2013. Horizontally transmitted symbions and host colonization of eco- logical niches. Current Biology 23: 1713–1717.

Heyworth ER, Ferrari JA. 2015. A facultative endosymbiont in aphids can provide diverse ecological benefits. Journal of Evolutionary Biology 28: 1753–1760.

Hills MD, Seiter N, Oszustowicz SD, Kerns D, Brown S, Beuzelin J, Guidry KM. 2015. Sugarcane aphid: a new invasive pest of sorghum. Louisiana Agriculture 58: 12–14.

Jiang AM, MacRae TH. 2015. Insect heat shock proteins during stress and dia- pause. Annual Review of Entomology 60: 59–75.

Kingsolver JG, Huey RB. 2008. Size, temperature, and fitness: three rules. Evolu- tionary Ecology Research 10: 1–18.

Koga R, Tsuchida T, Fukatsu T. 2003. Changing partners in an obligate symbiosis: a facultative endosymbiotic can compensate for loss of the essential endo- symbiont Buchnera in an aphid. Proceedings of the Royal Society of London B: Biological Sciences 270: 2543–2550.

Lactin DJ, Holliday NJ, Johnson DL, Craigen R. 1995. Improved rate model of temperature-dependent development by arthropods. Environmental Ento- mology 24: 68–75.

Langer A, Boivin G, Hance T. 2004. Oviposition, flight and walking capacity at low temperatures of four aphid parasitoid species (Hymenoptera: Aphidiidae). European Journal of Entomology 101: 473–480.

Leather SR, Dixon AFG. 1982. Secondary host preferences and reproductive ac- tivity of the bird cherry oat aphis, R hapalosiphum padi. Annals of Applied Biology 101: 219–228.

Leather SR, Dixon AFG. 1984. Aphid growth and reproductive rates. Entomolo- gia Experimentalis et Applicata 35: 137–140.

Lefebvre MP, Kieckhefer RW. 1997. Effect of fluctuating and constant tempera- tures on immature development and age-specific life tables of the aphid Megoura viciae Buckton – III. Further properties of the maternal switching mechanism in aper- tous aphis. Journal of Insect Physiology 9: 153–164.

Li Y, Zhao Q, Duan X, Song C, Chen M. 2017. Transcription of four R hapalosiphum padi (L.) heat shock protein genes and their responses to heat stress and ginseng extract. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 31: 48–57.

Liu SS. 1994. Production of alatae in response to low temperature in aphis: a trait of seasonal adaptation, pp. 245–261 in Banks HV [ed.], Insect Life-cycle Polymorphism. Kluwer, Dordrecht, Netherlands.

Logan JA, Wolkind DJ, Hoyt SC, Tanigoshi LK. 1976. An analytic model for de- scription of temperature dependent rate phenomena in arthropods. Envi- ronmental Entomology 5: 1133–1140.

Lopes-da-Silva M, Rocha DA, da Silva KT. 2014. Potential population growth of Melanaphis sacchari (Zehntner) reared on sugarcane and sweet sorghum. Current Agricultural Science and Technology 20: 21–25.

Ma G, Ma CS. 2007. Upper critical temperatures for behaviors of three spe- cies of cereal aphis in leaf temperature gradients. Acta Ecologica Sinica 27: 2449–2459.

Meyer JS, Ingersoll CG, McDonald LL, Boyce MS. 1986. Estimating the uncer- tainty in population growth rates jackknife vs bootstrap techniques. Ecology 67: 1156–1166.

Michaud JP, Zhang Y, Bain C. 2017. Feeding by Melanaphis sacchari (Hemiptera: Aphi- didae) facilitates use of sorghum by R hapalosiphum padi (Hemiptera: Aphi- didae), but reciprocal effects are negative. Environmental Entomology 46: 268–273.

Monteiro CB, Maxmen A, Purcell AH. 2002. Facultative bacterial endosymbions benefit pea aphis Acrystosiphon pisum under heat stress. Ecological Ento- mology 27: 189–195.

Müller CB, Williams IS, Hardie J. 2001. The role of nutrition, crowding and inter- specific interactions in the development of winged aphis. Ecological Ento- mology 26: 330–340.

Neven LG. 1998. Respiratory response of fifth instar codling moth to rapidly changing temperatures. Journal of Economic Entomology 91: 502–508.

Neven LG. 2000. Physiological responses of insects to heat. Postharvest Biology and Technology 31: 103–111.
Oliveira SA, Souza B, Auad AM, Silva DM, Souza LS, Carvalho CA. 2009. Development of a superclonal PloS ONE 13: 1–15.

NOAA — National Oceanic and Atmospheric Administration. 2017. National Centers for Environmental Information, Climate at a Glance: U.S. 2017. http://www.ncdc.noaa.gov/cag/ (Time Series, Average Temperature, retrieved Sep 2017) (last accessed 14 Jul 2019).

Okada Y, Teramura K, Takahashi KH. 2014. Heat shock proteins mediate trade-offs between early-life reproduction and late survival in Drosophila melanogaster. Physiological Entomology 39: 304–312.

Oliveira SA, Souza B, Auad AM, Silva DM, Souza LS, Carvalho CA. 2009. Development and reproduction of Sipha flavo (Forbes) (Hemiptera: Aphididae) at different temperatures. Neotropical Entomology 38: 70–80.

Park CG, Choi BR, Cho JY, Ahn JI. 2017. Thermal effects on the fecundity and life table parameters of Rhopalosiphum padi (Linnaeus) (Hemiptera: Aphididae) on barley. Journal of Asia-Pacific Entomology 20: 767–775.

Pigliucci M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends in Ecology & Evolution 20: 481–486.

Russell JA, Moran NA. 2006. Costs and benefits of symbiont infection in aphids: variation among symbionts and across temperatures. Proceedings of the Royal Society of London B: Biological Sciences 273: 603–610.

Sampaio MV, Bueno VH, Pérez-Maluf R. 2001. Parasitism of Aphidius colemani Viereck (Hymenoptera: Aphididae) in different densities of Myzus persicae (Sulzer) (Hemiptera: Aphididae). Neotropical Entomology 30: 81–87.

Schenck S, Lehrer AT. 2000. Factors affecting the transmission and spread of sugarcane yellow leaf virus. Plant Disease 84: 1085–1088.

Sharma S, Rohilla MS, Tiwari PK. 2007. Developmental and hyperthermia-induced expression of the heat shock proteins HSP60 and HSP70 in tissues of the housefly Musca domestica: an in vitro study. Genetics and Molecular Biology 30: 159–168.

Sibb RM, Barker D, Hone J, Pagel M. 2007. On the stability of populations of mammals, birds, fish and insects. Ecology Letters 10: 970–976.

Singh BU, Padmaja PG, Seetharama N. 2004. Biology and management of the sugarcane aphid, Melanaphis sacchari (Zehntner) (Homoptera: Aphididae), in sorghum: a review. Crop Protection 23: 739–755.

Sumner L, Dorschner K, Ryan J, Eikenbary R, Johnson R, McNew R. 1986. Reproduction of Schizaphis graminum (Homoptera: Aphididae) on resistant and susceptible wheat genotypes during simulated drought stress induced with polyethylene glycol. Environmental Entomology 15: 756–762.

Tofangsszi N, Kheradmand K, Shahrkohi S, Talebi AA. 2010. Temperature-dependent life history of Schizaphis graminum on barley. Bulletin of Entomology 63: 79–84.

van Lenteren JC, Kla F, Aplinkj JN, van Schelt JC, Steinberg S. 2003. Guidelines for quality control of commercially produced natural enemies, pp. 265–304 in van Lenteren JC [ed.], Quality Control and Production of Biological Control Agents: Theory and Testing Procedures. CAB International, Cambridge, Massachusetts, USA.

van Rensburg NJ. 1973a. Notes on the occurrence and biology of the sorghum aphid in South Africa. Journal of the Entomological Society of Southern Africa 36: 293–298.

van Rensburg NJ. 1973b. Population fluctuations of the sorghum aphid, Melanaphis (Longinius) pyrarius (Passerini) forma sacchari (Zehntner). Phytophylactica 5: 127–134.

van Schelt JC. 1994. Newsletter on biological control in greenhouse. Sting 14. OBC/WPRS, Wageningen, Netherlands.

Villanueva RT, Brewer MJ, Way MO, Biles S, Bynum E, Swart J, Crumley C, Knutson A, Porter P. 2014. Sugarcane aphid: a new pest of sorghum. Texas A&M Agrilife Extension, Ento-035. College Station, Texas, USA. https://ccag.tamu.edu/files/2014/07/2014sugarcaneaphidENTO-035.pdf (last accessed 14 Jul 2019).

Vorburger C, Lancaster M, Sunnucks P. 2003. Environmentally related patterns of reproductive modes in the aphid Myzus persicae and the predominance of two ‘superclones’ in Victoria, Australia. Molecular Ecology 12: 3493–3504.

Wang HH, Reitz SR, Wang LX, Wang SY, Xue L, Li ZR. 2013. The mRNA expression profiles of five heat shock protein genes from Frankliniella occidentalis at different stages and their responses to temperatures and insecticides. Journal of Integrative Agriculture 13: 2196–2210.

Warrington S, Mansfield T, Whittaker J. 1987. Effect of sulfur dioxide on the reproduction of pea aphids, Acyrthosiphon pisum, and the impact of sulfur dioxide and aphids on the growth and yield of peas. Environmental Pollution 48: 285–294.

Zhou XL, Carter N, Mumford J. 1989. A simulation model describing the population dynamics and damage potential of the rose grain aphid, Metopolophium dirhodum (Walker) (Hemiptera: Aphididae) in the UK. Bulletin of Entomological Research 79: 373–380.

Zuniga G, Salgado M, Corcuera L. 1985. Role of an indole alkaloid in the resistance of barley (Hordeum vulgare). Phytochemistry 24: 945–948.