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

M. F. Souza[1], and J. A. Davis[1,]*

Abstract

Sugarcane 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_m = 0.405 ± 0.030). Net reproductive rate (R_0) 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 nao 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, and 35 °C). A 20 °C *M. sacchari* apresentou o maior 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_m = 0,405 ± 0,030). A taxa líquida de reprodução (R_0) 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, 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 afídeo 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-

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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 (r_m) 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 founded 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 85G85 (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 85G85.' 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 Sampaio 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_x) and fecundity (m_x) were calculated for each temperature. Net reproductive rate, R_o, defined as the product of age-specific survival and age-specific fecundity, was calculated using the formula $R_o = \Sigma l_x m_x$, where l_x is the proportion of females alive on a given d, and m_x is the mean number of female births on that d. The intrinsic rate of increase, r_m, ($\Sigma e^{-rm} l_x m_x = 1$), finite rate of increase ($\lambda_F = e^{rm}$), mean

generation time [$T_G = \ln R_o / r_m$], and doubling time (DT = $\ln(2)/r_m$) of a generation were estimated according to Birch (1948). Jackknifing procedure was used to estimate r_m standard error. This procedure is based on recombining the original data and calculating pseudo-values of r_m for each recombination of the original data, and estimating the mean value and standard error of r_m 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 means and determine whether paired temperatures treatments were different 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:

$$r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} + \lambda$$

Where $r(T)$ is the mean developmental rate at temperature T (°C). Fitted parameters ρ (rate of increase at optimal temperature), T_{max} (upper developmental threshold), Δ (difference between optimal and upper developmental threshold), and λ (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; $P < 0.0001$). *Melanaphis 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 = 28.61; $P > 0.0001$). 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_0 values were 31.1 and 34.0, respectively, and the lowest R_0 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_m (Table 2). The finite rate of increase (λ_F) 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 *Melanaphis 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).

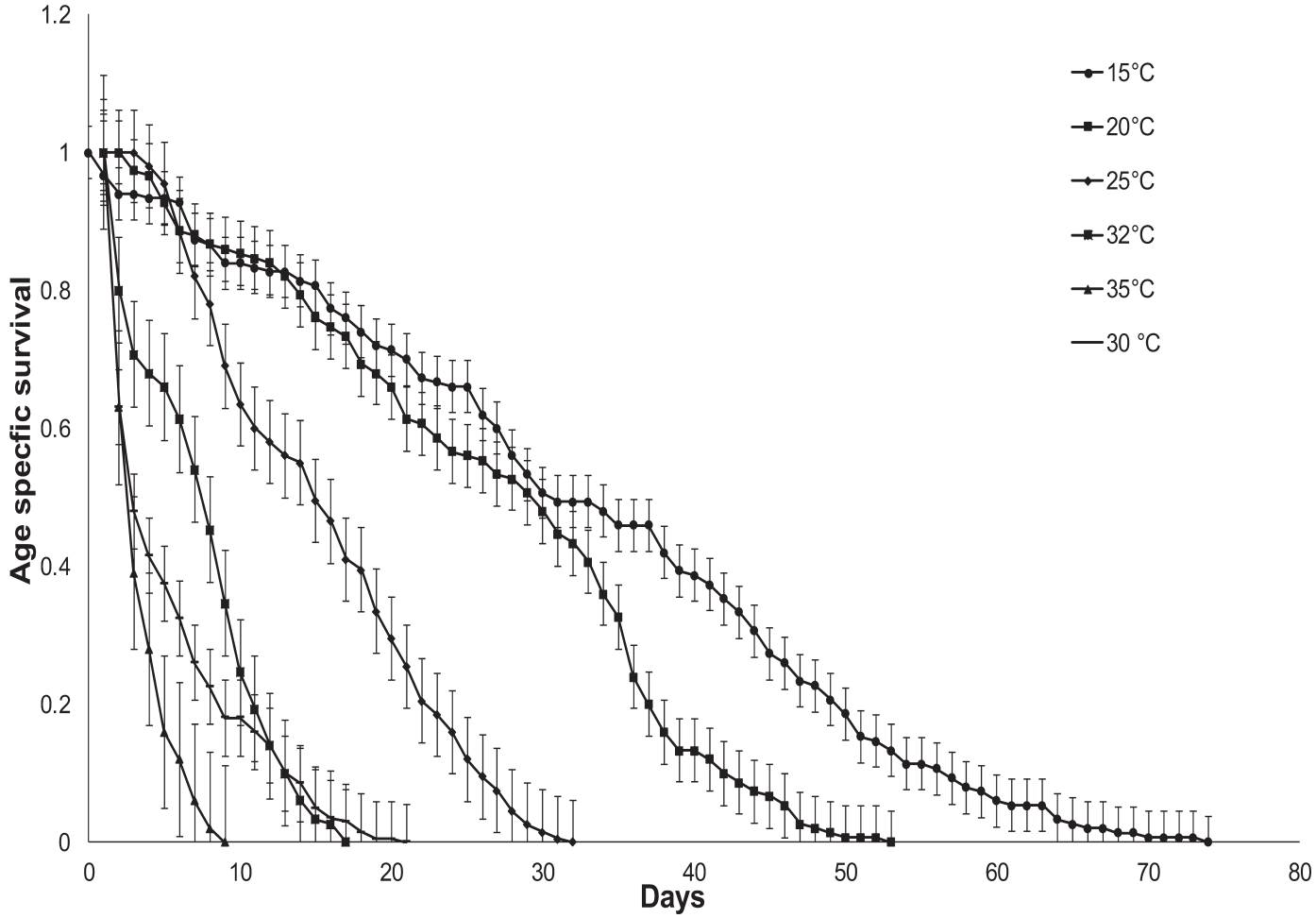

Fig. 1. Age-specific survivorship (proportion of alive individuals per day) of *Melanaphis sacchari* under 6 constant temperatures on grain sorghum.

THERMAL REQUIREMENTS

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 threshold. 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.

	Intrinsic rate of increase						
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

Table 3. Estimated parameters of Lactin model for constant temperature regimes: ρ = rate of increase at optimal temperature, T_{max} = upper developmental threshold, Δ = difference between optimal and upper developmental threshold, and λ = value that allows the curve to intercept x-axis.

Model	ρ	SE	T_{max}	SE	Δ	SE	λ	SE
Constant	0.01081	± 0.00035	37.808	± 0.517	2.506	± 0.242	−1.097	± 0.007

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 (Montllor et al. 2002; Russell & Moran 2006; Heyworth & Ferrari 2015) through nutritional compensation when heat impairs

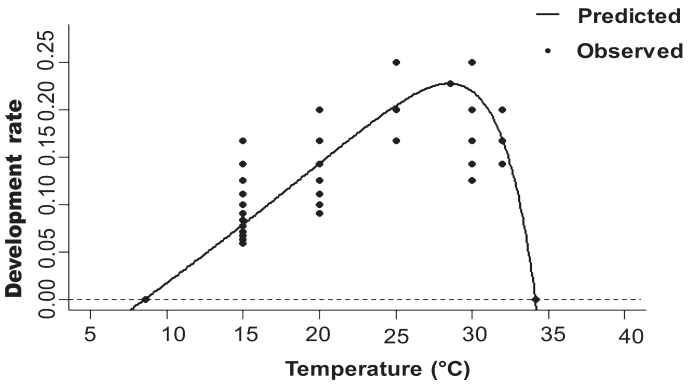

Fig. 2. *Melanaphis sacchari* constant temperature dependent development rate Lactin model estimation. Solid line representing the predicted values by Logan-Lactin model and dots represent the observed values.

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 increment 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_m 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_m increased from 0.390 at 25 °C to 0.450 under 30 °C, whereas in the present study the r_m decreased from 0.405 to 0.124 when the temperature increased from 25 to 30 °C. At 24 °C, *M. sacchari* R_0 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_m 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.

Table 4. Fifteen years average temperature (°C) in the US continental states throughout the year. Shaded area corresponds to *Melanaphis sacchari* active development.

State/temperature °C	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Alabama	7.1	8.4	13.6	17.5	21.6	25.7	26.8	26.7	23.9	18.1	12.3	8.8
Arizona	6.2	7.9	11.5	14.7	19.3	25.1	27.5	26.2	23.0	17.0	10.8	5.7
Arkansas	4.6	5.8	11.3	16.4	20.5	25.4	26.8	26.7	22.9	16.7	10.9	5.9
California	7.3	8.4	10.7	12.8	16.9	21.4	25.0	24.1	21.5	16.0	10.5	6.5
Colorado	−3.1	−2.2	2.8	6.7	11.5	17.5	20.6	19.1	14.9	8.6	2.2	−3.4
Connecticut	−2.9	−2.1	2.8	9.0	14.5	19.3	22.6	21.6	17.9	11.3	5.8	0.6
Delaware	1.4	2.1	7.1	12.6	17.8	22.8	25.5	24.4	20.9	14.5	8.9	4.4
Florida	14.3	15.4	18.6	21.4	24.6	27.2	27.9	28.0	26.7	23.1	18.6	16.2
Georgia	7.9	9.1	13.9	17.7	21.8	25.8	26.9	26.7	23.9	18.4	12.8	9.7
Idaho	−3.7	−2.2	1.8	5.3	9.8	14.5	19.7	18.3	13.6	7.2	0.5	−4.1
Illinois	−2.8	−1.8	5.6	12.0	17.3	22.5	24.1	23.3	19.6	12.7	6.2	−0.3
Indiana	−2.5	−1.6	5.4	11.6	16.9	22.0	23.4	22.8	19.2	12.4	6.2	0.3
Iowa	−6.7	−5.2	2.8	9.8	15.5	21.2	23.1	21.8	17.8	10.7	3.5	−4.1
Kansas	−0.3	0.9	7.6	12.7	17.7	23.8	26.3	25.3	20.6	13.6	6.9	0.4
Kentucky	1.1	2.2	8.5	14.0	18.4	23.0	24.6	24.3	20.7	14.2	8.2	3.5
Louisiana	9.8	11.0	15.6	19.6	23.4	27.1	27.9	28.1	25.6	20.2	14.9	11.1
Maine	−9.2	−8.0	−2.8	4.4	11.0	15.8	19.2	18.4	14.2	7.6	1.6	−5.2
Maryland	0.8	1.5	6.8	12.5	17.6	22.5	25.0	24.0	20.4	13.9	8.3	3.6
Massachusetts	−3.6	−2.8	2.0	8.3	14.0	18.6	22.1	21.1	17.2	10.7	5.4	0.0
Michigan	−6.5	−6.3	−0.4	6.4	12.7	18.1	20.7	19.8	16.0	9.1	3.0	−3.2
Minnesota	−11.8	−10.1	−2.2	6.0	12.4	18.1	21.0	19.4	15.3	7.6	−0.3	−8.7
Mississippi	7.4	8.6	13.8	18.0	22.0	26.2	27.1	27.1	24.3	18.4	12.7	8.9
Missouri	−0.5	0.8	7.6	13.5	18.0	23.4	25.3	24.6	20.3	13.7	7.7	1.4
Montana	−5.4	−4.4	0.4	5.2	9.9	14.9	19.9	18.4	13.4	6.4	−0.3	−6.0
Nebraska	−3.5	−2.4	4.2	9.4	14.6	20.8	23.9	22.6	17.8	10.5	3.6	−3.1
Nevada	0.4	2.1	5.7	8.6	13.4	19.2	23.7	22.0	17.6	11.1	4.6	−0.2
New Hampshire	−7.4	−6.2	−1.1	5.9	12.3	16.9	20.0	19.1	15.1	8.3	2.5	−3.5
New Jersey	−0.5	0.4	5.3	11.1	16.4	21.4	24.3	23.3	19.8	13.1	7.7	2.8
New Mexico	2.1	3.7	8.0	11.8	16.4	22.1	23.5	22.3	18.8	13.1	6.8	2.1
New York	−6.0	−5.3	0.0	7.0	13.4	18.1	20.7	19.8	16.2	9.4	3.8	−2.1
North Carolina	4.6	5.6	10.4	15.2	19.4	23.9	25.5	25.0	21.7	15.9	10.3	6.7
North Dakota	−11.2	−10.0	−2.7	5.5	11.5	17.5	21.0	19.7	14.8	6.7	−1.5	−9.4
Ohio	−2.5	−1.9	4.6	11.0	16.3	21.1	22.9	22.4	18.7	12.0	6.1	0.6
Oklahoma	3.6	5.0	11.0	15.7	20.2	25.5	27.7	27.4	22.9	16.4	10.2	4.3
Oregon	1.0	2.2	4.6	6.8	10.8	14.8	19.7	18.8	15.0	9.4	3.7	0.1
Pennsylvania	−3.3	−2.7	3.0	9.4	14.9	19.5	21.9	21.0	17.5	10.8	5.3	0.0
Rhode Island	−1.9	−1.3	3.3	9.0	14.3	19.1	22.7	21.9	18.1	11.8	6.7	1.7
South Carolina	7.1	8.2	13.0	17.4	21.4	25.7	27.1	26.6	23.6	17.9	12.2	9.0
South Dakota	−6.8	−5.7	1.1	7.5	13.0	19.2	23.2	21.6	16.7	8.8	1.3	−6.0
Tennessee	3.0	4.3	10.1	15.0	19.2	23.8	25.2	25.0	21.5	15.2	9.4	5.0
Texas	8.4	10.0	14.9	19.0	23.0	27.2	28.1	28.2	24.7	19.6	13.7	9.0
Utah	−2.4	−0.1	4.7	8.1	13.1	19.3	23.3	21.5	16.8	10.1	3.2	−2.4
Vermont	−8.3	−7.2	−1.8	5.4	12.1	16.7	19.5	18.6	14.8	7.9	2.1	−4.2
Virginia	1.8	2.8	8.0	13.3	17.7	22.3	24.3	23.7	20.2	13.9	8.4	4.1
Washington	0.1	1.7	4.4	7.3	11.4	14.8	19.0	18.5	14.5	8.8	2.9	−0.7
West Virginia	−0.8	0.2	6.1	11.8	16.2	20.6	22.3	22.0	18.6	12.2	6.6	2.0
Wisconsin	−9.1	−7.8	−0.7	6.6	12.9	18.4	21.0	19.7	15.7	8.4	1.5	−6.0
Wyoming	−5.3	−4.7	0.5	4.5	9.2	15.1	19.7	18.0	13.1	6.3	−0.4	−6.0
District of Columbia	0.9	1.5	7.2	12.9	18.0	22.8	25.3	24.6	20.7	13.8	8.1	3.5

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