



Effects of temperature on the development, performance and fitness of the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae): implications on its distribution under climate change

Guido A. Van Nieuwenhove*[†], Eduardo A. Frías[‡] and Eduardo G. Virla^{§§}

*Sección Zoología Agrícola, Estación Experimental Agroindustrial Obispo Colombres, Av. William Cross 3150, CP 4101, Las Talitas, Argentina,

[†]Facultad de Ciencias Naturales e IML-UNT, M. Lillo 205, CP 4000, San Miguel de Tucumán, Argentina, [‡]CONICET, PROIMI-Biotecnología, Av.

Belgrano & Pje. Caseros, CP 4000, San Miguel de Tucumán, Argentina, and ^{§§}Instituto de Entomología, Fundación M. Lillo, M. Lillo 251, CP 4000,

San Miguel de Tucumán, Argentina

- Abstract**
- 1 Maize and its wild teosinte (*Zea*) relatives are the only developmental hosts of the corn leafhopper. The leafhopper and the three phytopathogens that it transmits are found in a wide range of latitudes and elevations from the U.S.A. to Argentina.
 - 2 The vector's populations would be expected to respond to environmental conditions. Temperature plays a key role in the life history of insects, limiting its geographical range.
 - 3 We focus on the effect of different constant temperatures on the development and fitness of *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) to estimate its thermal constant and threshold temperature, which may represent useful information for studies aiming to predict its potential distribution.
 - 4 Temperature had a significant influence on egg-laying and hatchability, as well as development and pre-imaginal survival of the vector, whereas the offspring sex ratio was not influenced.
 - 5 *Dalbulus maidis* required 648.26 degree-days above a threshold of 4.9 °C to complete a life cycle; it had a wide oviposition range (15–40 °C), although its fitness occurred in a narrower range (17.5–35 °C). Apparently, the distribution range of *D. maidis* could be restricted by host plant availability more than by temperature.
 - 6 The vector is unlikely to develop permanent populations in temperate areas of the American continent because there is no availability of host plants for extended periods, with mean temperatures below 17 °C.

Keywords Corn diseases, fitness, phenology, range expansion, temperature-dependent development models, thermal performance breadth, vector.

Introduction

Human activities are increasingly altering the distributions of species as a result of modification of the habitat, changes in global climate and facilitation of pest species invasions (Parmesan, 2006). Insects are ectotherms and they are especially likely to be vulnerable to climate warming because their basic physiological functions such as locomotion, behaviour, development, performance and fitness are strongly influenced by environmental temperature (Inward *et al.*, 2012; Romo & Tylianakis,

2013; Piyaphongkul *et al.*, 2014). Two principle aspects of the thermal ectotherms play a central role in shaping patterns: temperature tolerance and dependent effects on performance. The effects of the temperature on performance traits within the zone of tolerance can be visualized using a thermal performance curve (TPC) (Schulte *et al.*, 2011). TPCs tend to take the same general shape: performance typically rises gradually with temperature from a minimum critical temperature, T_{min} , to an optimum temperature, T_{opt} , and then drops rapidly to a critical thermal maximum, T_{max} (Huey & Stevenson, 1979; Angilletta, 2006, 2009; Rotvit & Jacobsen, 2014; McKee & Aukema, 2015).

Currently, there has been resurgence in interest in TPCs because of their potential utility in helping to predict the

Correspondence: Eduardo G. Virla. Tel.: +54 381 434 4888; fax: +54 381 434 4887; e-mail: evirla@hotmail.com; evirla@proimi.org.ar

responses of populations or species to climate change (Deutsch *et al.*, 2008; Angert *et al.*, 2011; Dell *et al.*, 2011; Huey & Kingsolver, 2011). TPCs also can be incorporated into mechanistic based models of organism responses to climate change (Helmuth *et al.*, 2005; Kearney, 2006; Kearney & Porter, 2009; Angert *et al.*, 2011), which may have advantages relative to other approaches, such as climate envelope models (Pearson & Dawson, 2003; Guisan & Thuiller, 2005), for predicting the effects of climate change on species persistence (Kearney, 2006; Buckley *et al.*, 2010; Chown *et al.*, 2010). On the other hand, the relationship between temperature and duration of development can be modelled, either by a cumulative degree-day (DD) model, also known as the law of total effective temperature, or by nonlinear models (Campbell *et al.*, 1974; Lactin *et al.*, 1995; Brière *et al.*, 1999; Ikemoto & Takai, 2001). From these models, a threshold temperature (i.e. T_{\min} and T_{\max}), thermal constant and a T_{opt} are defined and these parameters are very useful for predicting the timing of pest outbreaks or the potential geographical limits of an insect's distribution (Dreistadt & Dahlsten, 1990; Horn *et al.*, 2012).

In tropical and subtropical America, corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) causes great damage to maize (*Zea mays* L.) because it efficiently transmits three important plant pathogens that adversely affect corn crop: corn stunt Spiroplasma, maize bushy stunt phytoplasma and maize rayado fino virus (Gamez, 1973; Nault, 1980). In those regions, corn stunt Spiroplasma is the most important pathogen affecting corn. The highest infection rates have been found in Central America, Peru, Brazil and Argentina, with many crops showing symptoms in 100% of plants (Virla *et al.*, 2004).

Dalbulus maidis shows a broad distribution throughout the Americas, from southeastern and southwestern U.S.A. to Argentina (Triplehorn & Nault, 1985). It is a monophagous species that only completes its development on plants of the genus *Zea* (maize and teosintes) and, although it prefers to live at low elevations, it is found in a wide range of altitudes on its host from sea level to 3200 m a.s.l. in the Peruvian Andes (Nault, 1990). In subtropical areas, corn leafhopper populations reach their peak during summer; however, when senescence of maize plants start and plants eventually die off at the end of the growing season, only a few adult insects may survive the cold winters (Virla *et al.*, 2003). Larsen *et al.* (1992), as a result of greenhouse and laboratory experiments, and Moya Raygoza *et al.* (2007), as a result of studies in Mexico, reported that the vector is capable of overwintering locally because it can survive at least 2 months in the absence of the maize host plants. Moreover, flight behaviour studies conducted by Taylor *et al.* (1992) suggest that the corn leafhopper can travel long distances.

At present, it is known that extreme temperatures limit the geographical range (through developmental rate and fitness) of insect populations, either by causing direct natural mortality or by limiting the range of host plants (Speight *et al.*, 1999). Identifying the environmental constraints that affect the geographical distribution and abundance of pest insects is fundamental to their effective management, particularly for invasive species (Wang *et al.*, 2009; Gutierrez *et al.*, 2011).

Because the American economy largely depends on agricultural activities, and corn stunting pathogens are a very important

adverse factor of corn crop productivity in essentially all of the American continent, the present study aimed to determine the effect of different temperatures on the development, performance and fitness of the vector. We also used diverse models to estimate the TPC, thermal constant, T_{\min} and T_{\max} to predict the potential range of *D. maidis* distribution throughout the continent.

Materials and methods

Origin of the specimens and D. maidis laboratory rearing

A *D. maidis* colony was established with individuals collected during the summer of 2011 in Los Nogales, Tucumán, Argentina (26°42'S to 65°13'W; elevation 588 m). The adults were placed in breeding cages (50 × 50 × 50 cm³), made of aluminum with the lateral and upper sides covered with nylon mesh (organdy type) to promote ventilation. Potted corn plants (pot of 6.3 dm³) were placed inside as food source and for reproduction. The maize variety 'Leales 25 plus' was used both for maintenance of the corn leafhopper colony and for all the assays. The colony was reared in a greenhouse at San Miguel de Tucumán (26°48'35.6'S to 65°14'24.6'W; elevation 500 m) under a natural photoperiod at between 20 and 30 °C and with no humidity control.

Oviposition range, egg hatchability, development time, pre-imaginal mortality, biological cycle and sex ratio of D. maidis at different constant temperatures

Oviposition range (i.e. thermal tolerance range) and egg hatchability (as a measure of performance and fitness, respectively) were assessed at 10 constant temperatures (13, 15, 17.5, 20, 25, 30, 35, 37.5, 40 and 42.5 °C with a range of ±1 °C), whereas developmental time [$D(T)$] and developmental rate [$D(r)$], percentage of pre-imaginal survival, biological cycle and sex ratio were assessed at nine constant temperatures (from 13 to 40 °C) in two environmental plant-growth chambers (model AR-36L; Percival Scientific, Perry, Iowa). Chambers were maintained under an LD 14:10 h photoperiod at 75 ± 10% relative humidity and 250 µmol/m²/s.

Oviposition range and egg hatchability. Fourth- and fifth-instar nymphs of *D. maidis* were randomly taken from the colonies and confined in cages under each selected temperature. As these individuals reached the adult stage, they were sexed and separated in groups of three pairs (4 days old) to be transferred to polyethylene-terephthalate cylindrical cages (height 35 cm, diameter 18 cm) for oviposition. The top end of the tube was covered with muslin fabric for ventilation,

These oviposition cages were randomly placed inside an incubator at each respective constant temperature. Then, a potted maize plant with three fully expanded leaves was placed inside each cage for oviposition. Twenty-four hours later, females were removed and plants were examined for eggs. Eggs were counted under a stereomicroscope at ×20 magnification (Stemi 2000-c; Carl Zeiss, Oberkochen, Germany), labelled and followed until they hatched. Each cage was considered as a replicate. For each temperature, there were at least, 20 replicates (Table 2).

Table 1 Nonlinear developmental models tested to describe the relationship between temperature and pre-imaginal development of *Dalbulus maidis*

| Model | Equation | Reference |
|-----------|---|-----------------------------|
| Lactin | $R(T)$ or $\frac{1}{D} = e^{P*T} - e^{(P*T_m - \frac{T_m - T}{\lambda})} + \lambda$ | Lactin <i>et al.</i> (1995) |
| Brière I | $R(T)$ or $\frac{1}{D} = aT (T - T_{\min}) (T_{\max} - T)^{1/2}$ | Brière <i>et al.</i> (1999) |
| Brière II | $R(T)$ or $\frac{1}{D} = aT (T - T_{\min}) (T_{\max} - T)^{1/m}$ | Brière <i>et al.</i> (1999) |

Developmental time at different constant temperatures. Once nymphs emerged from the different treatments, they were isolated in glass tubes (length 9 cm, diameter 1.5 cm) and capped with wetted cotton. Nymphs were fed with fresh pieces of corn replaced every day. At the same time, the occurrence of molts and survival were observed. Thus, it was possible to obtain the developmental time for each individual and stage. The total numbers of individuals used in the trials are summarized in Table 5.

Relationship between temperature and developmental rate

Linear and three nonlinear regression models were applied to determine the relationship between temperature and development rate of *D. maidis*. Those data points that deviated from the straight line were rejected for correct calculation of linear regression (Campbell *et al.*, 1974). For this reason, only data of the temperatures from 17 to 30 °C were used in the linear model.

Linear model. The linear model, commonly described as the DD model, was used to determine the lower threshold temperature and the thermal constant for pre-imaginal development: $D(r)$ or $1/D = a + bT$, where $D(r)$ is the rate of development or the inverse of development time ($1/D$), D is development time in days, T is the ambient temperature (°C), and a and b are estimates of the intercept and slope, respectively. The lower temperature threshold (T_{\min}) was estimated by the intersection of the regression line [$D(r) = 0$, $t_{\min} = -a/b$], and DD requirements (thermal constant, $K = 1/b$), were calculated using the inverse of the slope of the fitted linear regression line. Both parameters were calculated for all stages, from egg to adult, with their respective standard errors (Campbell *et al.*, 1974; Ikemoto & Takai, 2001).

Nonlinear model. The nonlinear relationship between developmental rate $D(r)$ and temperature T was modelled using Lactin and Brière-1 and 2 models, which allow for the estimation of the upper and lower developmental thresholds and the optimum temperature for development (T_{opt}) (Lactin *et al.*, 1995; Brière *et al.*, 1999). Lactin, Brière-1 and Brière-2 models are described in Table 1.

All of the above models were fitted to data by iterative nonlinear regression based on the Marquardt technique using JMP, version 9.0 (SAS Institute Inc., Cary, North Carolina). Fitting each model to the data set for the different temperatures tested was evaluated based on the criteria: (i) the coefficient of determination (r^2); (ii) the residual sum of squares (RSS); (iii) the Akaike information criterion (AIC); and (iv) the respective

adjusted coefficient of determination (r^2_{adj}). AIC is estimated according to the equation:

$$\text{AIC} = n \ln \left(\frac{\text{SSE}}{n} \right) + 2p$$

where n is the number of observations, p is the number of model parameters including the intercept and SSE is the sum of squares error. The adjusted coefficient of determination (r^2_{adj}) was estimated by the equation:

$$r^2_{\text{adj}} = 1 - \left(\frac{n-1}{n-p} \right) (1 - r^2)$$

where n is the number of observations, p is the number of model parameters and r^2 is the coefficient of determination of the nonlinear regression. For models with higher r^2 , r^2_{adj} and lower RSS, AIC fitted better to the recorded data (Burnham & Anderson, 2002; Quinn & Keough, 2002).

Egg hatchability and pre-imaginal survival

Egg hatchability and survival of five nymphal instars were estimated based on those that pass to the next stage-instars divided by the initial number of individuals alive at the beginning of each stage-instars $\times 100$.

Biological cycle and sex ratio

The total time to complete the biological cycle (time elapsed from egg stage until adult oviposition) was estimated by adding the duration of immature stages to the respective pre-ovipositional period (Kontodimas *et al.*, 2004).

The sex ratio of *D. maidis* offspring was calculated as the percentage of emerged females divided by the total number of emerged adults.

Statistical analysis

The data were checked for normality using the Kolmogorov–Smirnov test. To normalize the distribution of percentage and count data, arcsine $\sqrt{\%}$ and $\log_e(x+1)$ transformations were applied, respectively.

Therefore, data were subjected to one-way multivariate analysis of variance (MANOVA) at $\alpha = 0.05$ to determine the effect of temperature on the duration of immature stages, the oviposition range, egg hatchability, pre-imaginal survival and sex ratio of *D. maidis*. In the case of a significant MANOVA, one-way analysis of variance (ANOVA) at $\alpha = 0.05$ was performed for each significant outcome/dependent variable.

Data were also submitted to two-way ANOVA at $\alpha = 0.05$ to examine the effects of sex and temperature, and their interaction on the total adult developmental time, after which means were separated by the Unequal Tukey's honestly significant difference test at $\alpha = 0.05$. Data are reported as the untransformed mean \pm SE.

Data recorded at 42.5 °C were excluded from the analysis because all females died at this temperature before egg-laying occurred.

Table 2 Female mean egg numbers, and egg hatchability (mean \pm SE) of *Dalbulus maidis* at different constant temperatures

| Temperature ($^{\circ}$ C) | <i>n</i> | Female mean egg number | Egg hatchability (%) |
|-----------------------------|----------|-------------------------------|--------------------------------|
| 13 | 73 | 0.01 \pm 0.01 ^a | 0 ^a |
| 15 | 70 | 0.09 \pm 0.04 ^a | 0 ^a |
| 17.5 | 70 | 1.24 \pm 0.08 ^b | 33.33 \pm 3.79 ^b |
| 20 | 20 | 3.43 \pm 0.38 ^c | 63.90 \pm 3.87 ^{cd} |
| 25 | 20 | 5.03 \pm 0.36 ^d | 79.93 \pm 2.36 ^{cd} |
| 30 | 30 | 5.83 \pm 0.40 ^d | 85.59 \pm 0.62 ^d |
| 35 | 30 | 5.34 \pm 0.31 ^d | 46.65 \pm 1.40 ^c |
| 37.5 | 52 | 4.80 \pm 0.33 ^{cd} | 0 ^a |
| 40 | 46 | 5.54 \pm 0.35 ^d | 0 ^a |
| 42.5 | 28 | — | — |

Means within the same column followed by the same superscript letter are statistically equivalent (unequal Tukey–Kramer honestly significant difference test, $\alpha = 0.05$). Different superscript letters denote significant differences (Tukey $P \leq 0.05$). *n*, total replicates containing three females each.

Results

Using MANOVA, a significant multivariate effect for all variables as a group in relation to the temperature (λ Wilks = 0.0001, $F_{72,1850} = 128.23$, $P < 0.01$) was observed. Using one-way ANOVA, temperature was found to affect significantly oviposition range ($F_{8,402} = 279.86$, $P < 0.01$), egg hatchability ($F_{8,1173} = 297.37$, $P < 0.01$) and pre-imaginal survival of corn leafhoppers [N_I ($F_{4,654} = 2.94$, $P < 0.01$), N_{II} ($F_{4,528} = 2.23$, $P = 0.06$), N_{III} ($F_{4,449} = 3.67$, $P < 0.01$), N_{IV} ($F_{4,394} = 5.06$, $P < 0.01$) and N_V ($F_{4,330} = 1.82$, $P = 0.12$)]. Moreover, based on a one-way ANOVA, temperature was also found to influence significantly developmental time of eggs ($F_{4,1173} = 2756.60$, $P < 0.01$), nymphal instars [N_I ($F_{4,657} = 133.65$, $P < 0.01$), N_{II} ($F_{4,528} = 128.75$, $P < 0.01$), N_{III} ($F_{4,449} = 424.59$, $P < 0.01$), N_{IV} ($F_{4,394} = 161.63$, $P < 0.01$) and N_V ($F_{4,330} = 86.13$, $P < 0.01$)] and biological cycle [egg to egg ($F_{4,105} = 273.02$, $P < 0.01$)]. In *D. maidis*, offspring sex ratio was not influenced by temperature (ANOVA, $F_{4,328} = 0.84$, $P = 0.50$).

Thermal effects on performance

Dalbulus maidis performed successfully from 13 to 40 $^{\circ}$ C, where females laid eggs. No eggs were observed at 42.5 $^{\circ}$ C because all females died. However, at 13 and 15 $^{\circ}$ C, females of *D. maidis* practically failed or laid very few eggs (one egg from 219 females and 18 eggs from 210 females, respectively). From 20 $^{\circ}$ C, egg-laying is significantly increased as the temperature increases (Table 2).

From a linear model, the T_{\min} for egg-laying and for its hatchability was estimated to be 9.06 and 5.88 $^{\circ}$ C, respectively. The Brière-2 model showed the best fit data for egg-laying and hatchability (Table 3), estimating an T_{opt} for oviposition and hatchability of 33.61 and 27.61 $^{\circ}$ C, respectively, and a T_{\min} and T_{\max} for egg-laying and hatchability of 12.14 and 11.99 $^{\circ}$ C, and 42.5 and 37.5 $^{\circ}$ C, respectively (Fig. 1 and Table 3).

Table 3 Mean \pm SE values of fitted coefficients and parameters of four models describing eggs laid and hatchability of *Dalbulus maidis* on *Zea mays*

| Model | Parameter | Eggs | |
|----------|--------------------|---------------------------------|---------------------------------|
| | | Laid | Hatchability |
| Linear | <i>a</i> | 0.389 | 0.039 |
| | <i>b</i> | −5.25 | −0.235 |
| | <i>K</i> | — | — |
| | T_{\min} | 13.48 | 6.37 |
| | r^2 | 0.943 | 0.812 |
| | r^2_{Adj} | 0.929 | 0.719 |
| | RSS | 1.81 | 0.032 |
| | r^2 | 0.957 | 0.790 |
| | r^2_{Adj} | 0.935 | 0.486 |
| | RSS | 0.83×10^{-1} | 677.19 |
| Lactin | AIC | 8.15 | 38.36 |
| | <i>P</i> | $3.85 \pm 0.009 \times 10^{-1}$ | $38.04 \pm 1.65 \times 10^{-1}$ |
| | ΔT | 7.04 ± 2.63 | 4.51 ± 0.82 |
| | λ | -2.00 ± 0.55 | -4.04 ± 1.45 |
| | T_{\min} | 10.03 | 1.83 |
| | $T_L (= T_{\max})$ | 43.51 ± 1.53 | 35.96 ± 7.51 |
| | T_{opt} | 34.74 | 30.74 |
| | r^2 | 0.972 | 0.970 |
| | r^2_{Adj} | 0.959 | 0.930 |
| | RSS | 0.52×10^{-1} | 96.34 |
| Brière 2 | AIC | 3.50 | 26.66 |
| | <i>a</i> | $21.10 \pm 5.59 \times 10^{-4}$ | $24.05 \pm 5.89 \times 10^{-3}$ |
| | T_{\min} | 12.14 ± 2.54 | 11.99 ± 2.04 |
| | $T_L (= T_{\max})$ | 42.5 ± 0.36 | 37.5 ± 0.24 |
| | T_{opt} | 33.61 | 27.61 |
| | <i>m</i> | 1.55 | 1.07 |
| | r^2 | 0.970 | 0.890 |
| | r^2_{Adj} | 0.960 | 0.814 |
| | RSS | 5.82 | 559.25 |
| | AIC | 4.59 | 37.21 |
| Brière | <i>a</i> | $25.53 \pm 4.03 \times 10^{-4}$ | $28.35 \pm 2.40 \times 10^{-3}$ |
| | T_{\min} | 10.12 | 1.52 ± 0.21 |
| | $T_L (= T_{\max})$ | 42.5 ± 0.00 | 37.5 ± 2.31 |
| | T_{opt} | 34.98 | 29.62 |

AIC, Akaike information criterion; RSS, residual sum of squares.

Development time, pre-imaginal survival, sex ratio and biological cycle

Dalbulus maidis developed successfully to the adult stage within the temperature range of 17.5–35 $^{\circ}$ C. No significant differences were observed in egg hatchability at temperatures between 20 and 30 $^{\circ}$ C. However, these temperatures were significant at 17.5 and 35 $^{\circ}$ C. On the other hand, *D. maidis* did not succeed in completing its development at 13, 15, 37.5 and 40 $^{\circ}$ C because no eggs hatched at these temperatures. The presence of ‘eye spots’ on eggs was not detected until day 22 after oviposition, when host plants were dead or almost dead at 15 $^{\circ}$ C. Despite the fact that females laid numerous eggs at temperatures above 35 $^{\circ}$ C, these eggs failed to develop because of high constant temperatures. After 4 or 5 days, most (or all) plants died from thermal stress (desiccation) (Table 2).

Lowest survival was always observed at the egg stage, ranging from 0% (at 13, 15, 37.5 and 40 $^{\circ}$ C) to 85.59% (at 30 $^{\circ}$ C). Overall, immature survival tended to be the lowest both at

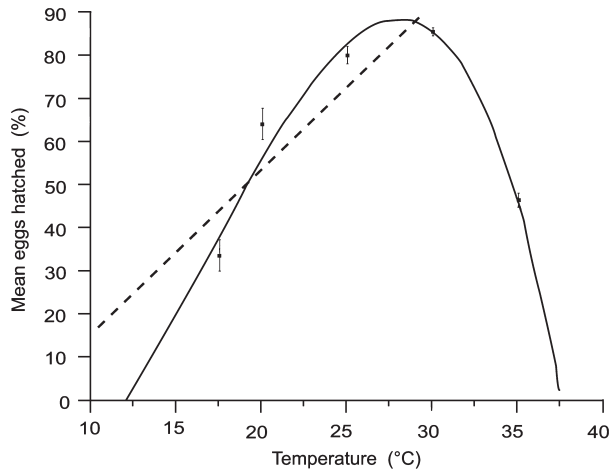


Figure 1 Fitting the linear (dashed line) and Brière 2 models (bold line) to observed values of egg hatchability (mean \pm SE) of *Dalbulus maidis* as a function of temperature ($^{\circ}$ C).

lower and at higher temperatures (Table 4). The sex ratio of the offspring was similar for all temperatures tested.

Two-way ANOVA showed that only temperature significantly affected developmental time to adult stage [Temperature ($F_{6,359} = 1636.26$, $P < 0.01$); Sex ($F_{1,359} = 0.14$, $P = 0.71$); Temperature \times Sex ($F_{6,359} = 1.25$, $P = 0.28$)]. Males and females had a similar development time, which decreased significantly when temperature increased until 30° C (Table 5). Overall, development time for egg hatch and pre-imaginal instars of *D. maidis* decreased significantly when temperature increased from 17.5° C to the upper limit of 30° C (Table 5).

Developmental rate

Linear model. The linear regression model showed a strong positive relationship between temperature and development rate until 30° C for eggs ($r^2 = 0.96$), five nymphal instars [N_I ($r^2 = 0.93$), N_{II} ($r^2 = 0.93$), N_{III} ($r^2 = 0.90$), N_{IV} ($r^2 = 0.95$) and N_V ($r^2 = 0.85$)] and adult stage ($r^2 = 0.94$) (Fig. 2 and Table 5). The number of degree-days required by *D. maidis* to complete development, from egg to adult stage, was 648.26 DD above a T_{min} of 4.98° C (Fig. 2 and Table 6).

Nonlinear models. All nonlinear models tested on pre-imaginal and total developmental rate fitted data of the current study, well. Using the values of r^2 , r^2_{adj} , RSS and AIC as indices to evaluate the goodness of fit, the Lactin model was shown to be the best fit data for all developmental stages (Table 6). On the other hand, the Brière-1 nonlinear model always gave the lowest fit of all the proposed models.

The Lactin model estimated a T_{opt} for total development of *D. maidis* on 33.48° C, whereas the estimated T_{min} and T_{max} were 4.98 and 37.5° C, respectively (Table 6).

Discussion

Temperature had a significant influence on egg-laying and hatchability, development and pre-imaginal survival of *D. maidis*. It is well known that diverse factors, such as temperature, humidity, pressure, insolation, etc., are expected to impact insect–plant interactions in several ways. They might affect insects directly, through changes in physiology, behaviour and life-history parameters, as well as indirectly, through changes experienced by host plants in their morphology (Barnes *et al.*,

Table 4 Eggs laid and hatchability, and pre-imaginal survival (mean \pm SE) of *Dalbulus maidis* on *Zea mays* at various constant temperatures

| Temperature | Eggs laid | Egg hatchability | Pre-imaginal survival | | | | |
|-------------|------------------------------|--------------------------------|-----------------------------|-----------------------------|-------------------------------|-----------------------------|----------------------------|
| | | | N_I | N_{II} | N_{III} | N_{IV} | N_V |
| 13 | 0.01 ± 0.01^a [73] | 0^a (1) | — | — | — | — | — |
| 15 | 0.09 ± 0.04^a [70] | 0^a (18) | — | — | — | — | — |
| 17.5 | 1.24 ± 0.08^b [70] | 33.33 ± 3.79^b (261) | 73.56 ± 4.76^a (87) | 89.06 ± 3.93^b (64) | 82.46 ± 5.08^{ab} (57) | 82.98 ± 5.54^b (47) | 97.50 ± 2.50^a (40) |
| 20 | 3.43 ± 0.38^c [20] | 63.90 ± 3.87^{cd} (206) | 86.51 ± 3.06^b (126) | 82.57 ± 3.65^b (109) | 85.56 ± 3.73^{ab} (90) | 79.22 ± 4.65^b (77) | 98.36 ± 1.64^a (61) |
| 25 | 5.03 ± 0.36^d [20] | 79.93 ± 2.36^{cd} (302) | 81.89 ± 2.48^b (243) | 88.95 ± 2.23^c (199) | 94.35 ± 1.74^c (177) | 92.81 ± 2.00^c (167) | 100^a (155) |
| 30 | 5.83 ± 0.40^d [30] | 85.59 ± 0.62^d (525) | 83.62 ± 3.45^b (116) | 84.54 ± 3.69^a (97) | 86.59 ± 3.79^{ab} (82) | 76.06 ± 5.10^a (71) | 100^a (54) |
| 35 | 5.34 ± 0.31^d [30] | 46.65 ± 1.40^c (481) | 71.11 ± 4.80^a (90) | 75.00 ± 5.46^a (64) | 77.08 ± 6.13^a (48) | 70.27 ± 7.62^a (37) | 96.15 ± 3.85^a (26) |
| 37.5 | 4.80 ± 0.33^{cd} [52] | 0^a (749) | — | — | — | — | — |
| 40 | 5.54 ± 0.35^d [46] | 0^a (764) | — | — | — | — | — |

Means within the same column followed by the same superscript letter are statistically equivalent (unequal Tukey–Kramer honestly significant difference test, $\alpha = 0.05$). The number given in parenthesis is the number of replicates (three females each); the number in parentheses is the sample size during each stage/instars.

Table 5 Duration (mean \pm SE) of development, biological cycle (days) and sex ratio of *Dalbulus maidis* on *Zea mays* at various constant temperatures

| Temperature | Developmental time (days) | | | | | | Females | Males | Biological cycle (egg-egg) | Sex ratio |
|-------------|--|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|-------------------------------|-------------------------------|
| | Eggs | N_I | N_{II} | N_{III} | N_{IV} | N_V | | | | |
| 13 | — [1] | — | — | — | — | — | — | — | — | — |
| 15 | — [18] | — | — | — | — | — | — | — | — | — |
| 17.5 | 19.36 \pm 0.13 ^a [261] | 5.98 \pm 0.10 ^a [87] | 4.86 \pm 0.10 ^a [64] | 4.95 \pm 0.16 ^a [57] | 5.85 \pm 0.12 ^a [47] | 7.10 \pm 0.17 ^b [39] | 46.00 \pm 0.45 ^a [22] | 46.29 \pm 0.36 ^a [17] | 51.69 \pm 0.66 ^a | 56.41 \pm 8.04 ^a |
| 20 | 16.03 \pm 0.08 ^b [206] | 4.67 \pm 0.11 ^b [126] | 4.70 \pm 0.11 ^a [109] | 5.06 \pm 0.12 ^a [90] | 5.84 \pm 0.12 ^a [77] | 7.79 \pm 0.20 ^a [61] | 43.74 \pm 0.39 ^b [34] | 43.92 \pm 0.43 ^b [26] | 49.17 \pm 0.43 ^b | 56.67 \pm 6.45 ^a |
| 25 | 14.66 \pm 0.07 ^c [302] | 4.10 \pm 0.07 ^c [243] | 3.52 \pm 0.08 ^b [199] | 3.77 \pm 0.07 ^b [177] | 4.00 \pm 0.06 ^b [167] | 6.12 \pm 0.08 ^c [155] | 35.87 \pm 0.31 ^c [75] | 35.52 \pm 0.25 ^c [80] | 42.48 \pm 0.68 ^c | 48.39 \pm 4.03 ^a |
| 30 | 9.98 \pm 0.06 ^d [158] | 2.70 \pm 0.07 ^d [116] | 2.44 \pm 0.06 ^c [97] | 2.48 \pm 0.08 ^c [82] | 2.85 \pm 0.10 ^c [71] | 4.35 \pm 0.07 ^d [54] | 24.04 \pm 0.40 ^d [23] | 25.07 \pm 0.45 ^d [31] | 29.61 \pm 0.51 ^d | 42.59 \pm 6.79 ^a |
| 35 | 7.91 \pm 0.05 ^e [251] | 3.90 \pm 0.09 ^d [90] | 2.42 \pm 0.08 ^c [64] | 2.65 \pm 0.11 ^c [48] | 3.35 \pm 0.16 ^c [37] | 4.96 \pm 0.18 ^d [26] | 25.29 \pm 0.57 ^d [14] | 24.82 \pm 0.72 ^d [11] | 30.64 \pm 0.68 ^d | 56.0 \pm 10.13 ^a |
| 37.5 | — [749] | — | — | — | — | — | — | — | — | — |
| 40 | — [764] | — | — | — | — | — | — | — | — | — |

Means within the same column followed by the same superscript letter are statistically equivalent (unequal Tukey–Kramer honestly significant difference test, $\alpha = 0.05$). The number given in parenthesis is the sample size during each stage/instars.

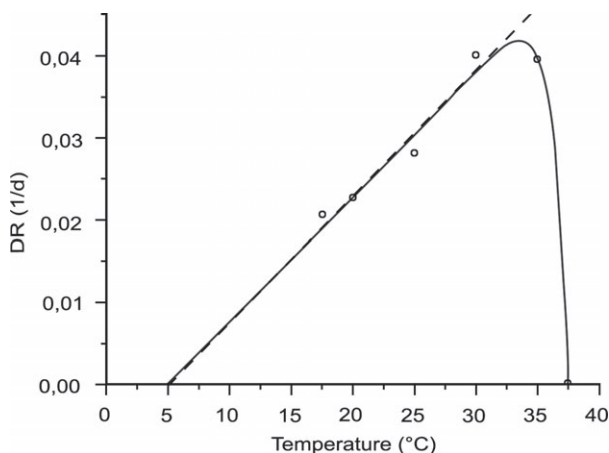


Figure 2 Fitted linear (dashed line) and nonlinear model (Lactin) (bold line) to observed values of developmental rates of *Dalbulus maidis* (from egg to adult stage) as a function of temperature ($^{\circ}\text{C}$). DR, rate of development.

1988; Morrison & Morecroft, 2006; Lake & Wade, 2009), biochemistry (Yuan *et al.*, 2009), physiology (Gifford *et al.*, 1996; Yadugiri, 2010), and patterns of richness, diversity and abundance (Thuiller *et al.*, 2005; Kazakis *et al.*, 2007).

The sex ratio of *D. maidis* offspring was not influenced by temperature. A similar result was reported by Waquil *et al.* (1999).

The present study showed that *D. maidis* has a wide oviposition range (15–40 $^{\circ}\text{C}$) but its best performance was observed within 25–40 $^{\circ}\text{C}$, where adult females oviposited approximately five eggs per day. Previous studies on the corn leafhopper (Davis, 1966; Madden *et al.*, 1984, 1986) have shown that egg-laying increased when the temperature increased, which is consistent with the present study (although they studied temperature ranges

between 20 and 29 $^{\circ}\text{C}$). However, Davis (1966) and Madden *et al.* (1986) reported a female egg average of almost the same result or more than twice that of the present study. These notable differences could be a result of the use of young females in the present study because Madden *et al.* (1984) reported that the number of eggs laid increased with the increasing age of females. There is generally an optimum temperature range outside which insects cannot maintain oogenesis and oviposition or cannot do so for long (Force & Messenger, 1964; Greenfield & Karandinos, 1976).

Although *D. maidis* was able to perform from 15 to 40 $^{\circ}\text{C}$, its fitness only occurred in a narrower range (17.5–35 $^{\circ}\text{C}$). Previous studies on *D. maidis* (Tsai, 1988; Waquil *et al.*, 1999) have shown that emergence of nymphs occurs from 20 to 29 $^{\circ}\text{C}$ because, under 20 $^{\circ}\text{C}$, development stopped and, over 32 $^{\circ}\text{C}$, the plants died (Waquil *et al.*, 1999). In the present study, nymph emergence was observed at 17.5 and 35 $^{\circ}\text{C}$. Moreover, at 15 $^{\circ}\text{C}$, egg development was observed until the appearance of eye spots, although there was no hatching as host plants failed. Considering that the vector can develop at higher or equal temperatures of 17 $^{\circ}\text{C}$, its ability to spread into temperate zones as reported by Carloni *et al.* (2013) is not unusual.

Dalbulus maidis required 648.26 DD above a T_{min} of 4.98 $^{\circ}\text{C}$ to complete a life cycle. Apparently, the fitness and therefore distribution range of *D. maidis* could be limited by host plant availability more than by temperature. Previous studies in other monophagous insects (Goehring & Oberhauser, 2002; Döring & Hoffmann, 2004; Hanspach *et al.*, 2014) indicate a close connection between the insects and their host plant where the latter limits the former's distribution, expansion or retraction and range. Biotic factors influence interspecific interactions affecting, positively or negatively, the performance and fitness of species (Brown *et al.*, 1996). Therefore, these factors also have a strong influence on them. Corn varieties have been developed to grow under a wide variety of conditions from Canada (58 $^{\circ}\text{N}$)

Table 6 Mean \pm SE values of fitted coefficients and parameters of four developmental rate models describing complete development of *Dalbulus maidis* on *Zea mays*

| Model | Parameter | Nymphal instars | | | | | | | Adult |
|--------------------|---------------------------------|---------------------------------|----------------------------------|---------------------------------|----------------------------------|----------------------------------|---------------------------------|---------------------------------|-------|
| | | N_I | N_{II} | N_{III} | N_{IV} | N_V | N_V | N_V | |
| Linear | a | $42.36 \pm 4.05 \times 10^{-4}$ | $15.13 \pm 2.90 \times 10^{-3}$ | $13.72 \pm 2.19 \times 10^{-3}$ | $16.44 \pm 3.81 \times 10^{-3}$ | $15.02 \pm 2.36 \times 10^{-3}$ | $7.52 \pm 2.23 \times 10^{-3}$ | $15.43 \pm 2.63 \times 10^{-4}$ | |
| | b | $-2.48 \pm 1.07 \times 10^{-2}$ | $-10.09 \pm 6.84 \times 10^{-2}$ | $-4.46 \pm 0.57 \times 10^{-2}$ | $-11.31 \pm 9.00 \times 10^{-2}$ | $-11.15 \pm 5.58 \times 10^{-2}$ | $-8.32 \pm 5.27 \times 10^{-3}$ | $7.68 \pm 6.22 \times 10^{-3}$ | |
| | K | 236.08 | 66.09 | 72.91 | 60.83 | 66.59 | 132.95 | 648.26 | |
| | T_{\min} | 5.84 | 6.67 | 3.25 | 6.88 | 7.43 | 1.11 | 4.98 | |
| | r^2 | 0.965 | 0.932 | 0.929 | 0.903 | 0.953 | 0.85 | 0.945 | |
| | r^2_{Adj} | 0.956 | 0.898 | 0.906 | 0.854 | 0.929 | 0.78 | 0.918 | |
| | RSS | 1.36×10^{-4} | 2.27×10^{-2} | 4.15×10^{-2} | 2.76×10^{-2} | 2.18×10^{-2} | 9.21×10^{-4} | 1.28×10^{-6} | |
| | r^2 | 0.992 | 0.949 | 0.984 | 0.96 | 0.98 | 0.924 | 0.97 | |
| | r^2_{Adj} | 0.979 | 0.872 | 0.959 | 0.89 | 0.94 | 0.811 | 0.93 | |
| | RSS | 3.24×10^{-5} | 2.32×10^{-3} | 1.36×10^{-3} | 2.49×10^{-3} | 1.08×10^{-3} | 9.29×10^{-4} | 1.29×10^{-5} | |
| | AIC | -54.47 | -37.14 | -40.37 | -36.73 | -41.72 | -42.64 | -68.3 | |
| | P | $38.39 \pm 3.24 \times 10^{-4}$ | $12.42 \pm 3.25 \times 10^{-3}$ | $12.42 \pm 1.63 \times 10^{-3}$ | $12.37 \pm 2.32 \times 10^{-3}$ | $11.76 \pm 1.77 \times 10^{-3}$ | $6.49 \pm 1.85 \times 10^{-3}$ | $14.90 \pm 2.58 \times 10^{-4}$ | |
| | ΔT | 0.13 ± 0.01 | 2.64 ± 0.96 | 1.26 ± 0.38 | 1.47 ± 0.54 | 1.93 ± 0.47 | 1.54 ± 0.62 | 1.23 ± 0.37 | |
| λ | -1.02 ± 0.01 | -1.08 ± 0.09 | -1.06 ± 0.05 | -1.07 ± 0.07 | -1.08 ± 0.05 | $-0.97 \pm 0.49 \times 10^{-1}$ | -1.01 ± 0.01 | | |
| T_{\min} | 5.43 | 6.53 | 4.87 | 5.42 | 7.06 | 0.23 | 4.98 | | |
| $T_L (= T_{\max})$ | 37.77 ± 0.13 | 40.58 ± 1.03 | 37.5 ± 1.68 | 39.17 ± 0.59 | 39.83 ± 0.54 | 39.87 ± 0.89 | 37.5 ± 1.68 | | |
| T_{opt} | 36.81 | 31.24 | 33.58 | 33.16 | 33.15 | 32.69 | 33.48 | | |
| r^2 | 0.916 | 0.921 | 0.965 | 0.87 | 0.96 | 0.90 | 0.96 | | |
| r^2_{Adj} | 0.79 | 0.803 | 0.912 | 0.68 | 0.90 | 0.74 | 0.90 | | |
| RSS | 3.26×10^{-4} | 3.58×10^{-3} | 2.92×10^{-3} | 7.10×10^{-3} | 1.72×10^{-3} | 1.26×10^{-3} | 1.87×10^{-5} | | |
| AIC | -42.34 | -34.55 | -35.76 | -30.43 | -38.94 | -40.83 | -66.24 | | |
| a | $11.05 \pm 3.62 \times 10^{-5}$ | $16.15 \pm 4.04 \times 10^{-5}$ | $2.45 \pm 4.70 \times 10^{-4}$ | $2.0 \pm 0.5 \times 10^{-4}$ | $23.18 \pm 5.33 \times 10^{-6}$ | $79.99 \pm 8.60 \times 10^{-6}$ | $23.18 \pm 5.33 \times 10^{-6}$ | | |
| T_{\min} | 5.61 ± 2.94 | 6.53 ± 1.85 | 2.49 ± 0.15 | 2.5 ± 0.85 | 4.59 ± 0.53 | 1.03 ± 0.15 | 1.82 ± 0.15 | | |
| $T_L (= T_{\max})$ | 37.5 ± 1.68 | 37.5 ± 0.92 | 37.5 ± 1.47 | 37.5 ± 1.63 | 37.5 ± 1.10 | 37.5 ± 2.66 | 37.5 ± 1.56 | | |
| T_{opt} | 30.31 | 33.15 | 32.61 | 31.26 | 32.09 | 33.39 | 33.15 | | |
| m | 5.1 | 1.86 | 3.32 | 2.4 | 2.77 | 4.02 | 4.04 | | |
| r^2 | 0.887 | 0.948 | 0.923 | 0.899 | 0.96 | 0.863 | 0.88 | | |
| r^2_{Adj} | 0.812 | 0.914 | 0.871 | 0.832 | 0.93 | 0.772 | 0.80 | | |
| RSS | 1.75×10^{-3} | 3.52×10^{-3} | 9.64×10^{-3} | 8.36×10^{-3} | 2.7618×10^{-3} | 2.52×10^{-3} | 8.40×10^{-5} | | |
| AIC | -38.84 | -34.65 | -28.60 | -29.43 | -36.12 | -36.64 | -57.06 | | |
| a | $7.03 \pm 2.05 \times 10^{-5}$ | $16.10 \pm 3.45 \times 10^{-5}$ | $25.31 \pm 5.71 \times 10^{-5}$ | $23.58 \pm 5.31 \times 10^{-5}$ | $19.14 \pm 3.05 \times 10^{-5}$ | $10.69 \pm 2.92 \times 10^{-5}$ | $23.39 \pm 5.33 \times 10^{-6}$ | | |
| T_{\min} | 10.52 ± 4.51 | 4.82 ± 1.38 | 9.62 ± 3.58 | 9.32 ± 3.65 | 8.29 ± 2.73 | 4.30 ± 0.57 | 8.44 ± 3.87 | | |
| $T_L (= T_{\max})$ | 37.5 ± 0.00 | 37.5 ± 0.00 | 37.5 ± 0.00 | 37.5 ± 0.00 | 37.5 | 37.5 ± 0.00 | 37.5 ± 0.00 | | |
| T_{opt} | 30.88 | 30.47 | 30.93 | 30.90 | 30.73 | 30.42 | 30.81 | | |

AIC, Akaike information criterion; RSS, residual sum of squares.

to Argentina (40°S) (Paliwal *et al.*, 2001). Based on this, we can explain wide distribution of corn leafhoppers and many biological differences among tropical and subtropical areas of the American continent (Oliveira *et al.*, 2004).

Although the models showed that average optimum temperature for different developmental stages was within the range of 31.24–36.81 °C, survival data suggested an optimum temperature between 20 and 30 °C. Extreme temperatures (both lower and higher) produced the highest mortality rates, particularly for the eggs and nymphs of *D. maidis*. Tsai (1988) and Waquil *et al.* (1999) found that lower and higher temperatures produced a higher mortality, or a lower viability, in *D. maidis* eggs. Moreover, Waquil *et al.* (1999) also reported a high mortality of host plants at temperatures above 32 °C. Previous studies in other Cicadellidae species such as *Homalodisca vitripennis* (Germar) [formerly known as *Homalodisca coagulata* (Say)] showed that higher temperatures reduced significantly hatchability of eggs (Al-Wahaibi & Morse, 2003). According to Hallman and Denlinger (1998), temperature extremes caused significant natural mortality in insect populations.

Dalbulus maidis showed slightly prolonged nymphal developmental periods at lower temperatures, although there is no evidence, at least as far as we are aware, that it has a diapause stage. Similar results were also reported in other subtropical species of Cicadellidae (Valle *et al.*, 1986; Gutierrez *et al.*, 2011). Previous studies have established that the corn leafhopper overwinters as an adult, taking refuge in winter crops and wild grasses (Virla *et al.*, 2003). Ebbert and Nault (1994) showed that some populations are capable of withstanding a few hours at –5 °C at low humidity, and that the adults can survive up to 75 days without food and temperatures between 9 and 17 °C. Virla *et al.* (2013) reported that the distribution pattern of *D. maidis* in subtropical South America is mainly affected by climatic conditions and host plant availability throughout the year, and described four different regions along a latitudinal gradient in areas below elevations of 1000 m a.s.l. The information reported in the present study supports the assertion that *D. maidis* is unable to develop permanent populations in temperate areas (e.g. south of latitude 30°S) because there is no availability of host plants from late fall to early spring, with mean temperatures below 17 °C.

Lactin-2 and Briere-2 models are more applicable than the Briere-1 model, respectively. Previous studies (Burnham & Anderson, 2002; Kontodimas *et al.*, 2004; Angilletta, 2006) have shown that models with more parameters typically describe major variation compared with a model with few parameters. The Lactin-2 model overestimated, with the exceptions of N_{II} and adult stage, the upper developmental threshold (T_L). Recently, Wang *et al.* (2013) reported that T_L is not a direct parameter in Lactin model, and numerical computations are needed to obtain their approximation. Therefore, an ordinary method to evaluate the accuracy of estimated critical temperatures is based on the comparison with experimental data (Kontodimas *et al.*, 2004).

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