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Thermal time clock for estimating phenological development of *Schistocerca piceifrons piceifrons* Walker (Orthoptera: Acrididae) in northeastern Mexico

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Abstract

The Central American locust, *Schistocerca piceifrons piceifrons* Walker, is an economically important agricultural pest in Mexico and Central America. This species is characterized by its ability to gregarize and migrate long distances. High infestations of *S. p. piceifrons* have occurred in northeastern Mexico since 1998, particularly in the Huasteca region (South Tamaulipas, East San Luis Potosí, North Veracruz and the State of Hidalgo). The aim of this study was to develop a model that relates the life cycle of the Central American locust with the climatic conditions of northeastern Mexico. The model is expressed in terms of a Thermal Time Clock calculated from mean monthly temperatures and photoperiod. Historic temperature data of 20 y, from 20 meteorological stations, were used to calculate average monthly (Ψ_{month}) and yearly (Ψ_{year}) values for thermal time (units are °C-days). For these calculations we used the Allen sine method, a lower temperature threshold ($k_1 = 15.3^\circ\text{C}$) and an upper thermal threshold ($k_2 = 38.5^\circ\text{C}$). An average Thermal Time Locust Development Clock (TTLDC) was calculated using the relationship $(\Psi_{month}/\Psi_{year}) \times 360$, which quantifies the monthly angular contribution on the clock ($\Psi = 10.6^\circ$). Essentially, the clock is a translator between thermal time and calendar time (or vice versa) and may be used to forecast locust-stage development dates, starting from a given "Bio-fix" point. This clock can be used to program management activities of this pest. Field observations from 2001 to 2008, on population density and development stages of the Central American locust, were consistent with the development times recorded in the TTLDC.

Resumen

La langosta centroamericana, *Schistocerca piceifrons piceifrons* Walker, es una plaga agrícola de importancia económica en México y Centro América; esta especie se caracteriza por su capacidad de gregarización y migración. A partir de 1998 se presentaron severas infestaciones de esta plaga en la región noreste de México, particularmente en la región Huasteca (Sur de Tamaulipas, Oriente de San Luis Potosí, Norte de Veracruz y Estado de Hidalgo). El objetivo del presente trabajo fue desarrollar un modelo que relacione el ciclo de vida de la langosta centroamericana con las condiciones climáticas del noreste de México. El modelo se expresa por medio de un Reloj en Tiempo Térmico Promedio para el Desarrollo de la Langosta (RTTDL), calculado a partir de temperatura media mensual y fotoperíodo. Se calculó el tiempo térmico promedio mensual y anual, a partir de datos históricos de temperatura de 20 años, provenientes de 20 estaciones meteorológicas ubicadas dentro del área de influencia de la plaga. Para estos cálculos se utilizó el método de la curva sinusoidal de Allen, una temperatura umbral mínima ($k_1 = 15.3^\circ\text{C}$) y máxima ($k_2 = 38.5^\circ\text{C}$). Los datos permitieron calcular un Reloj en Tiempo Térmico Promedio (RTTDL) promedio, mediante la relación $(\Psi_{mes}/\Psi_{año}) \times 360$, que cuantifica la contribución angular de cada mes en el reloj ($\Psi = 10.6^\circ$). Básicamente este reloj es un traductor del tiempo térmico y el tiempo calendario (o viceversa) y puede usarse para pronosticar las fechas en que se presentarán los distintos estados del ciclo de vida de la

langosta, a partir de una determinada fecha "punto Bio-fix"; lo cual permite programar actividades de manejo de esta plaga. Las observaciones de campo de 2001 a 2008 sobre densidad de población y estados de desarrollo de la langosta centroamericana fueron congruentes con los tiempos de desarrollo consignados en el RTTDL.

Key words

Central American locust, life history, thermal time clock, northeastern Mexico

Introduction

The Central American locust, *Schistocerca piceifrons piceifrons* Walker, is an economically important agricultural pest in Mexico and Central America, affecting almost all crops. Heavy infestations of this pest have occurred since early in 1998, causing severe damage to a diversity of annual and perennial plants in the Huasteca region (South Tamaulipas, East San Luis Potosí, North Veracruz and the State of Hidalgo) (DGSV 2003, Barrientos-Lozano *et al.* 2004). Biology, ecology and integrated management of *S. p. piceifrons* have been the subject of numerous studies (Barrientos-Lozano 2001a, b, c, d; Barrientos-Lozano 2005; Barrientos-Lozano *et al.* 2004; Poot 2005; Ávila-Valdez *et al.* 2005; Ávila-Valdez *et al.* 2006). These works have been crucial in understanding the behavior and the interaction of this insect in the ecosystem.

The species has two generations per year: the first generation occurs from May to August-September (60-80 d) and the second from October-November to May (155-180 d). Second generation, sexually immature adults go through a diapause period from December to April; diapause ends in Spring (March-April) and with the onset of the rainy season adults become sexually mature and begin mating (Barrientos-Lozano 2001b, c).

As poikilotherms, all insects adopt the temperature of the environment and therefore their rates of development are directly related to the air temperature within a particular interval (k_1 , k_2). In contrast to homeotherms, whose rate of development is conveniently expressed as a function of Julian or calendar time (day^{-1}), in poikilotherms, this is not so, unless the temperature remains constant during the whole developmental cycle. Instead, the rate of development of poikilotherms is best expressed as a function of thermal time, whose units are degree-days [$^\circ\text{C-days}$] $^{-1}$ (Higley *et al.* 1986). For insect species which enter a diapause period, as is the case of the Central American locust, besides air temperature the day length may

also play an important role in regulatory mechanisms. An insect's phenology models, expressed as a function of thermal time, may be useful in predicting pest development dates, monitoring scheduling, risk assessment analysis, predicting migration tracks and planning control actions (Mellors & Bassow 1983, Kauffman *et al.* 1985, Pinto *et al.* 2002). Online data bases are available to support insect model designs, for example, temperature thresholds and thermal times for insect development of many crop pests economically important: *e.g.*, (UC-IPM Online): (1) www.ipm.ucdavis.edu/_WEATHER/ddconcepts.html), (2) www.nappfast.org/pdf/IDD%202007.pdf.

Temperature and light are the most important single nonbiotic factors associated with the rate of growth and development of the Central American locust; however, other climatic variables also play significant roles. For example, early rain promotes copulation as well as egg laying, whereas a high relative humidity protects eggs and immature stages from dehydrating, and by so doing improves locust fertility and survival rates. High relative humidity may also increase locust susceptibility to the attack of naturally occurring entomopathogenic fungi, which might result in a decrease in locust population growth. Locust food availability (plant growth) is positively related with rain frequency and total precipitation. Finally, temperature gradients, solar radiation and light intensity may also play a role in migration, inasmuch as locusts show positive thermo- and phototropic effects (Porter *et al.* 1991; Cornford 1991 cited by Retana 2003; Barrientos-Lozano 2001a, b). While studying the effects of temperature on locust swarm migration, Uvarov (1935) reported two types of responses: a) an increase in swarm excitability when in contact with a warm soil surface and b) an increase in reflex actions, as expressed in terms of an increased jump length of individuals belonging to young swarms. More recent work (Retana 2003), establishes the relationship between sea surface temperatures "El Niño Southern Oscillation (ENSO), and the potential of this pest.

The aim of this study was to design an easy-to-use model, a Thermal Time Locust Development Clock (TTLDC), of help to biologists, entomologists and agronomists making decisions in

locust management, such as predicting pest development dates, monitoring scheduling, making risk assessment analyses, predicting migration tracks and planning control actions.

Materials and methods

The work was conducted in southern Tamaulipas, México, in an area between parallels 22°00'00" and 23°15'00" north latitude and meridians 98° 00'00" and 100°00'00 west longitude, at elevations from 0 to 380m a.s.l., from the coastal plain of the Gulf of Mexico, to the foothills of the Sierra Madre Oriental (SMO). Climatic conditions are defined by latitude, elevation and proximity to the Gulf of Mexico. The Tropic of Cancer divides the state into two climatic zones — the south with warm, humid climate and the north, less warm, with its little rain distributed throughout the year (INEGI 1983).

The grand mean monthly thermal time of the study area was calculated from the mean monthly minimum and mean monthly maximum temperatures of each of 20 meteorological stations (Table 1). Thermal time (°C-days) was calculated by the Allen sine method (1976), locating the axis of coordinates at the point (0, T_{med}). Thermal thresholds for the Central American locust, k_1 and k_2 , were taken from Barrientos-Lozano *et al.* (2004). Comparing temperature thermograms T_{max} and T_{min} with k_1 and k_2 there were six possible cases, but only three of them occurred in the area. This meant it required only three different equations for calculating thermal time: case 1, all thermogram temperatures are within the interval $k_1 \leq T \leq k_2$ (Fig. 1a); case 2, the daily minimum temperature is less than the lower threshold ($T_{min} < k_1$) and the maximum is located within the threshold values ($k_1 \leq T_{max} \leq k_2$) (Fig. 1b); this condition occurs frequently during the winter months, when locusts are in diapause; case 3, the thermogram maximum daily temperature is greater than the upper threshold ($T_{max} > k_2$) and the minimum is located within the interval [$k_1 \leq T_{min} \leq k_2$] (Fig. 1c); this usually occurs during spring and summer months (April-August). Cases 4, 5 and 6 are theoretically possible, but not probable in the area under study: [case 4 ($T_{min} <$

Table 1. Meteorological stations located in south Tamaulipas, México. Comisión Nacional del Agua (CNA-2006).

Meteorological Station	Lat North	Long West	Altitude meters a.s.l	Mean annual Precipitation mm
Aldama	22° 55'44"	98° 04'30"	130	959.4
Barberena	22° 37'15"	98° 10'15"	66	957.7
Chamal Nuevo	22° 50'30"	99° 01'30"	108	1210.7
El Nacimiento	22° 57'47"	98° 07'41"	140	836.4
González	22° 48'51"	98° 25'11"	55	899.5
El Refugio	22° 43'36"	99° 01'23"	230	NA*
Lázaro Cárdenas	22° 29'56"	98° 49'30"	67	943.1
Ocampo	22° 50'40"	99° 01'54"	320	1544
San Gabriel	23° 05'03"	98° 47'15"	140	1950
Xicoténcatl	22° 59'36"	98° 59'29"	100	1023
El Apuro	23° 15'18"	97° 52'17"	45	901.6
El Lajal	22° 50'46"	98° 43'46"	80	783.4
El Mayab	22° 54'56"	98° 20'44"	120	935.9
Gómez Farías	23° 01'43"	99° 08'45"	380	1842.3
Mante	22° 43'36"	98° 58'39"	100	1016.5
La Servilleta	22° 51'00"	99° 07'10"	94	1304.2
Estación Manuel	22° 43'31"	99° 18'30"	80	840
Nuevo Morelos	22° 31'49"	99° 12'50"	290	1062.3
San Felipe	22° 00'00"	98° 50'57"	68	966.9
El Oyul	22° 33'00"	99° 05'12"	NA*	1038.7

NA* = not available

k_1) and $(T_{\max} > k_2)$, case 5 ($T_{\min} \geq k_2$), case 6 ($T_{\max} \leq k_1$).

Day length (photoperiod), was obtained from latitude values given in Tables 1 and 2, which present monthly average day-length values (hours) for different latitudes (Mexican National Meteorological Service). For latitude values not listed in Table 2, linear extrapolation was used.

To calculate the daily number of hours at which the air temperature is less than 15.3 °C, diapause cool hours (case 2, Fig. 1b), the thermogram was adjusted by the method of Rodríguez-Absi *et al.* (2007) and Rodríguez-Absi (1997), using two functions: a sine function for the photoperiod and a decreasing exponential function for the night portion, as shown in Figure 2. It is convenient to separately analyze each part of the thermogram for establishing the equations which are needed in each case (Fig. 3).

Microsoft® Office Excel 2003 (Microsoft Corp., 2003) was used for: a) calculating daily thermal time using the derived equations for the three cases (1a,b,c) already discussed; b) calculating the day length (photoperiod) by linear extrapolation; c) calculating the number of hours below 15.3 °C which occur during diapause, using the derived cooling hours equations of Figure 3.

Input data included mean monthly minimum and mean monthly maximum temperatures of the 20 meteorological stations listed in Table 1, latitude values and temperature threshold values (k_1 and k_2). The program also calculated the monthly angular contribution to the clock and also the relationship between thermal time and a clock's angle. Thus, the following equations were also incorporated into the Excel program:

a) average monthly thermal time:

$$\Psi_{\text{monthly}} = \Psi_{\text{mean daily}} * (\text{days/month})$$

b) average yearly thermal time:

$$\Psi_{\text{yearly}} = \sum_{i = \text{january}}^{\text{december}} \Psi_{\text{month}_i}$$

c) average angular monthly contribution to the thermal clock:

$$\alpha_{\text{month}_i} = \frac{\Psi_{\text{month}_i}}{\Psi_{\text{yearly}}} * 360$$

d) relationship between thermal time and a clock's angle:

$$\Psi = \frac{\Psi_{\text{yearly}}}{360^\circ} \alpha$$

Once those calculations were performed and the clock was drawn, average locust phenological development data and other relevant information were incorporated into the clock, including dates at which developmental stages do occur, diapause period, *etc.*, (Barrientos-Lozano 2001a,b,c,d; Barrientos-Lozano 2005; Barrientos-Lozano *et al.* 2004; Ávila-Valdez *et al.* 2005; Ávila-Valdez *et al.* 2006).

Results and Discussion

The calculated yearly thermal time (Ψ_{yearly}) and Diapause Cool Hours (DCH) for the 20 meteorological stations are shown in Table 2. Maximum (Ψ_{yearly}) thermal time variation between the two more discrepant stations (Table 2) was 29%, (*i.e.*, 4272.3/3311.2-1*100),

Table 2. Calculated thermal time (°C-days) and Diapause Cool Hours (DCH) ($T \leq 15.3^\circ\text{C}$), for 20 meteorological stations located in south Tamaulipas, Mexico

Meteorological Station	(Ψ yearly) °C-days	Diapause Cold Hours (DCH) November 15th to April 10th $T < 15.3^\circ\text{C}$
Aldama	3389.9	1925
Barberena	3827.1	1655
Chamal Nuevo	3874.1	1913
El Nacimiento	3424.3	1892
González	3789.5	1900
El Refugio	3932.4	2018
Lázaro Cárdenas	3996.8	1857
Ocampo	3470.3	2065
San Gabriel	3715.9	2039
Xicoténcatl	4272.3	1908
El Apuro	3343.5	1773
El Lajal	4150.5	1850
El Mayab	3418.4	2063
Gómez Farías	3311.2	1941
Mante	3916.3	2038
La Servilleta	4041.1	1887
Estación Manuel	4062.7	1765
Nvo. Morelos	4202.6	1927
San Felipe	4036.5	1873
El Oyul	NA*	1985
	3798.71	1913.70
SD	314.93	105.76

NA* = not available

while DCH hours variation was about 25% (*i.e.*, 2065/1655-1*100). However, a better estimate of variability is obtained by dividing the values by the average value of the group, *e.g.*, when (Ψ_{yearly}) thermal time largest and smallest values are compared with the grand mean, the variability drops to 12.5 and 14.7% respectively. Analogous calculations for DCH result in a variation of 8 and 15.6% for extreme values, when such values are compared to the grand mean.

A TTLDC for south Tamaulipas, Mexico is shown in Figure 4. Note that in contrast to a regular calendar time clock in which all month angles would be approximately equal (30°), the monthly angles in a TTLDC may be quite different; for example, May's angle is 50°, whereas December's is only 16°. This means that May offers more than three times as many degree days for locust development as does December, *i.e.*, locust development rate in May is more than three times faster than that in December.

The relationship between (Ψ_{yearly}) thermal time (°C-days) and the angular values α is $\Psi = 10.6 \alpha$, as expressed in the center of the clock (Fig. 4). This means that a unit angle in the clock = 10.6 °C-days of thermal time. For example, an egg laid on 25th April, may hatch on May 15th (first instar nymph); the angle comprised between these two dates is ~30°, resulting in $\Psi = 10.6 * 30 = 318$ °C-days, as shown in Fig. 4. The thermal time involved in transition from one stage to another is calculated in an analogous manner, *i.e.*, by multiplying the constant 10.6 by the angle which comprises the change of stage.

The period from November to April is particularly interesting. This is when second generation adult locusts are in diapause. During this period not only do the lowest temperatures of the year occur, but also the photoperiod shortens. The average monthly number of cold days and the average monthly photoperiod for October to

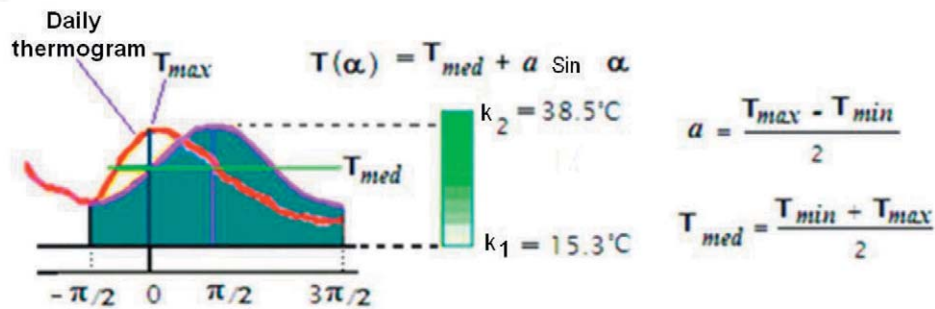


Fig.1a. All thermogram temperatures are within the $[k_1, k_2]$ interval. For color versions, see Plate II.

$$\Psi_{daily} = \frac{1}{2\pi} \int_{-\pi/2}^{3\pi/2} [T_{med} + a \sin \alpha - k_1] d\alpha$$

$$\Psi_{daily} = T_{med} - k_1$$

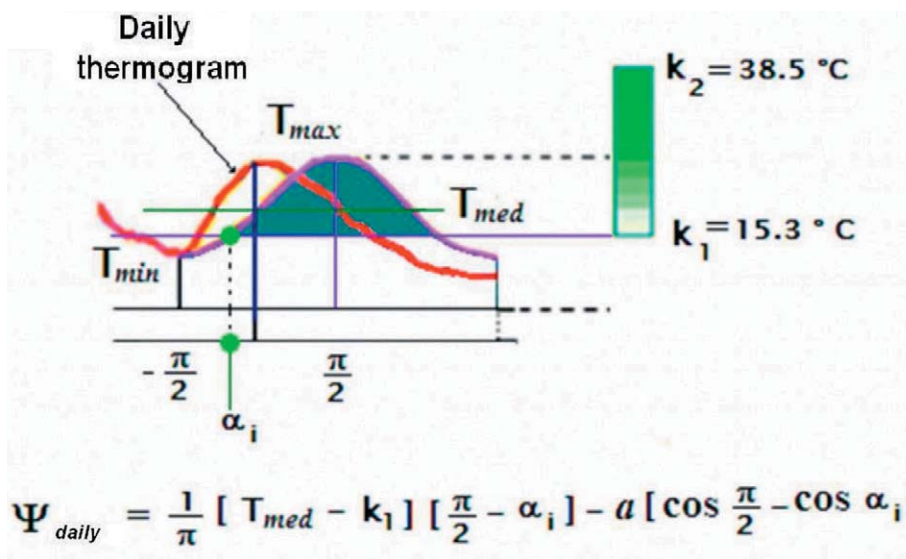


Fig.1b. The maximum daily temperature is located within the k_1, k_2 interval, but the minimum is less than k_1 .

$$\Psi_{daily} = \frac{1}{\pi} [T_{med} - k_1] \left[\frac{\pi}{2} - \alpha_i \right] - a [\cos \frac{\pi}{2} - \cos \alpha_i]$$

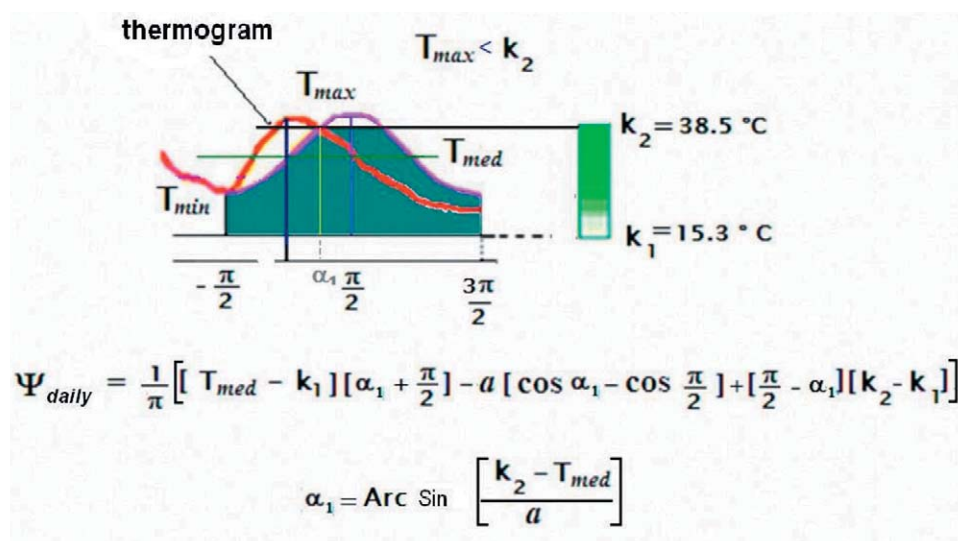


Fig.1c. The maximum daily temperature of the thermogram is greater than the upper threshold ($T_{max} > k_2$) and the minimum is located within the interval $[k_1 \leq T_{min} \leq k_2]$; this usually occurs during spring and summer months (April - August).

$$\Psi_{daily} = \frac{1}{\pi} [T_{med} - k_1] \left[\alpha_1 + \frac{\pi}{2} \right] - a [\cos \alpha_1 - \cos \frac{\pi}{2}] + \left[\frac{\pi}{2} - \alpha_1 \right] [k_2 - k_1]$$

$$\alpha_1 = \text{Arc Sin} \left[\frac{k_2 - T_{med}}{a} \right]$$

April are shown in Fig. 5. It is suggested that the input signal to initiate diapause is controlled by day length (F_p), particularly when $F_p \leq 11h$: this occurs November 18th to 30th; the number of cooling hours is increasing at an approximate rate of 288 hours per month as shown in Figure 5.

The diapause stage continues whenever the rate of cooling is greater than 288 hours month⁻¹ (12 to 13 cold-days/month; $T \leq 15.3^\circ\text{C}$ /month) and concludes when $F_p \geq 12h$. The average total number of cooling hours, which occurs during the whole diapause interval, is around 1914 (Table 2).

Immature individuals of the Central American locust, similar to other locust migratory species, show phenotypic plasticity; this is defined as the capacity of a given genotype to produce different phenotypes in response to varying environmental conditions (Pigliucci 2001). For example, diapause entrance of *S. p. piceifrons* occurs with last instar, green-color nymphs. These individuals are solitary and avoid encounters with other individuals. As the number of solitary nymphs increases, they develop pink to red color with intense black pigments and become gregarious (Fig. 6).

Changes occur not only in color but also in behavior; a density-dependent gregarious mechanism is activated and may result in swarms of millions of individuals. The dorsal black stripes allow the insect to be more efficient at absorbing solar radiation, raising its body temperature and metabolic activity; this is important during the winter (diapause stage) because temperature may drop several degrees below k_1 (15.3°C).

To incorporate Locust Development Stages, Diapause Cooling Hours and Day length data into the TTLDC, three circles were added (Fig. 7); the outermost circle comprises life history stages of the Central American locust. This circle moves in phase with the 10° -angle graduated circle. The inner two circles correspond to photoperiod (day length) and cold hours, respectively. For example, when the zero of the angular section (10° degrees graduated circle) is set at the date when last instar nymphs are initially observed (i.e., Nov 15th) (Bio-fix point), the average dates at which other stages of development occur, may be read on the scale dates: since the angle remains constant (it is proportional to thermal time), variation is only in dates. Data on life history, ecology and field observations from 2001 to 2008 on the Central American locust (Barrientos-Lozano 2001a, b, c; Barrientos-Lozano 2005; Barrientos-Lozano et al. 2004; Ávila-Valdez et al. 2005; Ávila-Valdez et al. 2006) are consistent with the development time estimated in the average TTLDC. Variation is

due to fluctuations of temperature and moisture typical of different years, so the life cycle of this pest is advanced or delayed.

Conclusions

This average Thermal Time Locust Development Clock (TTLDC), obtained for the Central American locust, can be used to predict timing of phenological stages of this pest; this implies a starting date (Bio-fix). This date is experimentally established after obtaining quality data on population dynamics and on the life cycle of the pest. Reliability of predictions depends upon accuracy of the starting date and deviations in weather condition from the average year. When the TTLDC was compared with field observations, the differences were relatively small.

Building a TTLDC involved calculations using average values: temperature, day length, diapause cool hours and calendar dates. Thus it may be expected that the clock provides reasonably good estimates for predicting locust phenological development in south Tamaulipas, México. However, more accurate clocks may be built, incorporating other variables such as relative humidity, rain etc. More specific clocks could be developed for smaller areas and used in local pest management programs. At present, several minimetereological stations connected to the web have been installed throughout. This may facilitate analysis on pests' life cycle vs climate data using the methods already discussed.

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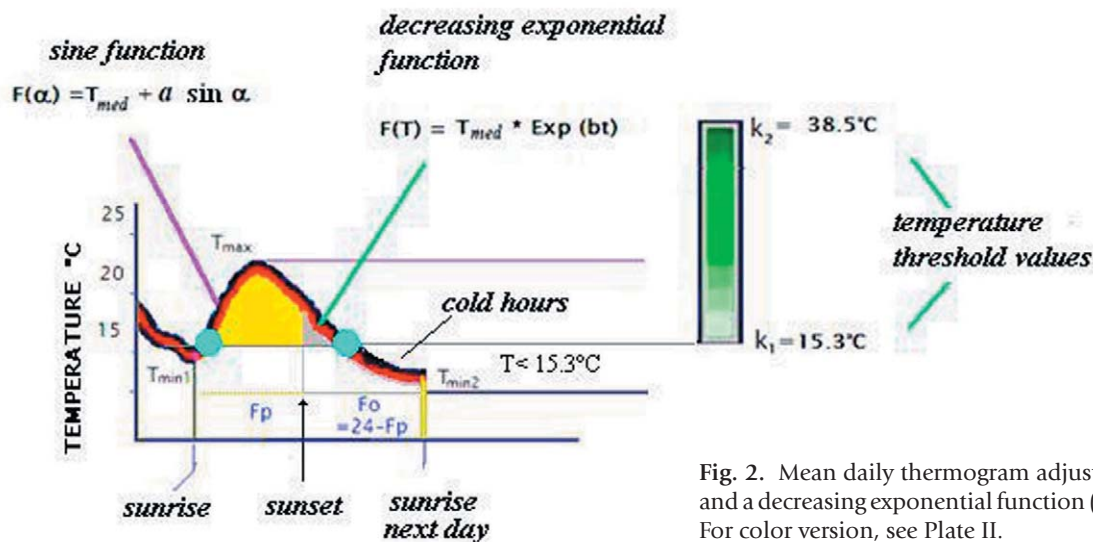


Fig. 2. Mean daily thermogram adjusted by two functions: a sine and a decreasing exponential function (Rodríguez-Absi et al. 2007). For color version, see Plate II.

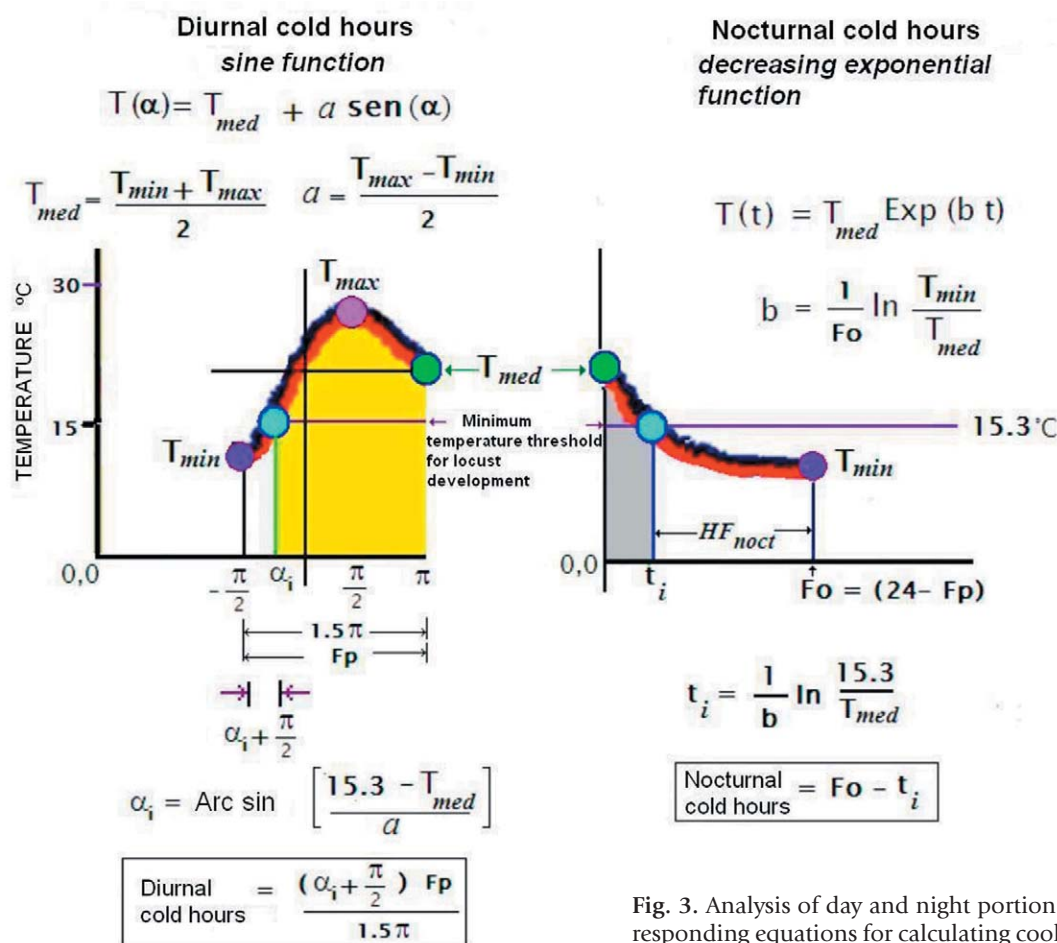


Fig. 3. Analysis of day and night portion of the thermogram and corresponding equations for calculating cool hours. For color version, see Plate II.

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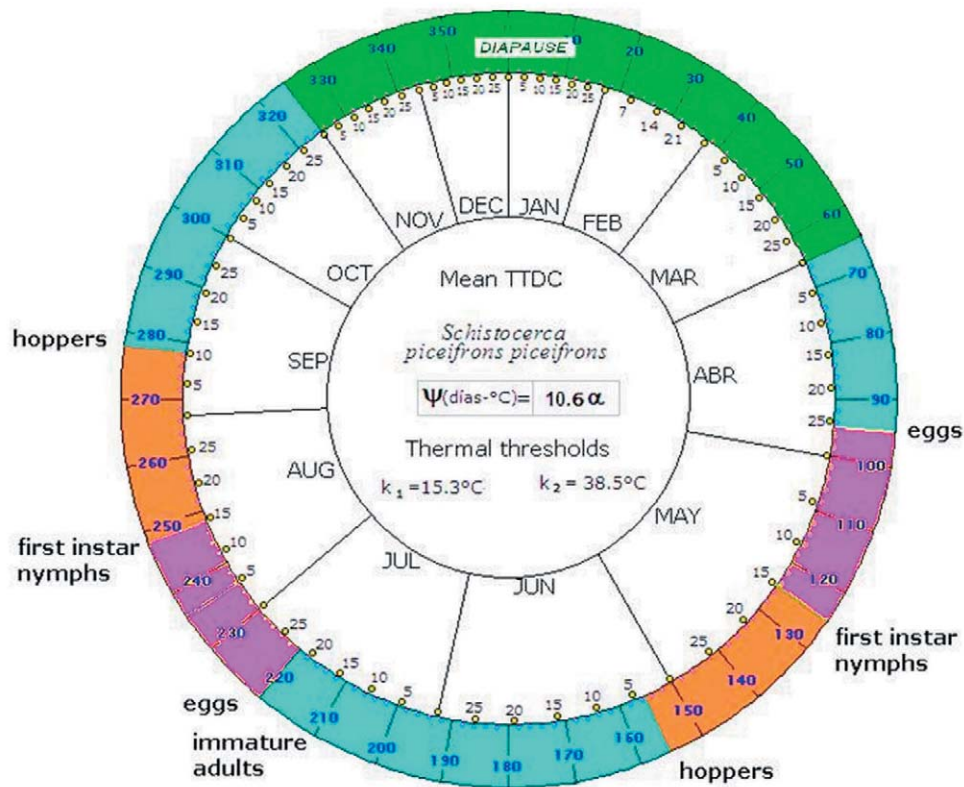


Fig. 4. Mean Thermal Time Locust Development Clock (TTLDC) for the Central American locust (*Schistocerca piceifrons piceifrons*) showing the angular sectors involved for different stages of development. For color versions, see Plate III.

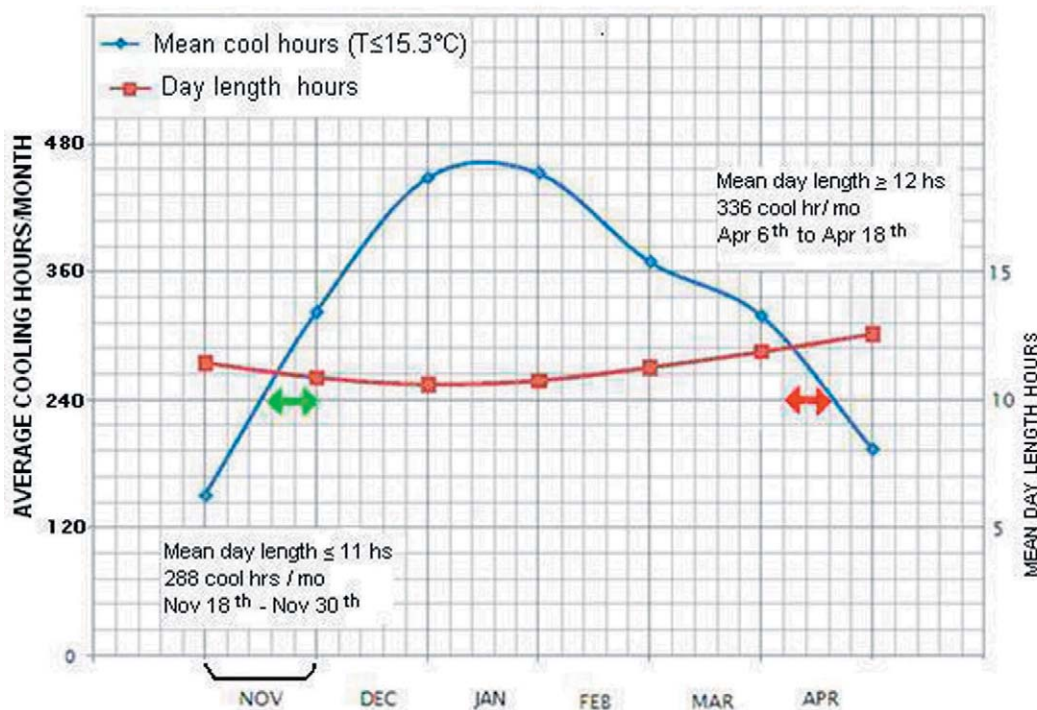


Fig. 5. Mean monthly values of cool hours and average daylight hours in south Tamaulipas, Mexico. For color versions, see Plate III.



Fig. 6. Phenotypic plasticity in *S. p. piceifrons*. Solitary green-color nymphs change to gregarious pink-reddish with black pigmentation, in response to population density. For color versions, see Plate III.

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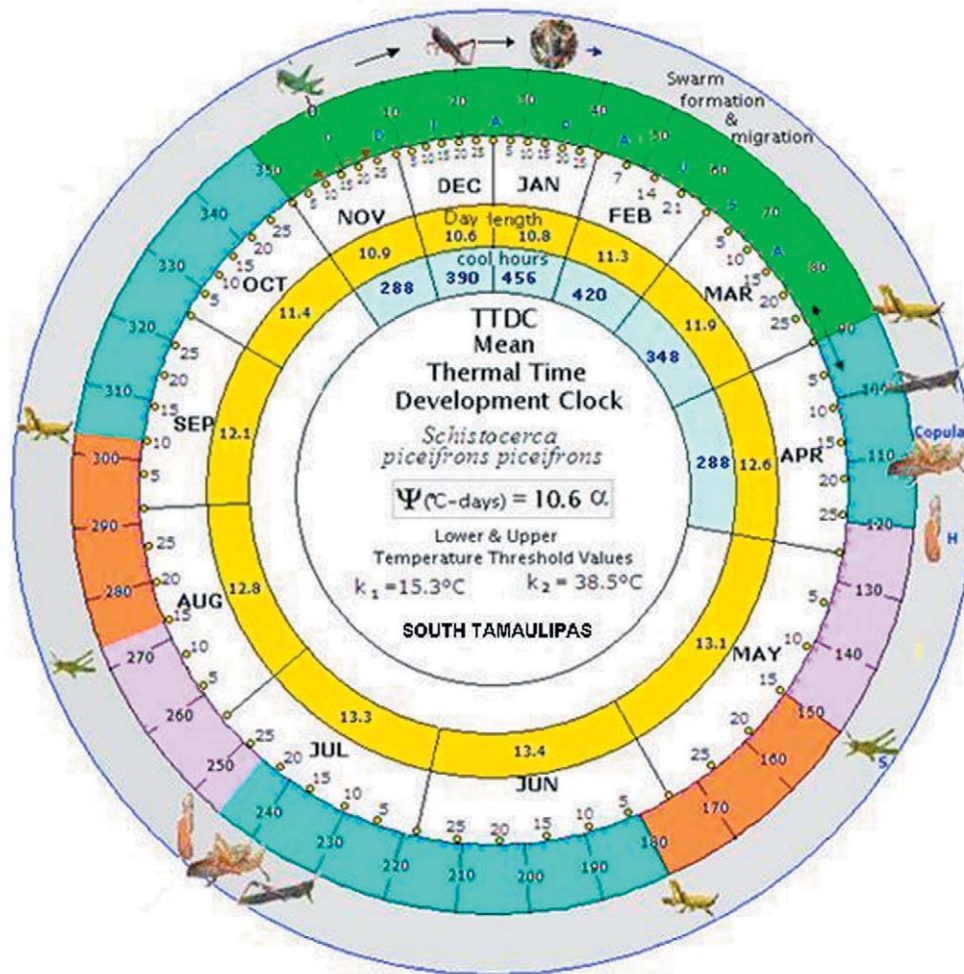


Fig. 7. Mean TTLDC with additional scales: average monthly cool hours and average monthly day length (photoperiod). For color versions, see Plate III.