DYNAMIC SIMULATION MODEL OF CENTRAL AMERICAN LOCUST *SCHISTOCERCA PICEIFRONS* (ORTHOPTERA: ACRIDIDAE)

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ABSTRACT

Locusts, large gregarious and migratory grasshoppers, are pests of economic importance in several regions of the world because of the severe damage they can cause to crops. The Central American locust, *Schistocerca piceifrons* is the most important locust species in the Americas, and it is distributed in zones of Mexico, Central and South America. In Mexico, despite the efforts to survey and monitor *S. piceifrons* (Walker) populations, outbreaks are still difficult to predict and prevent, and high economic and ecological costs are incurred in controlling them. The purpose of this study was to build a dynamic model of locust growth and development as a function of environmental conditions in order to identify suitable conditions for the high reproduction rates of this insect. This information can be used to assist in locust management. A modular approach and numerical integration techniques were applied in model building. The main inputs of the model were daily rainfall and temperature data, and physical soil properties such as texture and depth. The model estimates the growth of non-cultivated grass in breeding zones and oviposition rates as a function of soil moisture. The development rates of the different locust stages are calculated as a function of temperature. The model satisfactorily represents *S. piceifrons* behaviour, and generates 2 generations per yr, the first in summer and the second in winter. In locations with suboptimal temperatures the second generation does not complete development until the next year. A good agreement was found between model outputs and field data from Yucatan, Mexico for 2008 to 2010. Based on these results the model is proposed for use as a tool to support *S. piceifrons* monitoring by the National Locust Control Program.

Key Words: *Schistocerca piceifrons*, model, population dynamics, life cycle, locust

RESUMEN

Langosta, el nombre común dado a los chapulines gregarios y migratorios son considerados como plaga de importancia económica en el mundo debido a los daños que causa a los cultivos. La langosta centroamericana *Schistocerca piceifrons* (Walker) es la más importante en el continente americano y se encuentra distribuida en zonas de México, Centro y Sudamérica. En México, a pesar de los esfuerzos de seguimiento y control de las poblaciones de *Schistocerca piceifrons*, los brotes de este insecto siguen siendo difíciles de predecir y prevenir ocasionando altos costos económicos y ecológicos para controlarlos. El objetivo de este estudio fue construir un modelo dinámico del crecimiento y desarrollo de la langosta en función de las condiciones ambientales con el fin de identificar las condiciones adecuadas para altas tasas de reproducción y darle soporte al manejo de la langosta. Un enfoque modular y métodos de integración numérica fueron utilizadas en la construcción del modelo. Las principales entradas del modelo son datos diarios de temperatura y precipitación y propiedades físicas del suelo como la textura y la profundidad. Las tasas de desarrollo de las diferentes etapas de la langosta son calculadas en función de la temperatura. Se encontró una buena concordancia con las salidas del modelo y los datos de campo del 2008 al 2010 en el estado de Yucatán, México. Con base en estos resultados, el modelo se propone como una herramienta de apoyo a la Campaña Nacional de Langosta para el monitoreo de *S. piceifrons.*

Palabras Clave: *Schistocerca piceifrons*, modelo, dinámicas poblacionales, ciclo de vida, langosta

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Locusts are among the most feared and devastating pests of agriculture. They are gregarious and migratory grasshoppers (Orthoptera: Acrididae). When congregated in swarms and bands, locusts have the capacity often to reduce yields up to 80% or even to completely destroy entire fields of crops (Song 2004). Only some locust species present the characteristics of acting in coordination and migrating long distances as destructive swarms of adults or bands of wingless nymphs called hoppers. Swarms and bands may contain billions of individuals acting as a cohesive unit (Buj 1996; Cressman 1997; Song 2005). Two migratory species of locust are present in the Americas: the Central American locust (CAL), *Schistocerca piceifrons* (Walker), and the South American locust, *Schistocerca cancellata* (Serville) (Harvey 1983; Shannon & Arboleda-Sepúlveda 1988). The first of these is considered to be the most dangerous migratory locust in the Americas.

CAL is distributed in Mexico, Central America, Colombia, Venezuela, Guyana, Ecuador, and Peru. Permanent populations of this insect are present in the state of Yucatan, Mexico, northern Honduras, and the Pacific coast of Central America (Harvey 1983). CAL presents 2 behavioral phases: the gregarious and the solitarious (Sword 2003; Song et al. 2006). During the solitarious phase, locust populations are sparse, individuals remain scattered or isolated, and they act independently. These characteristics make it difficult to perceive their presence or locate them in the field. While in the gregarious phase, the locust population congregates in dense groups acting in coordination and devastating crops and other vegetation. The change of phase from solitarious to gregarious, and vice versa, is associated with the increase and decrease of population densities in response to variations in the coverage and biomass of the vegetation (van Huis et al. 2007). The life cycle of CAL includes 3 different stages: egg, nymph and adult. Under the conditions of central and southern Mexico this insect completes 2 generations per yr (Harvey 1983). The first generation occurs from May to Sep and the second from Oct to May. Under warm and humid climates, and therefore with an abundant food availability, this locust is capable of high reproductive rates by the end of each generation, and this results in significant increases in population densities, as occurs in the southeastern Mexican states of Campeche and Yucatan. In other states with a well-defined winter season, such as Tamaulipas and San Luis Potosi, the preoviposition period at the end of the second generation can take several months because of the delay in the rate of development caused by the cold and dry climate and the lack of food (Ramirez & Romero 2008). Although the life cycle and the behavioral phases of CAL are well understood, the high dependence of the processes of development and oviposition on weather and vegetation conditions obstructs the application of opportune measures to prevent swarm formation. In Mexico the CAL is categorized as a pest of economic importance with control actions being the responsibility of government (SENASICA 2012). One of the main concerns of the official research program is the development of weather-based tools to support the monitoring of this insect (SENASICA 2012).

Modelling techniques have been used as a tool to support management and control of some locust species in several regions of the world. Models of *Schistocerca gregaria* (Reus & Symmons 1992) and *Locustana pardalina* (Tilch & Hanrahan 2000) are used to support the monitoring of locusts in Africa (Price & Brown 1999; Roffey & Magor 2003). In both cases the models help to forecast outbreaks of the pest based on the locust life cycle and the process of migration (Tilch & Hanrahan 2000; Roffey & Magor 2003). For CAL, Galván-Martínez et al. (2008), developed a simulation model that estimates the populations of the second generation of this insect for the southern region of the state of Tamaulipas in Mexico by using statistical estimates of growth and mortality, but without taking into consideration the influence of weather. This limits considerably the model's capacity to simulate locust behaviour. Rodríguez-Absi et al. (2009) built a thermal time clock to calculate the phenological stages of CAL in northeastern Mexico using mean monthly temperatures and photoperiod. This model serves as a general reference to locate the different stages of locust throughout the yr but does not provide information about the reproductive period, because rainfall and food availability are not considered in the model.

The objective of this study was to construct a dynamic simulation model of the CAL, which would particularly include the effects of weather and vegetation variables on the population biology of this species.

Materials and Methods

The present study is based on a comprehensive approach, which takes into consideration the process of growth and development of the CAL and its interactions with the climatic conditions and the availability of food. The population dynamics of the insect were modelled through stock-flow feedback relationships to represent the different life stages and the size of the insect population. Food availability depends on the grass biomass in the breeding zones, and the growth rate of grass is calculated as a function of solar radiation (SRad) and potential evapotranspiration (PET). The model is intended to begin calculations at the end of the second generation, i.e., when adults have completed their development. The first estimation consists of determining if these adults are sexually mature or not, depending on temperature and food availability conditions. From this point, the model calculates the timing for reproduction and oviposition of CAL and the course of growth and development of subsequent generations.

The model was built and parameterized using the available knowledge of CAL biology regarding its development stages, reproduction rates and feeding habits (Hunter-Jones 1967; Retana 2000; Ramirez & Romero 2008). Model inputs include dai-

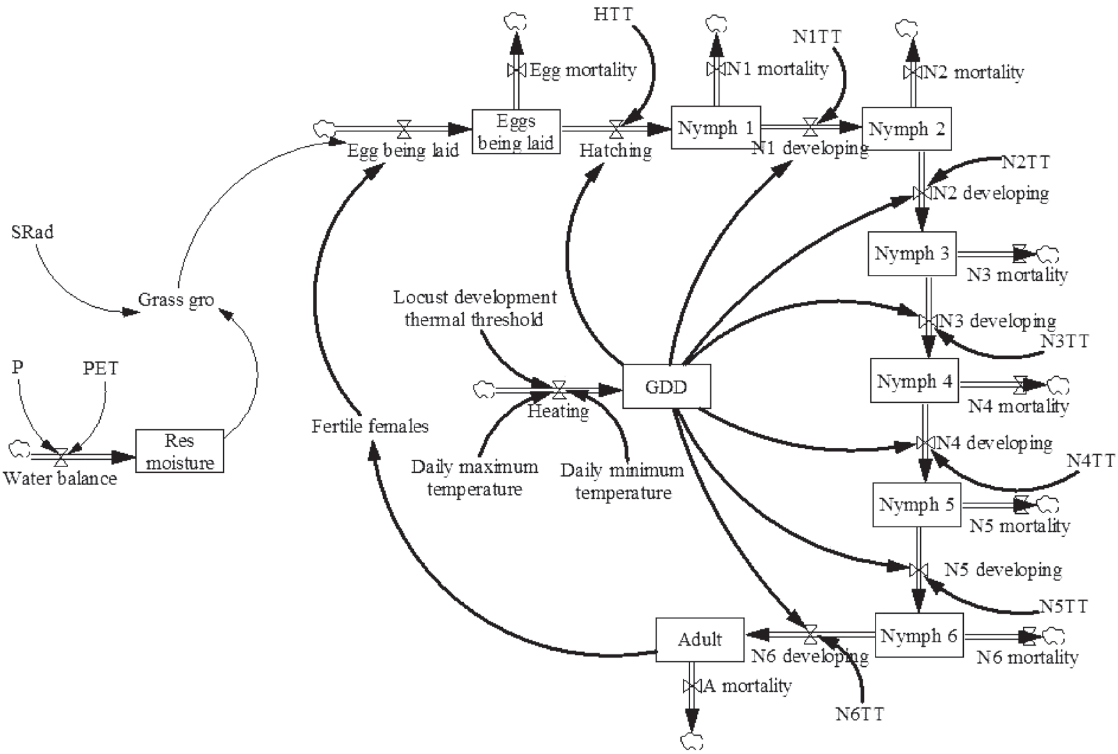

Fig. 1. Diagram of conceptual model of the development of the Central American Locust (CAL), *Schistocerca piceifrons*. The diagram indicates that rate of development in the life cycle is driven by the cumulative temperature (growing degree days) and food availability.

ly weather data (temperature and rainfall), which were obtained from the National Weather Service (SMN) of Mexico database and from the national agro-meteorological network (http://clima.inifap.gob.mx/redclima/), initial CAL population density according to the field survey data provided by the Mexican Plant Protection Organization (SENASICA), grass biomass, and soil physical properties (INIFAP 2001). The main output of the model is the population dynamics of the insect, i.e., the number of individuals and the date of appearance of the different life stages. CAL field survey data provided by SENASICA were used to validate the model.

The CAL Life Cycle Module

The life cycle of CAL was modelled considering its 8 developmental stages (Ramirez & Romero 2008), i.e., the egg, the first to the sixth instar and the adult. As described previously, *S. piceifrons* completes 2 generations in 1 yr. In every life cycle, the transition between successive life stages is calculated as a function of accumulated growing degree days (GDD). Adult sexual maturity requires temperatures above 20 °C and growth of new leaves to guarantee that enough food is available (Symmons & Cressman 2001). If these conditions are not present, adults remain immature or in diapause until the temperature rises and the rainfall permits vegetation growth (Ramirez & Romero 2008). The period with new vegetative growth of grass becomes available when enough humidity is calculated to exist based on a simple climatic water balance in which rainfall (P) is compared with potential evapo-transpiration (PET) following the method proposed by FAO (1996). When P exceeds half the PET, the grass growing period is considered to start and residual moisture storage is calculated as a function of soil physical properties. The growing period ends when residual moisture is completely exhausted. Fig. 1 shows the flow diagram of the model in terms of the stock and flow variables that represent the life cycle of the insect.

The model algorithm was constructed using the program Vensim 4.2a, which consists of a graphical environment that permits users to draw the flow diagram of the model, and an assisted module to write the numerical integration equations (Ventana Systems 1999). A complete description of the developed model equations are presented in Table 1.

Data to parameterize the developmental times were taken from Retana (2000) and Hunter-

TABLE 1. LIST OF VARIABLES AND EQUATIONS FOR A MODEL OF THE POPULATION DYNAMICS OF THE CENTRAL AMERICAN LOCUST (CAL), *SCHISTOCERCA PICEIFRONS*.

Variable name	Equation	Description
State Variables		
Egg	$Egg_{(t+\Delta t)}$ = Eggt + Δt(Egg being laid – Egg mortality – Hatching)	Egg population
Nymph 1	Nymph $1_{(t+\Delta t)}$ = Nymph 1t + Δt(Hatching – N1 mortality – N1 developing)	Nymphal 1 population
Nymph 2	Nymph $2_{(t+\Delta t)}$= Nymph 2t + Δt(N2 developing – N2 mortality – N2 developing)	Nymphal 2 population
Nymph 3	Nymph $3_{(t+\Delta t)}$= Nymph 3t + Δt(N3 developing – N3 mortality – N3 developing)	Nymphal 3 population
Nymph 4	Nymph $4_{(t+\Delta t)}$= Nymph 4t + Δt(N4 developing – N4 mortality – N4 developing)	Nymphal 4 population
Nymph 5	Nymph $5_{(t+\Delta t)}$= Nymph 5t + Δt(N5 developing – N5 mortality – N5 developing)	Nymphal 5 population
Nymph 6	Nymph $6_{(t+\Delta t)}$= Nymph 6t + Δt(N6 developing – N6 mortality – N6 developing)	Nymphal 6 population
Adult	$Adult_{(t+\Delta t)}$= Adultt + Δt(N6 developing – A mortality)	Adult population
GDD	$GDD_{(t+\Delta t)}$= GDDt + Δt(Heating)	Degree days
Res moisture	Res $moisture_{(t+\Delta t)}$= Res moisturet + t(water balance)	Residual moisture
	Rate Variables	
Egg mortality	f(Egg, T)	Egg mortality
N1 mortality	f(Nymph1, T)	Nymph 1 mortality
N2 mortality	f(Nymphs2,T)	Nymph 2 mortality
N3 mortality	f(Nymphs3,T)	Nymph 3 mortality
N4 mortality	f(Nymphs4,T)	Nymph 4 mortality
N5 mortality	f(Nymphs5,T)	Nymph 5 mortality
N6 mortality	f(Nymphs6,T)	Nymph 6 mortality
A mortality	f(Adult,T)	Adult mortality
Hatching	f(Egg, GDD, HTT)	Nymph hatching
N1 developing	f(Nymph 1, GDD, N1TT)	Nymph 1 developing
N2 developing	f(Nymph 2,GDD, N2TT)	Nymph 2 developing
N3 developing	f(Nymph 3,GDD, N3TT)	Nymph 3 developing
N4 developing	f(Nymph 4,GDD, N4TT)	Nymph 4 developing
N5 developing	f(Nymph 5,GDD, N5TT)	Nymph 5 developing
N6 developing	f(Nymph 6, GDD,N6TT)	Nymph 6 developing
Heating	F(Locust development thermal threshold, Daily maximum temperature, Daily minimum temperature)	Heating
Water balance	f(P, PET)	Water balance

TABLE 1. (CONTINUED) LIST OF VARIABLES AND EQUATIONS FOR A MODEL OF THE POPULATION DYNAMICS OF THE CENTRAL AMERICAN LOCUST (CAL), *SCHISTOCERCA PICEIFRONS*.

Variable name	Equation	Description
	Auxiliary variables and constants	
HTT	Constant	Nymph hatching degree days
N1TT	Constant	Nymph 1 degree days
N2TT	Constant	Nymph 2 degree days
N3TT	Constant	Nymph 3 degree days
N4TT	Constant	Nymph 4 degree days
N5TT	Constant	Nymph 5 degree days
N6TT	Constant	Nymph 6 degree days
Daily maximum temperature	Constant	Daily maximum temperature
Daily minimum temperature	Constant	Daily minimum temperature
Locust development thermal threshold	Constant	Locust development thermal threshold
P	Data	Rain
PET	Data	Evapotranspiration
Grass gro	f(Srad, Res moisture)	Grass growth
SRad	Data	Solar Radiation

Jones (1967) as shown in Table 2, whereas the required GDD for every developmental stage was taken from Retana (2000) as shown in Table 3. A temperature of 13 °C was used as threshold for GDD accumulation. The life cycle duration from egg to adult varies from 60 to 80 days in the summer and reaches approximately 155 days in the winter (Ramirez & Romero 2008).

CAL mortality was calculated based in the data reported by Astacio & Landaverde (1988) about the temperature for development of CAL, and data from Gangwere (1991) on the temperature range for development of Acrididae, as is shown in Table 4.

Model Validation

Data of bi-monthly surveys provided by the Mexican locust control program in Yucatan, Mexico were utilized for validating the model. These data consisted in a report of the presence of the different stages of CAL and their densities classified as low, medium or high as described by (Ramirez & Romero 2008).

Simulations of population dynamics of CAL were performed with daily data from the meteorological stations of the state of Yucatan covering the 2010 and 2011 yrs. The variables used were rainfall, maximum and minimum temperatures, and estimated values of Solar Radiation (W/m^2) and Potential Evapotranspiration (PET).

Field data for the dates of appearance of the different stages of CAL were collected in 2010 and 2011 at Tizimin, in the state of Yucatan, Mexico. These data were provided by the National Service of Food Health, Safety and Quality (SENASICA-SAGARPA-Mexico).

The model was evaluated by comparing simulated and observed data on dates of appearance for the different stages of the life cycle of the CAL. A linear regression analysis was performed to verify the statistical significance of this relationship and the predictive capacity of the simulation model.

TABLE 2. DEVELOPMENT TIMES (DAYS) OF THE CENTRAL AMERICAN LOCUST (CAL), *SCHISTOCERCA PICEIFRONS* BASED ON RETANA (2000) AND HUNTER-JONES (1967).

	Duration (days)	
Stage	26.5-27.4 °C (Retana 2000)	32 °C (Hunter-Jones 1967)
Egg	30	19
1 Nymph	8	6
2 Nymph	10	6
3 Nymph	10	6
4 Nymph	11	6
5 Nymph	11	8
6 Nymph		12

TABLE 3. GROWING DEGREE DAY (GDDS) ACCUMULATION FOR THE CENTRAL AMERICAN LOCUST (CAL), *SCHISTOCERCA PICEIFRONS* BASED ON RETANA (2000).

Stage	GDD
Egg	405-432
1 nymph	110-114
2 nymph	137-143
3 nymph	137-144
4 nymph	151-157
5 nymph	166-173

RESULTS

Population Dynamics of the CAL

As a first trial of the model, the population dynamics of CAL at Panaba, Yucatan, Mexico was simulated. Simulation was carried out from 1 Jan 1 2008 to 31 Dec 2009. The model was initialized with 40,000 adults assuming that at the beginning of the yr the adults of the second generation of 2007 were finishing the maturation process . The initial number of eggs and nymphs was assumed to be zero. In 2008 adults of the first generation were present from the beginning of Aug to early Nov, while the adults of the second generation occurred from Jan to Jul 2009. In 2009 adults of the first generation were estimated to exist from Aug to Nov and those of the second generation appeared in Dec and remained until the next yr (Fig. 2). In both yrs, the population of the second generation was higher than that of the first one. In 2008, nymphs of the first generation emerged at the beginning of Jul and continue their development until Sep. The immatures of the second generation appeared at the end of Oct of 2008 and finished development in Jan of 2009. In 2009 nymphs of the first generation occur from Jul to Aug and those of the second generation

TABLE 4. PERCENT MORTALITY OF THE CENTRAL AMERICAN LOCUST (CAL), *SCHISTOCERCA PICEIFRONS*.

Temperature	% mortality
16	50
28	0
32	0
38.5	40
40	50

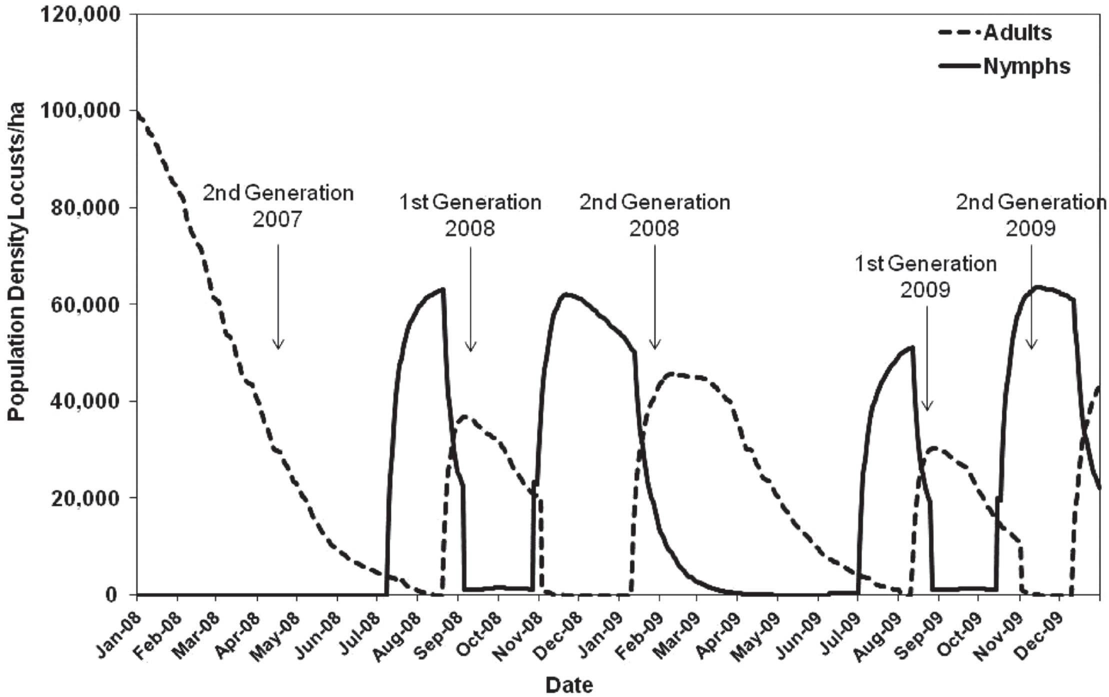

Fig. 2. Population dynamics of the Central American Locust (CAL), *Schistocerca piceifrons*, in Yucatan, Mexico from Jan 2008 to Dec 2009. Nymphs are represented by the continuous line and adults by the discontinuous line and adults by the continuous line.

appeared in Oct and continue developing into the next yr. These results are consistent with the description of the CAL life cycle presented by Ramirez & Romero (2008).

Model Validation

Fig. 3 shows the comparison of observed (open circles) and simulated (dashed line) data of adult population dynamics of CAL for Tizimin, Yucatan, Mexico in 2010. It is clear that there were 2 population peaks; the first generation of adults began in Aug and the second appeared in Dec.

There was good agreement between experimental and simulated data using our model. Also there existed a remarkable difference in population densities between the first and the second generations.

The simulated dates of adult appearance were compared with the observed data to evaluate the predictive capacity of the model (Fig. 4). A simple linear regression model was obtained to relate the observed and simulated data. As can be seen, the model performance was very similar to that of the observed data with a coefficient of determination (R^2) of 91%. These results indicate that the model can be used as a reliable tool to estimate the timing of the different stages of CAL, and to support decisions on the need for management interventions to limit population growth.

To explore the model's capacity for long term predictions of CAL population dynamics, the insect populations were simulated over the period from 2001 to 2010 in Yucatan, Mexico. There was a well-defined annual pattern of nymphal appearance (Fig. 5). Two complete generations were estimated every yr, and the population abundance of the first one was always lower in than the second. In early of 2009 and 2010 the population densities were higher. According to field data for these yrs, locust bands and swarms occurred early in those 2yr in the state of Yucatán.

Discussion

The model outputs adequately represented the population dynamics of CAL, registering 2 generations per yr, as reported by Ramirez & Romero (2008). Higher densities of the second generation are attributed to the suitable conditions of humidity and food availability for the reproduction and development of the locust in the summer (Rodriguez-Absi et al. 2009). In the

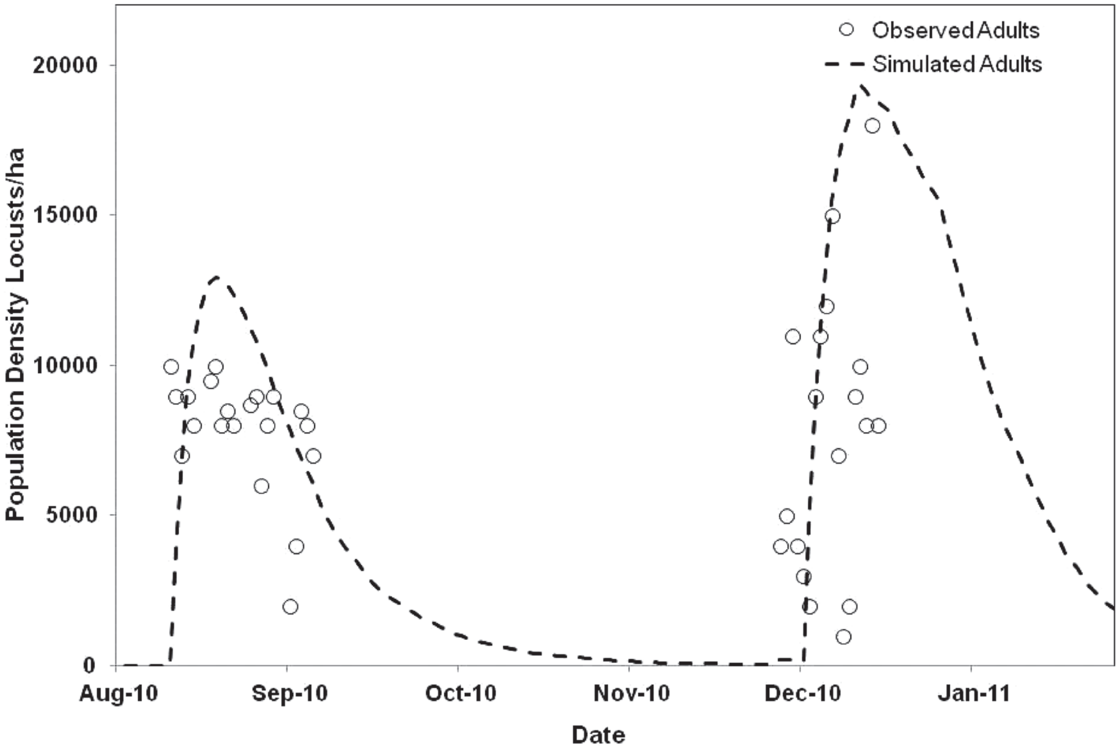

Fig. 3. Comparison of simulated and observed data on adults of the Central American Locust (CAL), *Schistocerca piceifrons*, in Yucatan, Mexico, during Jul 2010 to Feb 2011. The simulated adult population is represented by the dashed line and the observed population is represented by open circles.

first generation of each yr the population was low because their parents (the adults of second generation of the previous yr) appear in the winter period when temperatures were low and food was scarce. The latter conditions caused both an increase in adult mortality and delayed sexual maturity, which resulted in low egg production.

The estimated periods of nymphal and adult occurrence were similar to those reported by Ramirez & Romero (2008). Some differences occurred in the periods of emergence between the model output and data reported by Ramirez & Romero (2008), but these were attributable to variations in weather conditions from one yr to another.

Considering that weather is the main factor influencing the development of the insects (Rodriguez-Absi et al. 2009) the shorter duration of nymphs and adults of the first generation can be explained by the prevalence of suboptimal temperatures during the winter. These conditions determine that adults of the second generation do not become sexually mature until the next yr. The model structure was designed to estimate the dates of appearance of the different stages of CAL as a function of weather conditions. This is a very important feature because the National Locust Control Program relies on the intense monitoring of CAL phenology, where the timely identification of critical events, especially reproduction and emergence of immatures are crucial to the effectiveness of preventive measures.

In this sense, model estimations of CAL phenology showed close agreement with observed data even when weather inputs did not correspond exactly with the sites of CAL sampling. Based on these results, the model developed is being proposed to enhance the monitoring capacity of the Locust Control Program. Model simulations of locust population dynamics can be combined with the physical surveys so that simulated and observed data may be displayed in a Geographic Information System that integrates them into a weather-based monitoring CAL system.

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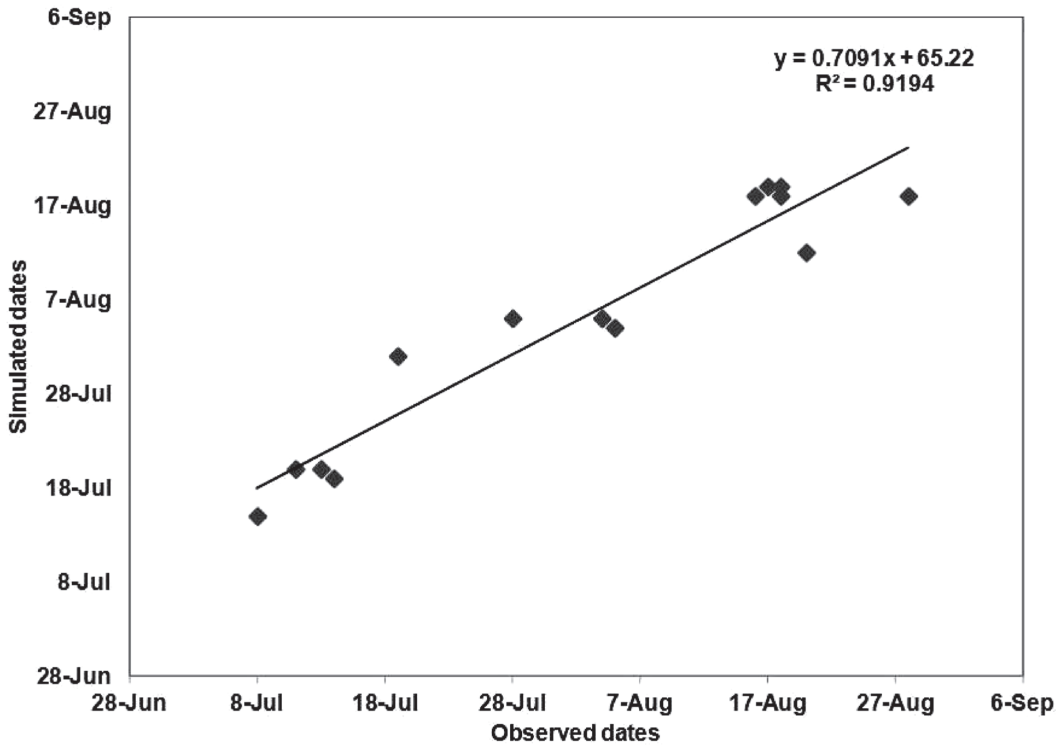

Fig. 4. Simulated and observed dates of appearance of adults of the Central American Locust (CAL), *Schistocerca piceifrons*, in Yucatan, Mexico in 2010.

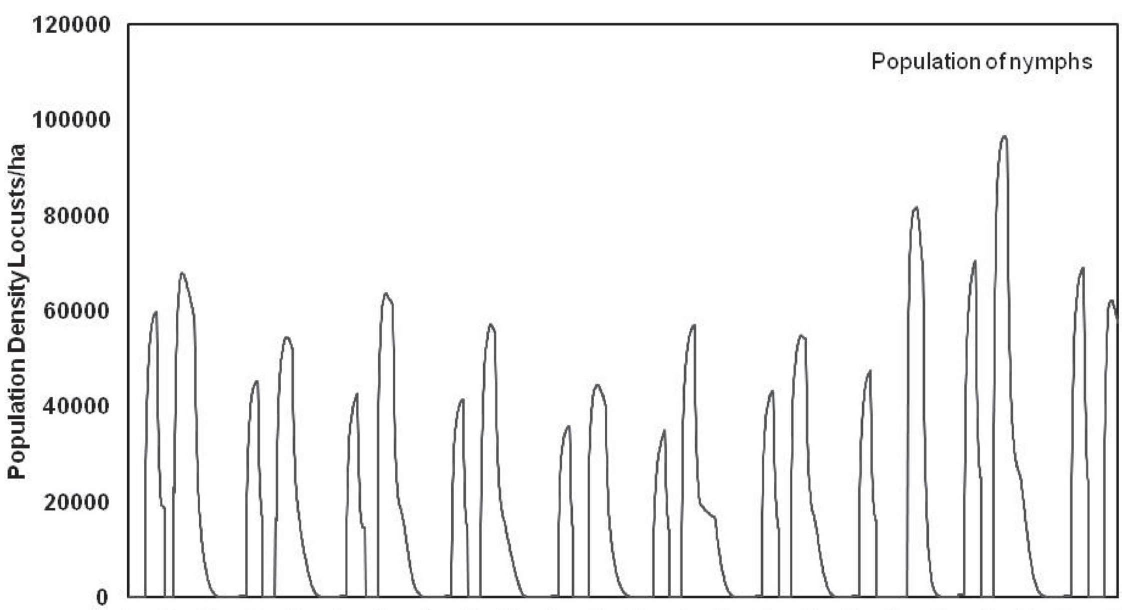

Fig. 5. Population dynamic of nymphs of the Central American Locust (CAL), *Schistocerca piceifrons*, in Yucatan, Mexico, 2001-2010. The nymph populations are represented by the continuous line.

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