Temperature-Dependent Reproductive and Life Table Parameters of Elasmopalpus lignosellus (Lepidoptera: Pyralidae) on Sugarcane

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TEMPERATURE-DEPENDENT REPRODUCTIVE AND LIFE TABLE PARAMETERS OF *ELASMOPALPUS LIGNOSELLUS* (LEPIDOPTERA: PYRALIDAE) ON SUGARCANE

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Abstract

The lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae) is an important pest of sugarcane (a complex hybrid of *Saccharum* spp.) in southern Florida. Reproductive and life table parameters for *E. lignosellus* were examined at nine constant temperatures from 13 to 36 °C with sugarcane as the larval food source. The pre- and post-oviposition periods decreased with increasing temperatures and reached their minimums at 33 and 36 °C, respectively. The oviposition period was longest at 27 °C. The mean fecundity, intrinsic rate of increase (r), and finite rate of increase (λ) were greatest at 30 °C and decreased with increasing or decreasing temperature. The net reproductive rate (R_0) was greatest at 27 °C. The Brière-1 model best described the relationship between temperature and r. The generation (T) and population doubling times (DT) were shortest at 33 and 30 °C, respectively. The temperatures around 27 to 30 °C are most favorable for *E. lignosellus* population growth and significant damage can be expected under these climatic conditions. This data in combination with population monitoring of *E. lignosellus* under field conditions can be effectively used in population predictions of this pest in field and severe damage can be prevented by timely implementation of control measures.

Key Words: Oviposition, fecundity, intrinsic rate of increase, net reproductive rate, Brière-1

Resumen

El barrenador menor del tallo de maíz *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae) es una plaga importante de la caña de azúcar (un híbrido complejo de *Saccharum* spp.) en el sur de la Florida. Se examinaron los parámetros reproductivos y la tabla de vida para *E. lignosellus* en nueve temperaturas constantes de 13 a 36 °C, con caña de azúcar como fuente de alimento para las larvas. Los períodos del pre-y de pos-oviposición disminuyeron con el aumento de las temperaturas y alcanzó sus mínimos en 33 y 36 °C, respectivamente. El período de oviposición más largo fue a 27 °C. El promedio de la fecundidad, la tasa intrínseca de crecimiento (r) y la tasa finita de crecimiento (λ) fueron mayores a 30 °C y disminuyeron con el aumento o disminución de la temperatura. La tasa neta de reproducción (R_0) fue mayor a 27 °C. El modelo Brière-1 describe mejor la relación entre la temperatura y r. El tiempo de generación (T) y de duplicación de la población (DT) fueron más cortos a los 33 y 30 °C, respectivamente. Las temperaturas alrededor de 27 a 30 °C son las más favorables para el crecimiento de la población de *E. lignosellus* y se puede esperar daño significativo bajo estas condiciones climáticas. Estos datos, en combinación con el monitoreo de la población de *E. lignosellus,* en condiciones de campo puede ser utilizado eficazmente en la predicción de la población de esta plaga y se puede prevenir daño severo por la aplicación puntual de medidas de control.

Palabras Clave: oviposición, fecundidad, tasa intrínseca de crecimiento, tasa neta de reproducción, Brière-1

Sugarcane (a complex hybrid of *Saccharum* spp.) (Poales: Poaceae) is an important crop grown in many southern temperate through tropical regions of the world [United States Department of Agriculture (USDA 2012)]. Florida, Louisiana, Texas and Hawaii are the main sug-

arcane producing states in the USA. Florida was the leading sugarcane producing state in the U.S. in 2010 with 392,000 acres (158,600 ha) (397,000 acres [160,700 ha] in 2011). The total value of Florida sugarcane in 2010 was $492.9M (USDA 2012). The lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae), is a polyphagous, semi-subterranean pest that is widely distributed in USA and Central and South America (Heinrich 1956; Genung & Green 1965; Chang & Ota 1987). Eggs are deposited mostly on the soil surrounding plants. Larvae bore into sugarcane stems below the soil surface and produce a silken tunnel at the entrance hole outward into the soil from which they attack the plants, as well as rest, molt and pupate (Schaaf 1974). *Elasmopalpus lignosellus* requires 548 degree days to complete development on sugarcane with lower and upper developmental thresholds estimated at 9.3 and 37.9 °C, respectively (Sandhu et al. 2010). Dead heart symptoms are produced when larvae reach the center of the shoot and damage or sever the youngest leaves or apical meristem. Non-lethal damage is caused when larvae chew only a few mm into the shoot evidenced by several symmetrical rows of holes revealed as the leaves emerge from the whorl. Larval feeding damage reduces plant stand and vigor, sugarcane photosynthesis, number of millable stalks and sugar yield (Carbonell 1977).

Reproductive studies of the lesser cornstalk borer have been conducted on cowpeas or southern peas (Luginbill & Ainslei 1917; Dupree 1965), peanuts (King et al. 1961), soybean (Leuck 1967), and sugarcane (Carbonell 1978). In all these studies, temperature and relative humidity were allowed to vary with the climatic conditions. Stone (1968) and Mack & Backman (1984) reported the longevity and oviposition rates of *E. lignosellus* on an artificial diet under controlled environmental conditions. However, quantitative information on life table parameters, such as intrinsic rate of increase (r), net reproductive rate (R_0), finite rate of increase (λ), mean generation time (T), and population doubling time (DT) was not published in their studies.

Life tables are powerful tools for analyzing and understanding the impact of external factors such as temperature on the growth, survival, reproduction, and rate of increase of insect populations (Sankeperumal et al. 1989). The intrinsic rate of increase can vary with the larval host or diet (Carey 2003). For example, female *Helicoverpa assulta* Guenee (Lepidoptera: Noctuidae) reared as larvae on artificial diet had significantly greater r values than females reared as larvae on pepper (*Capsicum frutescens* L.) (Solanales: Solanaceae) (Wang et al. 2008). To predict the lesser cornstalk borer population parameters on sugarcane, it is important to study its life history on the same host. Development and survivor-

ship rates for *E. lignosellus* reared on sugarcane at constant temperatures were determined in a recent study (Sandhu et al. 2010). The purpose of this experiment was to measure the effect of a range of constant temperatures on reproductive (pre-oviposition, oviposition, post-oviposition periods, and fecundity) and life table parameters (r, R_0, λ, T, and DT) of the lesser cornstalk borer reared on sugarcane.

MATERIALS AND METHODS

Reproductive Parameters

Pre-oviposition, oviposition, post-oviposition periods, and fecundity for *E. lignosellus* were determined at nine constant temperatures [13, 15, 18, 21, 24, 27, 30, 33, and 36 °C (± 0.05 °C)] at 14:10 (L:D) and 65-70% RH in temperature controlled chambers (Custom made, Department of Entomology and Nematology, University of Florida, Gainesville, FL) to construct time-specific life tables. This study was conducted in 2006-2008. Using two chambers, two temperatures were tested simultaneously with pairs of temperatures tested staggered over time. The range of tested temperatures was selected based on those experienced by lesser cornstalk borer in sugarcane in southern Florida. The experiment design was a randomized complete block with three cohorts at each temperature and it was replicated through time; repeated for three generations at each temperature. Adults were obtained from immatures reared on sugarcane used for companion developmental studies (Sandhu et al. 2010) conducted at the same temperatures and relative humidity as indicated above. Details on materials and methods used to rear immature stages are available in Sandhu et al. (2010). Ten male:female pairs of newly emerged adults (< 12 h old) were first released into each of three oviposition cages (17 × 17 × 17 cm) to facilitate mating. Adults were provided with a 10% honey solution for free feeding (ad libitum feeding), because sugarcane does not produce a food source for adults. After 24-h, individual pairs were moved to transparent plastic cylinders (one pair per cylinder) (11 cm length and 5 cm diameter; Thornton Plastic Co., Salt Lake City, UT) lined with tubular synthetic stockinette (Independent Medical Co-Op, Ormond Beach, FL) as an oviposition substrate as the females prefer rough, dry substrates for oviposition. We used stockinette because females preferred it over the Handy Wipes (The Chlorox Co., Oakland, CA) used by previous workers (e.g., Chalfant 1975). Adults were observed daily to record the limits of the reproductive parameters. The stockinette was replaced daily during oviposition periods. The orange-colored eggs were easily observed against the white background of the material and were counted using a hand lens. Fecundity was

reported as the number of eggs deposited by an individual female during her entire life period. Age-specific female survival (l_x, percentage of females alive at specific age x) and age-specific fecundity (m_x, number of female offspring produced by a female in a unit of time) were recorded for each day (x) they were alive. Age specific fecundity was calculated as $(f / (m + f)) \times n$, where f = number of females, m = number of males, and n = number of offspring. The l_x and m_x were calculated for each cohort of 10 females. Age-specific survivorship curves were constructed using adult l_x and m_x values for cohorts at each temperature treatment.

Life Table Parameters

The age-specific life table method was used to calculate the life table parameters for *E. lignosellus* (Birch 1948). The values of lx used in life table calculations were obtained by combining age specific adult female survival with the survival of immatures reported under same environmental conditions in a concurrent study (Sandhu et al. 2010). Similarly, the age of adults (x) used in these calculations also includes the development time of immatures reared on sugarcane under the same environmental conditions (Sandhu et al. 2010). The intrinsic rate of increase (r) was calculated through iteration of the Euler-Lotka equation ($\sum e^{-rx} l_x m_x = 1$). The l_x and m_x values were used to calculate the net reproductive rate ($R_0 = \sum l_x m_x$, mean number of female offspring / fe-

male) and the mean generation time ($T = \sum(x l_x m_x)$ / $\sum(l_x m_x)$, mean age of the mothers in a cohort at the birth of female offspring). The values for r at each temperature were used to calculate the finite rate of increase ($\lambda = e^r$, the number of times the population multiplies in a unit of time) and population doubling time ($DT = \ln(2) / r$, the time required for the population to double). To compare the thermal sensitivities of r and R_0, we plotted these alternative fitness measures against the tested temperatures.

Model Evaluation

A non-linear distribution was observed when r was plotted against the temperature treatments. To find an equation that best fit the observed relationship between r and temperature, eight non-linear models (Table 1) previously used (Roy et al. 2003; Bonato et al. 2007; Sandhu et al. 2010; Shi & Ge 2010) to describe temperature dependent development or other population parameters of different insects were tested. The parameters of the nonlinear models were estimated with the nonlinear regression model of Marquardt (1963) using SAS (SAS Institute 2008). Sigma Plot (Systat Software, Inc., San Jose, CA) was used to plot the regressions of the non-linear models. The models were evaluated based on the coefficient of determination (r^2), the adjusted coefficient of determination (r^2_{adj}, a modified r^2 that adjusts for the number of explanatory terms in the model), the residual sum of squares (RSS), and the corrected

TABLE 1. MATHEMATICAL EQUATIONS OF THE MODELS TESTED TO DESCRIBE THE RELATIONSHIP BETWEEN TEMPERATURE AND INTRINSIC RATE OF INCREASE IN LESSER CORNSTALK BORER ON SUGARCANE.

Model	Equation	References
Brière	$r = \begin{cases} aT(T - T_0) \sqrt{T_m - T} & \text{(Brière - 1)} \\ aT(T - T_0)(T_m - T)^{1/d} & \text{(Brière - 2)} \end{cases}$	Brière et al. (1999)
Logan	$r = \psi \left[\exp(\rho T) - \exp\left(\rho T_m - \dfrac{T_m - T}{\delta} \right) \right]$	Logan et al. (1976)
Lactin	$r = \exp(\rho T) = \exp[p T_m - (T_m - T/\delta)] + \lambda$	Lactin et al. (1995)
Polynomial (4th order)	$r = a + bT + cT^2 + dT^3 + eT^4$	Lamb et al. (1984)
Ratkowsky	$\sqrt{r} = b(T - T_o \bullet [1 - \exp[c(T - T_m)]]$	Ratkowsky et al. (1983)
Taylor	$r = r_f \cdot \exp\left[-\dfrac{1}{2}\left(\dfrac{T - T_f}{T_o} \right)^2 \right]$	Taylor (1981)
Wang-Lan-Ding	$r = \dfrac{m \cdot [1 - \exp[- K_1(T - T_o)] \cdot [1 - \exp[K_2(T - T_m)]]}{1 + \exp[- c(T - T_o)]}$	Wang et al. (1982)

r, intrinsic rate of increase; ψ, developmental rate at given base temperature; ρ, increase rate at optimal temperature; T, ambient temperature above the lower developmental threshold; T_m, upper developmental threshold; δ, no. of degrees over the base temp over which thermal inhibition becomes predominant; , maximum developmental rate; T_f, optimum temperature; T_o, lower temperature threshold; a, b, c, d, e, empirical constant; λ, empirical constant which forces the curve to intercept the y-axis at a value below zero; m, constant; K_1, increase in enzymatic reaction rate; K_2, decrease in reaction rate.

Akaike Information Criterion (AIC_C) (Burnham and Anderson 2004). The r^2 and r^2_{adj} indicate better fits with higher values, whereas RSS and AIC_C indicate better fits with lower values. The corrected AIC value was calculated using the formula:

$$AIC_C = n \log(RSS / n) + 2Kn / (n-K-1)$$

where n denotes the sample size; RSS denotes the residual sum of squares; K is the number of model parameters including an error item (namely the number of free parameters in the model itself). The AIC_C was preferred over the AIC because of the small sample sizes ($n/K < 40$) in this study, for which AIC_C is recommended (Hurvich & Tsai 1989; Burnham & Anderson 2004).

Statistics

PROC MIXED (SAS Institute 2008) was used to analyze the variance due to the potential covariance structure associated with taking repeated measures over time at each temperature. Normality of the data was tested with the Shapiro-Wilk normality test (Shapiro & Wilk 1965). The oviposition cages were treated as cohorts and replications through time were treated as generations for data analysis. Temperatures, cohorts, generations, and their interactions were used in the analysis of variance models. Generations were used as the repeated variable and the cohorts were nested under temperature in the repeated measures statement. Several covariance structures were fitted to the data. The unstructured covariance type fit well and was used for the analysis (Littell et al. 1998). Data for each pair of adults were used for analysis of effects of temperature, cohort, and generation for reproductive parameters. Daily values by cohort were used for analysis of effects of temperature and generation on l_x and m_x. The percentage of females alive at age x (l_x) was arcsin square root transformed for normality purposes before analysis and retransformed for presentation purposes. The Tukey's HSD test (SAS Institute 2008) was used for means separation with $\alpha = 0.05$.

RESULTS

Reproduction

Temperature significantly affected the lengths of the lesser cornstalk borer pre-oviposition, oviposition, and post-oviposition periods (Table 2). Cohorts, generations and the modeled interactions were not significant sources of variation in the models for any of these periods. Therefore, data were pooled across cohorts and generations to calculate means for these periods. The mean pre-oviposition period decreased with an increase in temperature from 9.7 d at 13 °C to 2.3 d at 33 °C (Table 3). The mean oviposition period was

TABLE 2. ANALYSIS OF VARIANCE FOR EFFECTS OF TEMPERATURE, COHORT AND GENERATION ON REPRODUCTIVE PARAMETERS OF *ELASMOPALPUS LIGNOSELLUS* ON SUGARCANE.

Source	Pre-oviposition			Oviposition			Post-oviposition			Fecundity		
	df	F	P	df	F	P	df	F	P	df	F	P
Model	80	249.20	< 0.0001	80	593.49	< 0.0001	80	439.28	< 0.0001	80	523.10	< 0.0001
Error	570			570			570			570		
Temp.	8	236.10	< 0.0001	8	579.60	< 0.0001	8	395.10	< 0.0001	8	457.80	< 0.0001
Cohort	8	1.05	0.3511	8	0.19	0.8291	8	0.77	0.4640	8	2.15	0.2420
Generation	2	0.78	0.5881	2	0.18	0.9820	2	0.84	0.5380	2	3.04	0.1941
T × C	64	0.69	0.9670	64	0.41	1.0000	64	0.51	0.9990	64	1.54	0.6412
T × G	16	0.74	0.6421	16	0.69	0.5240	16	0.76	0.6120	16	2.15	0.3540
C × G	16	1.02	0.3950	16	1.11	0.4520	16	1.25	0.4550	16	1.89	0.5411
T × C × G	128	0.89	0.5490	128	0.86	0.5131	128	0.78	0.6290	128	0.97	0.6242

F, df, and *P* values represent ANOVA of temperature, cohort and generation treatments within a reproductive stage (PROC MIXED, SAS Institute 2008).

TABLE 3. MEAN (± SEM) PRE-OVIPOSITION, OVIPOSITION, POST-OVIPOSITION PERIODS AND FECUNDITY FOR *ELASMOPALPUS LIG-NOSELLUS* ON SUGARCANE.

Temp (°C)	Pre-oviposition (d)	Oviposition (d)	Post-oviposition (d)	Fecundity (eggs / female)
13	9.7 ± 0.06 a	2.2 ± 0.05 f	5.9 ± 0.07 a	29.2 ± 3.13 f
15	7.2 ± 0.07 b	2.8 ± 0.06 e	5.3 ± 0.07 b	42.3 ± 4.21 e
18	5.8 ± 0.05 c	4.5 ± 0.05 c	4.2 ± 0.05 c	51.1 ± 4.66 d
21	3.5 ± 0.05 d	4.5 ± 0.07 c	4.0 ± 0.06 d	56.3 ± 4.89 d
24	2.9 ± 0.05 e	4.8 ± 0.05 b	3.8 ± 0.06 e	97.5 ± 5.31 c
27	2.7 ± 0.06 f	5.6 ± 0.06 a	3.2 ± 0.05 fg	158.4 ± 6.14 a
30	2.5 ± 0.06 g	4.5 ± 0.05 c	3.3 ± 0.05 f	165.3 ± 6.52 a
33	2.3 ± 0.05 h	3.2 ± 0.05 d	3.1 ± 0.07 g	110.2 ± 5.07 b
36	4.4 ± 0.07 d	2.8 ± 0.06 e	2.5 ± 0.05 h	62.3 ± 4.22 d

Means within a column followed by the same letters are not significantly different (Tukey's test, α = 0.05).

longest (5.6 d) at 27 °C and decreased with an increase or decrease in temperature from 27 °C. The post-oviposition period became progressively shorter from a maximum at 13 °C to a minimum at 36 °C (Table 3).

Fecundity was also significantly affected by temperature (Table 2). Cohort, generation and modeled interactions were not significant sources of variation in the fecundity model. Therefore, the fecundity data were pooled across cohorts and generations to calculate mean fecundity at each temperature. Fecundity increased with an increase in temperature from 13 to 30 °C and decreased at 33 and 36 °C. Mean fecundity ranged from 29.2 (13 °C) to 165.3 eggs (30 °C) (Table 3) which indicates that warm temperatures are more favorable for fecundity than cool temperatures.

LIFE TABLE PARAMETERS

Temperature had a significant effect on l_x ($F = 50.19$; df = 8, 333; $P < 0.0001$) and m_x values ($F = 16.05$; df = 8, 333; $P < 0.0001$). Generations and the modeled interactions did not provide significant sources of variation in the models for l_x ($F = 0.52$; df = 2, 333; $P = 0.5972$; $F = 0.75$; df = 16, 333; $P = 0.7384$) or m_x ($F = 0.13$; df = 2, 333; $P = 0.8805$; $F = 0.26$, df = 16, 333, $P = 0.9984$). Therefore, the data were pooled across generations to calculate means for these periods. Both l_x and m_x increased with an increase in temperature from 13 to 27 °C and then decreased at or above 33 °C except at 15 °C where m_x was unexpectedly greater than 18, 21, and 24 °C (Fig. 1).

Data were pooled across generations (i.e., 90 different pairs were pooled for each temperature, total 810 pairs) to calculate the life table parameters r, R_0, λ, T, and DT at each temperature, because pre-oviposition, oviposition, post-oviposition and fecundity were significantly affected by temperature, but not by cohort or generation (Table 2). The intrinsic rate of increase (r) and the finite rate of increase (λ) both increased with an increase in temperature from 13 to 30 °C before starting to decrease at > 33 °C (Table 4). The negative value of r at 13 °C (-0.0021) indicates a decrease rather than an increase in lesser cornstalk borer population with time at this temperature. The net reproductive rate (R_0) was greatest at 27 °C (53.8537). Comparing the values of r and R_0 versus temperature resulted in similar increases to maximum values, but the curve for r was shifted slightly to the right of the curve for R_0 (Fig. 2). The mean generation time (T) decreased from the maximum at 13 °C (130.7 d) to the minimum at 33 °C (27.7 d) (Table 4). The population doubling time (DT) was negative (-334.8537) at 13 °C which indicates that the population will reduce to half of its original population in 334.9 days rather than increase in population. The value of DT was lowest (5.6386) at 30 °C which means population doubles in size in 5.6 days at this temperature.

Model Evaluation

The model evaluation parameters, and the predicted optimum temperatures (temperatures for maximum intrinsic rate of increase) are presented in Table 5. The predicted optimum temperature ranged from 28.8 °C (Taylor model) to 31.3 °C (Logan model). In general, all the tested models showed satisfactory fitted results with $r^2 > 0.9312$ and $r^2_{adj} > 0.8623$. The polynomial (fourth order) and Wang-Lan-Ding models showed the best fit to the data based on their higher r^2 and r^2_{adj} and lower RSS values than other models (Table 5). However, the greater number of fitted parameters in the polynomial model resulted in greater AIC_C value (-39.09) than the other models and the AIC_C for Wang-Lan-Ding could not be calculated, because (n-K-1) in the AIC_C formula equaled zero. Based on the lowest AIC_C (-62.43) values, the Brière-1 was found to be the best model to describe the relationship between r and temperature.
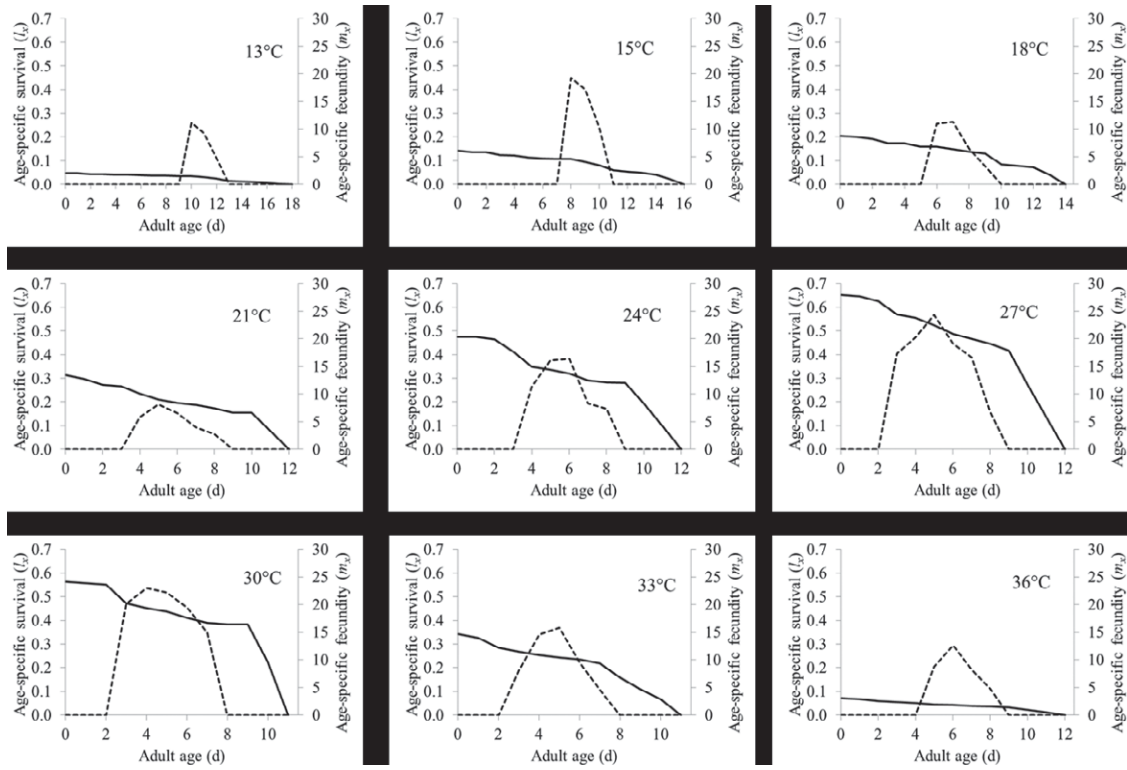
Fig. 1. Relationships between the adult age (d) and age-specific survival l_x (solid line) and age specific daily fecundity m_x (dashed line) for *Elasmopalpus lignosellus* at 9 constant temperatures.

The fitted curves for all the tested models representing the relationship between r and temperature for the lesser cornstalk borer on sugarcane are presented in Figs. 3a and 3b. In general, the shape of these curves estimated by different models is quite similar. However, some models had different lower and upper temperatures where the curve intersected x-axis. For example, in Brière-1, Brière-2, Lac-tin, Ratkowsky and Wang-Lan-Ding models, curve intersected the x-axis at approximately 12-13 °C which indicates their estimated lower temperature threshold. However, in Logan and Taylor models, curve did not intersect x-axis at lower temperature which indicate the estimated lower temperature threshold to be < 10 °C. Similarly, the estimated upper temperature threshold was 36-37 °C in most of the models,

TABLE 4. LIFE TABLE PARAMETERS FOR *ELASMOPALPUS LIGNOSELLUS* ON SUGARCANE AT NINE CONSTANT TEMPERATURES.

Temp. (°C)	r	R_0	T	DT	λ
13	-0.0021	0.7631	130.6554	-334.8537	0.9979
15	0.0146	4.4649	102.7285	47.6063	1.0147
18	0.0199	4.7123	77.9978	34.8841	1.0201
21	0.0310	5.5819	55.4920	22.3596	1.0315
24	0.0644	18.8646	45.6598	10.7633	1.0665
27	0.1109	53.8537	36.0535	6.2485	1.1173
30	0.1229	43.3763	30.7755	5.6386	1.1308
33	0.0924	12.8691	27.7046	7.5000	1.0968
36	0.0085	1.4335	42.1790	81.1648	1.0086

r, intrinsic rate of natural increase (female/female/day); R_0, net reproductive rate (female/female/generation); T, generation time (d); DT, population doubling time (d); λ, finite rate of increase (female/female/day).

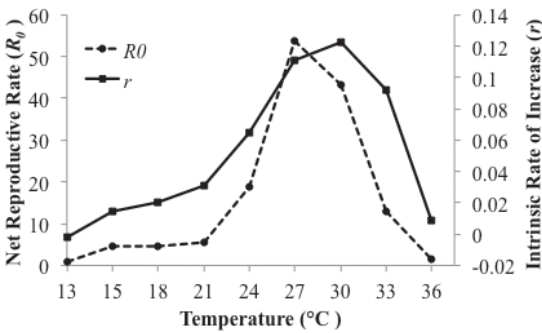Fig. 2. Effect of temperature (°C) on *Elasmopalpus lignosellus* intrinsic rate of increase (*r*) and net reproductive rate (R_0).

but in Taylor model it was > 40 °C, because curve did not intersect x-axis even at 40 °C.

DISCUSSION

Reproduction

The values for reproductive parameters on sugarcane fell mostly within the ranges of those determined for *E. lignosellus* on other crops such as southern pea and soybean. The mean (± SEM) pre-oviposition period found in this study (2.3 ± 0.05 d at 33 °C to 9.7 ± 0.06 d at 13 °C) is similar to the value of 2.8 d reported by Stone (1968) for *E. lignosellus* on an artificial diet at 27 °C. The mean oviposition period on sugarcane (2.2 ± 0.05 d at 13 °C to 5.6 ± 0.06 d at 27 °C) was shorter than those reported on artificial diets (10.4 d, Luginbill and Ainslei 1917; 11.8 d, Stone 1968; and 6.4 d, Simmons and Lynch 1990), but within the range determined by Dupree (1965) on southern pea (mean: 4.1 d, range 1 to 9 d). The 4.7 d post-oviposition period reported by Leuck (1967)

on soybean is consistent with that found on sugarcane (2.5 ± 0.05 to 5.9 ± 0.07 d).

Fecundity on sugarcane (29 to 165 eggs per female) mostly fell within the range reported by others on leguminous crops and artificial diets. The lesser cornstalk borer mean fecundity (number of eggs/female) reported in earlier studies was 192 on cowpeas (Luginbill & Ainslei 1917), ranged from 124 to 129 on soybean (King et al. 1961; Dupree 1965; Leuck 1967), and ranged from 67 (Calvo 1966) to 419.5 on artificial diet (Stone 1968). The results of our study are similar to those of Mack and Backman (1984) who reported an increase in fecundity with an increase in temperature from 17 to 27.5 °C, peaks at 27.5 and 30.5 °C, and large decreases at 17 and 35 °C.

Life Table Parameters

Elasmopalpus lignosellus reached its maximum reproductive rate within the same temperature range where generation time and population doubling time were the lowest (30 to 33 °C). Life table parameters for lesser cornstalk borer on other hosts are not available for comparison, but such values have been published for other stalk boring Lepidoptera pests of monocots (Table 6). Intrinsic rate of increase (*r*) at 25 °C on corn and artificial diet for *Diatraea lineolata* (Walker) (Lepidoptera: Crambidae), a neotropical cornstalk borer (Rodríguez-del-Bosque et al. 1989), were slightly lower than those found in this study for *E. lignosellus* that developed as larvae on sugarcane at 24 °C. The sugarcane borer, *D. saccharalis* (F.), and the Mexican rice borer, *Eoreuma loftini* (Dyar) (both Lepidoptera: Crambidae), recorded lower *r* and λ, and higher *T* and *DT* parameters at 30 °C on an artificial diet that included dried, ground sugarcane leaf sheaths (Sétamou et al. 2002) than those reported in our study for *E. lignosellus*. The Mexican rice borer had greater R_0 than the lesser cornstalk borer that indicates its

TABLE 5. COMPARISON OF DIFFERENT NON-LINEAR MODELS TESTED TO DESCRIBE THE RELATIONSHIP BETWEEN INTRINSIC RATE OF INCREASE (r) AND TEMPERATURE (°C).

Model	T_f(°C)	RSS	R^2	R^2_{adj}	AIC_C
Brière-1	30.7	0.00118	0.9342	0.8947	-62.43
Brière-2	31.1	0.00116	0.9353	0.8707	-50.59
Logan	31.3	0.00115	0.9358	0.8715	-50.66
Lactin	30.9	0.00118	0.9343	0.8685	-50.45
Polynomial	30.3	0.00029	0.9839	0.9570	-39.09
Ratkowsky	30.9	0.00124	0.9312	0.8623	-50.03
Taylor	28.8	0.00119	0.9336	0.8938	-62.36
Wang-Lan-Ding	29.8	0.00011	0.9939	0.9511	NA

T_f, the predicted temperature at which the intrinsic rate of increase could reach its maximum; RSS, Residual Sum of Squares; R^2, coefficient of determination; R^2_{adj}, adjusted coefficient of determination; AIC_C, corrected Akaike Information Criterion.

A
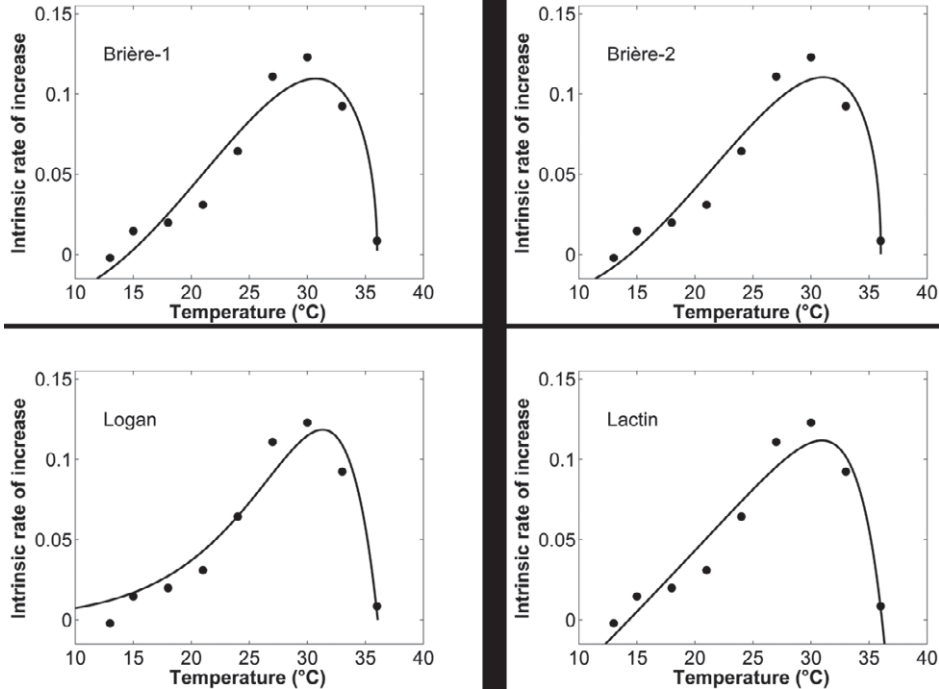
B

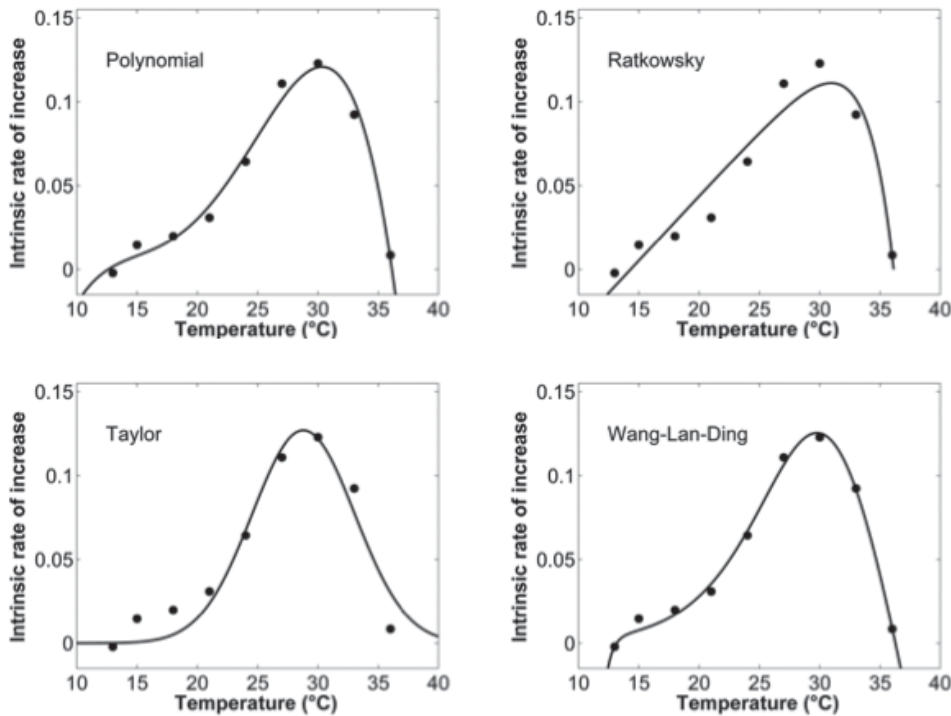Fig. 3a-b. Relationship between temperature (°C) and intrinsic rate of natural increase (*r*) for *E. lignosellus* on sugarcane described by different non-linear models.

TABLE 6. LIFE TABLE PARAMETERS FOR SELECTED STEM-BORING LEPIDOPTERA PESTS OF SUGARCANE AND CORN.

Species (Lepioptera family)	Temp. (°C)	Food sources	Life table parameters					Reference
			r	R_0	T	DT	λ	
Diatraea lineolata (Crambidae)	25	corn	0.053	15.6	51.5	—	1.055	Rodríguez-del-Bosque et al. 1989
Diatraea lineolata (Crambidae)	25	artificial diet	0.054	19.9	55.4	—	1.055	Rodríguez-del-Bosque et al. 1989
Diatraea saccharalis (Crambidae)	30	artificial diet[a]	0.059	12.0	42.0	11.7	1.06	Sétamou et al. 2002
Diatraea saccharalis (Crambidae)	27	corn	0.124	345.8	—	—	1.132	Bessin and Reagan 1990
Diatraea saccharalis (Crambidae)	27	sugarcane[b]	0.124	332.9	—	—	1.132	Bessin and Reagan 1990
Eoreuma loftini (Crambidae)	30	artificial diet[a]	0.088	84.0	50.3	7.9	1.09	Sétamou et al. 2002

r, intrinsic rate of natural increase; R_0, net reproductive rate; T, generation time (d); DT, population doubling time (d); λ, finite rate of increase; — values not available.
[a] Including 6.25% by weight leaf sheaths of sugarcane variety CP 65-357.
[b] Variety CP 61-37.

high reproductive potential, but the r for the Mexican rice borer was lower on an artificial diet than for the lesser cornstalk borer on sugarcane. Our studies determined that r and λ for *E. lignosellus* reared on sugarcane were slightly lower than *D. saccharalis* reared on corn and on sugarcane at 27 °C (Bessin & Reagan 1990). However, the net reproductive rate (R_0) for *D. saccharalis* on both of these host plants was approximately seven times greater than for *E. lignosellus* on sugarcane. The results of Bessin & Reagan (1990) and Sétamou et al. (2002), who found very different r and R_0 values for *D. saccharalis* that developed on corn and sugarcane compared to an artificial diet containing <10% sugarcane leaf sheaths, provide further evidence that larval host or diet affects the intrinsic rate of increase.

In most ectotherms, r reaches its maximum value at a greater temperature than for R_0. Huey & Berrigan (2001) attributed this to r (but not R_0) being sensitive to the accelerating effect of high temperature on generation time. Because r is inversely related to generation time and R_0 is independent of it (Cole 1954; Lewontin 1965), the normal shortening of the generation time associated with rising temperatures will work to increase r without affecting R_0. This leads to a shift to the right in the thermal fitness curve for r relative to R_0, as was observed in this study. This right shift of the r curve relative to the R_0 curve observed for *E. lignosellus* on sugarcane may be due to the shortest generation time occurring at a temperature 3 and 6 °C greater than the maximum r and R_0 values, respectively.

Model Evaluation

Mathematical models used in this study were also tested to describe the relationship between temperature and r for *Tetranychus mcdanieli* McGregor (Acarina: Tetranychidea) and *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) on red raspberry (*Rubus idaeus* L.), *Sitotroga cereallela* (Olivier) (Lepidoptera: Gelechiidae) on corn (*Zea mays* L.), and *Halyomorpha halys* (Stal) (Hemiptera: Pentatomidae) on green beans [*Vigna radiata* (L.) Wilczek] (Roy et al. 2003; Hansen et al. 2004; Nielsen et al. 2008). High r^2 values were used to choose the Lactin-2 model for *T. mcdanieli* and the Brière-1 model for *S. punctillum*, *S. cereallela*, and *H. hays*. In the present study, the Wang-Lan-Ding model provided the best fit between temperature and r based on r^2 and RSS. However, Angilletta Jr (2006) reported that the selection of model based on r^2 and RSS can be erroneous to select the best model. Based on AIC_C values, the Brière-1 model was the best to describe the relationship between r and temperature. Shi and Ge (2010) also reported the Brière-1, Brière-2 and Performance models to be the most suitable for explaining temperature-dependent develop-

ment rates of insects. Additional factors such as soil moisture and natural enemies have been reported to affect *E. lignosellus* populations under field conditions. For example, elevated moisture levels at the soil surface play an important role in reducing oviposition and larval survival under field conditions (Smith & Ota 2002). Larval parasitoids and predators may also play an important role in regulating *E. lignosellus* population growth in sugarcane (Falloon 1974).

CONCLUSION

Life table analyses determined that the lesser cornstalk borer has the potential to quickly increase its population in sugarcane. Temperatures in the range of 27 to 33 °C were most favorable for reproduction and survival. The results of this temperature-dependent study on reproduction and estimation of life table parameters provides important information that may ultimately be used for predicting outbreaks of the lesser cornstalk borer and improving its management in sugarcane. This data in combination with population monitoring of *E. lignosellus* under field conditions can be effectively used in population predictions of this pest in the field and severe damage can be prevented by timely implementation of control measures. Additional information is necessary to be able to predict *E. lignosellus* populations in the field, including relationships among air temperatures and temperatures inside the shoots and in the soil where larvae feed, and the relative attractiveness of stockinette material versus plant tissue and the soil surface for oviposition. Models in this study require field testing before they can reach their full potential for predicting the population dynamics of the lesser cornstalk borer.

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