Temperature-Dependent Development of Xyleborus glabratus (Coleoptera: Curculionidae: Scolytinae)

Authors: Brar, Gurpreet S., Capinera, John L., Kendra, Paul E., Smith, Jason A., and Peña, Jorge E.

Source: Florida Entomologist, 98(3) : 856-864

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.098.0307

Temperature-dependent development of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae)

Gurpreet S. Brar[1,*], *John L. Capinera*[2], *Paul E. Kendra*[3], *Jason A. Smith*[4], *and Jorge E. Peña*[5]

Abstract

Redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae), is a nonnative pest that transmits the pathogenic fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva (Ophiostomatales: Ophiostomataceae), which causes laurel wilt disease in trees of the family Lauraceae. Laurel wilt is present in the commercial avocado (*Persea americana* Mill.; Laurales: Lauraceae) growing areas of Florida and poses a potential threat to the avocado industries of California and Mexico. The life cycle of *X. glabratus* was studied in avocado logs at 16, 20, 24, 28, and 32 °C. *Xyleborus glabratus* successfully completed its life cycle at 24, 28, and 32 °C, with the greatest oviposition and development rate at 28 °C. Development of the egg and pupal stages was studied at 12, 16, 18, 20, 24, 28, 32, and 36 °C. One linear and 7 nonlinear developmental models were used to estimate the temperature-dependent development of both stages. The linear model estimated the lower threshold temperatures for egg and pupal development to be 13.8 °C and 11.1 °C, respectively, and the degree-days (DD) for egg and pupal development to be 55.1 DD and 68.2 DD, respectively. The Brier-2, Ratkowsky, Logan, and polynomial models gave the best estimates for the temperature-dependent development of the egg stages, whereas the Brier-1, Logan, and polynomial models gave the best estimates of temperature-dependent development of the pupal stages. Our results suggested that the optimal temperature for development of *X. glabratus* was around 28 °C, and that temperature will play an important role in the spread and successful establishment of *X. glabratus*.

Key Words: avocado; redbay, temperature; development models

Resumen

El escarabajo ambrosia del laurel rojo, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae) es una plaga no nativa y el vector del hongo patógeno *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva, que causa la enfermedad de la marchitez del laurel en los árboles de la familia Lauraceae. La marchitez del laurel está presente en áreas de la Florida donde se siembra el aguacate comercial (*Persea americana* Mill) y representa una amenaza potencial para las industrias de aguacate en California y México. Se estudió el ciclo de vida de *X. glabratus* en troncos de aguacate a los 16, 20, 24, 28 y 32 ° C. *Xyleborus glabratus* completó con éxito su ciclo de vida a los 24, 28 y 32 °C, con la tasa de oviposición y desarrollo más alto a los 28 °C. Se estudió el desarrollo del huevo y pupa a los 12, 16, 18, 20, 24, 28, 32 y 36 °C. Un modelo lineal y 7 modelos no lineales de desarrollo fueron utilizados para modelar el desarrollo del huevo y pupa dependiente de la temperatura. El modelo lineal resultó en un estimado del umbral de la temperatura inferior para desarrollo de huevos y pupas de 13.8 °C y 11.1 °C, respectivamente, y del número de grados-día (GD) para el desarrollo de huevos y pupas a 55.1 GD y 68.2 GD, respectivamente. Los modelos Brier-2, Ratkowsky, Logan y polinomiales dio las mejores estimaciones para el desarrollo del estadio de huevo dependiente de la temperatura, mientras que los modelos Brier-1, Logan y polinomiales dieron las mejores estimaciones para el desarrollo del estadio de pupa dependiente de la temperatura. Nuestros resultados sugieren que la temperatura óptima para el desarrollo de *X. glabratus* es alrededor de 28 °C, y que la temperatura va a jugar un papel importante en la propagación y establecimiento exitoso de *X. glabratus*.

Palabras Clave: aguacate; laurel rojo; temperatura; modelos de desarrollo

The exotic redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae) has become a serious pest of trees of the family Lauraceae in the United States. The beetle is native to Southeast Asia and was introduced accidentally in the southeastern United States around 2002 (Haack 2003; Rabaglia et al. 2008; Peña et al. 2012). The redbay ambrosia beetle transmits the fungus *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva (Ophiostomatales: Ophiostomataceae), (Fraedrich et al. 2008; Hanula et al. 2008) that causes laurel wilt, a lethal vascular disease. Since the introduction of the beetle, the laurel wilt pathogen has been detected in the following Lauraceae species: redbay (*Persea borbonia* [L.] Spreng.), avocado (*Persea americana* Mill.), swampbay (*Persea palustris* [Raf.] Sarg.), silkbay (*Persea humilis* Nash), sassafras (*Sassafras albidum* [Nutt.] Nees), northern spicebush (*Lindera benzoin* [L.] Blume), pondspice (*Litsea aestivalis* [L.] Fernald), pondberry (*Lindera melissifolia* [Walter] Blume), and camphor tree (*Cinnamomum camphora* [L.] J. Presl). It sometimes causes mortality of 90% of infested trees (Fraedrich et al. 2008; Mayfield et al. 2008; Smith et al. 2009a, b; Hughes et al. 2013). Experimental inocula-

---

[1] Everglades Research and Education Center, University of Florida, IFAS, 3200 E Palm Beach Rd, Belle Glade, FL 33430, USA
[2] Entomology and Nematology Department, University of Florida, IFAS, Gainesville, FL 32611, USA
[3] Subtropical Horticulture Research Station, USDA-ARS, Miami, FL 33158, USA
[4] School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, USA
[5] Tropical Research and Education Center, University of Florida, IFAS, Homestead, FL 33031, USA
*Corresponding author; E-mail: gpsbrar@ufl.edu

tions with *R. lauricola* indicate that California bay laurel (*Umbellularia californica* [Hook & Arn.] Nutt.) and Gulf licaria (*Licaria triandra* [Sw.] Kosterm.) also are susceptible (Fraedrich 2008; Ploetz & Konkol 2013). Identical rates of development of *X. glabratus* were observed in avocado, redbay, and swampbay logs held at 25 ± 2 °C, with teneral adult stages encountered approximately 1 mo after gallery initiation (Brar et al. 2013). The emissions of α-cubebene, α-copaene, α-humulene, and calamenene from host trees were correlated with attraction of adult beetles to the host trees (Kendra et al. 2011, 2014). Laurel wilt currently is present in commercial avocado groves in southern Florida (FDOACS 2012) and has been the subject of recent reviews (Kendra et al. 2013; Ploetz et al. 2013).

Since its introduction, the redbay ambrosia beetle has been reported in North Carolina, South Carolina, Georgia, Florida, Alabama, and Mississippi, USA, and its range has expanded more quickly than predicted by Koch & Smith (2008). Beetle population dynamics studies in South Carolina and Georgia, USA, have shown that adult beetles were active throughout the year, with greater flight activity in Sep compared with Jan and Feb (Hanula et al. 2008, 2011). In Alachua County, Florida, USA, strong activity of the beetles was recorded in Apr 2010, Oct 2010, and Mar 2011, whereas little activity was recorded in Nov 2010, Dec 2010, and Jan 2011 (Brar et al. 2012). This suggests that the beetles are more active in the summer months than in colder months in northern Florida. Variation in temperature, along with other climatic variables, might play an important role in the population dynamics of this species (Brar et al. 2012). Given the potential impact of the beetle–fungus complex on the avocado industry of Florida and California, USA, and its potential threat to other lauraceous plants throughout North, Central, and South America (Gramling et al. 2010; Peña et al. 2012), it is desirable to develop phenological and population dynamics models to help predict pest infestations, and to initiate control measures.

Climate limits the distribution of insect pests, with temperature being one of the abiotic factors that play a major role. Knowledge of insect development in relation to temperature is critical in order to understand insect population dynamics, but knowledge of temperature relations is also essential to create phenological predictive models. During the last few decades, various mathematical models have been used to model temperature-dependent development of insects. These models range from simple linear models (Campbell et al. 1974; Roy et al. 2002) that can predict the lower developmental threshold temperature within limited ranges of temperature, to nonlinear mathematical models (Logan et al. 1976; Taylor 1981; Ratkowsky et al. 1983; Lamb at al. 1984; Lactin et al. 1995; Briere et al.1999) that can describe temperature-dependent development over wider ranges of temperatures. Nonlinear models have been compared to find the model that reliably predicts development close to actually observed values based on commonly used criteria such as higher r^2 (coefficient of determination) and lower RSS (residual sum of squares) and AIC Akaike information (Walgama & Zalucki 2007b; Aghdam et al. 2009; Sandhu et al. 2010, 2013). The objectives of this study were to 1) evaluate temperature-dependent development of the egg and pupal stages of *X. glabratus*, 2) develop a valid model based on various linear and nonlinear models, and 3) study the life cycle and temperature-dependent development of *X. glabratus* in avocado logs placed at different constant temperatures.

Materials and Methods

BEETLE SOURCE

Redbay and swampbay trees with high infestations of *X. glabratus* were scouted at 3 locations in Florida, USA, i.e., Austin Cary Memorial Forest (Alachua County), Ordway-Swisher Biological Station (Putnam County), and Hammock Dunes Club Golf Course, Palm Bay (Brevard County). Infested logs were collected, and a beetle colony was maintained at the University of Florida, Entomology and Nematology Department, Gainesville (Alachua County), Florida, USA, by methods previously reported (Brar et al. 2013).

REARING OF *X. GLABRATUS* FOR DEVELOPMENTAL STAGES

Avocado 'Booth 7' logs measuring 4.5 to 6.5 cm in diameter and 8 to 10 cm in length from healthy trees without beetle infestation were procured from the University of Florida, Tropical Research and Education Center, Homestead (Miami Dade County), Florida, USA. Logs were soaked in tap water for 48 h, removed, and individually placed in 946 mL clear plastic containers (American Plastics, Gainesville, Florida, USA). Each container was covered with Plankton netting (150 microns, BioQuip, Rancho Dominguez, California, USA). To keep the logs moist, approx. 100 mL of water were maintained in each container throughout the experiment. Twenty sclerotized female adult beetles were placed directly on the bark of each log and were allowed to bore. Logs were kept in an incubator (Precision® illuminated incubator, Precision Scientific Inc., Chicago, Illinois, USA) at 25 ± 2 °C in complete darkness. The number of logs infested on a given day was dependent on the number of adult females available. Infested logs were divided into 2 sets, one for collection of eggs and the other for collection of pupae. Based on data previously obtained regarding the life cycle of *X. glabratus* on avocado (Brar et al. 2013), the logs were split and galleries carefully opened with a hand pruner (Fiskars compound anvil hand pruner, Lowes, Gainesville, Florida, USA) on the 10th to 13th day after gallery initiation, and eggs were carefully extracted with sterilized needles. In like manner, the logs were split, galleries carefully opened on the 24th to 26th day after gallery initiation, and pupae were extracted.

DEVELOPMENT OF EGG AND PUPAL STAGES AT CONSTANT TEMPERATURES

The duration of development from egg to larval stage and from pupal to adult stage was studied at constant temperatures. Eggs extracted from avocado logs were placed in Petri dishes (50 × 9 mm, BD Falcon, Franklin Lakes, New Jersey, USA) lined with moist paper towel. Petri dishes were placed in Florida Reach-In incubators (Walker et al. 1993) held at constant temperatures of 12, 16, 20, 24, 28, 32, and 36 °C (± 0.1 °C) and kept under constant darkness. For each temperature, the numbers of larvae that hatched were recorded daily. Numbers of eggs used for each temperature study were dependent on the numbers available after splitting the logs. The number of eggs placed at each temperature ranged from 20 to 60. Pupae extracted from avocado logs were placed in Petri dishes following the same method used for eggs. Numbers of pupae placed at each temperature treatment ranged from 20 to 45. The number of days required for the development of egg to the 1st instar and from the pupal to the adult stage for all temperature treatments was recorded daily. Paper towels were kept moist to prevent desiccation of insects. The study was conducted between Mar and Jun 2012. Temperature-dependent development of the various larval instars was not studied due to lack of an adequate artificial medium on which to rear larvae.

LIFE CYCLE AND DEVELOPMENT OF *X. GLABRATUS* IN AVOCADO LOGS AT CONSTANT TEMPERATURES

The life cycle and development of *X. glabratus* in avocado logs were studied at 5 constant temperatures (16, 20, 24, 28, and 32 °C) during Sept 2011 to May 2012. Avocado 'Booth 7' logs of 4.5 to 6.5 cm diameter were cut from healthy trees without any beetle infestation from the University of Florida, Tropical Research and Education Center, Homestead (Miami Dade County), Florida, USA. The logs were cut to 8 to 10 cm length, soaked in tap water for 48 h, and then placed in a 946 mL clear plastic container (American Plastics, Gainesville, Florida, USA). Depending on the availability of beetles, 5 to 20 sclerotized adult female beetles were placed on each log and allowed to bore for 24 h at 25 ± 2 °C. Each container was covered with Plankton netting (150 microns, BioQuip, Rancho Dominguez, California, USA). After 24 h of infestation, infested logs were placed in Florida Reach-In incubators (Walker et al. 1993) held at 5 constant temperatures (16, 20, 24, 28, and 32 °C [± 0.1 °C]) under complete darkness. For each temperature treatment, 60 logs were infested and studied for 40 d. For each temperature treatment, every other day, 3 logs or 3 replicates were randomly removed from the incubators, and for each log, 5 active galleries (with signs of fresh frass) were marked with a permanent marker (Sharpie pen). The logs were split to expose the marked galleries, and galleries were further dissected to record the number of insects at each developmental stage. The whole study was repeated twice.

MATHEMATICAL MODELS AND STATISTICAL ANALYSES

The development rate of eggs and pupal stages was regressed against temperature in linear and nonlinear models. Seven nonlinear models (Table 1) used to describe temperature-dependent development of insects—such as *Halyomorpha halys* (Stal) (Hemiptera: Pentatomidae) (Nielsen et al. 2008), *Cydia pomonella* L. (Lepidoptera: Tortricidae) (Aghdam et al. 2009), *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Golizadeh et al. 2007), and *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae) (Sandhu et al. 2010, 2013)—were used to describe temperature-dependent development of the egg and pupal stages of *X. glabratus*. The estimated parameters were T_0 (the temperature at, or below, which no measurable development was visible; also called lower development threshold) (Howell & Neven 2000; Sandhu et al. 2010), T_m (upper development threshold, temperature at, or above, which no visible development takes place) (Kontodimas et al. 2004; Sandhu et al. 2010), T_{opt} (temperature at which highest rate of development takes place) (Briere & Pracros 1998; Sandhu et al. 2010), and K (thermal constant; the number of degree-days required by an immature stage to complete its development) (Campbell et al. 1974; Aghdam et al. 2009). The value of T_0 can be estimated from a linear model and from 3 nonlinear models (Briere-1, Briere-2, and Ratkowsky and Taylor). T_m can be estimated by nonlinear models (Briere-1, Briere-2, Lactin, and Logan). T_{opt} can be calculated with the Taylor, Briere-1, Briere-2, and Lactin and Logan models. In the Briere-1 and Briere-2 models, T_{opt} can be calculated by Equation 1.

$$T_{opt} = [2mT_m + (m + 1)\ T_0] + \surd 4m^2T_m{}^2 + (m + 1)^2\ T_0{}^2 - 4m^2\ T_mT_0 / 4m + 2 \qquad (1)$$

The m is the empirical constant with value 2 for the Briere model (Briere & Pracros 1998). In the Lactin and Logan models, T_{opt} can be estimated as the parameter value for which the first derivative equals zero. In the Taylor model, T_{opt} can directly be estimated from the model (Table 1). The value of K can be estimated by linear regression (Campbell et al. 1974). Criteria used to compare performance of nonlinear mathematical models were (1) coefficient of determination (r^2), wherein the higher value indicates a better fit of the model, and (2) residual sum of squares (RSS), wherein the lower value indicates a better fit of the model (Aghdam et al. 2009). A third additional criterion, the Akaike information criterion (AIC) was used to compare nonlinear models. The model that has the lower AIC value has a better fit when comparing models. AIC was calculated by Equation 2.

$$\text{AIC} = n\ ln(SSE\ /\ n) + 2p \qquad (2)$$

where n is the sample size, p is the number of parameters, and SSE is the sum of the squared errors.

Data for different experiments were tested with Shapiro–Wilk normality tests (Shapiro & Wilk 1965) to ensure that the assumptions of homogeneity of variance and normality were met before the data were analyzed. To determine differences between the duration of development from egg to larval stage and from pupal to adult stage at different constant temperatures, we subjected the data to separate 1-way analysis of variance (ANOVA) and Tukey–Kramer tests, by Proc GLM in SAS (SAS 2003). Linear regression (SAS) was used to model the rate of development for each stage at 16, 20, 24, and 28 °C. The linear model $y = a + bx$ (Campbell et al. 1974) was used to estimate the lower developmental threshold temperature ($T_{min} = -a / b$), and thermal constant ($K = 1 / b$). Seven nonlinear models (Table 1) were used to model temperature-dependent development of the egg and pupal stages. The nonlinear models were fitted with the Marquardt algorithm (Marquardt 1963) in SAS software. The differences in time to occurrence of different development stages after initial infestation of avocado logs at different constant temperatures were analyzed by conducting ANOVA in SAS. Tukey–Kramer tests were conducted to ascertain differences in duration of developmental stages of the beetle in logs at constant temperatures using SAS.

Results

EGG DEVELOPMENT

Temperature had a significant effect on egg development (F = 192.3; df = 5, 188; $P < 0.0001$) (Table 2). No development was observed

Table 1. Mathematical equations of nonlinear developmental models tested to describe the relationship between temperature and development of egg and pupal stages of *Xyleborus glabratus.*

Developmental model	Mathematical equation	References
Briere-1 model	$r = aT(T - T_0)\ ´\ [\text{sqrt}(T_m - T)]$	Briere et al. (1999)
Briere-2 model	$r = aT(T - T_0)\ ´\ [(T_m - T)^{(1/d)}]$	Briere et al. (1999)
Logan model	$r(T) = e^{\rho T} - e^{[\rho T_m - (T_m - T)/\Delta]}$	Logan et al. (1976)
Lactin model	$r(T) = e^{\rho T} - e^{[\rho T_m - (T_m - T)/\Delta]} + l$	Lactin et al. (1995)
Polynomial model	$r = a(T)^4 + b(T)^3 + c(T)^2 + d(T) + e$	Lamb et al. (1984)
Taylor model	$r = R_m\ ´\ \exp\{-0.5[(T - T_{opt}) / T_0]^2\}$	Taylor (1981)
Ratkowsky model	$\surd r = b(T - T_0)[1 - \exp\{c(T - T_m)\}]$	Ratkowsky et al. (1983)

r = rate of development; T = treatment temperature ; T_0 = lower temperature threshold; T_m = lethal maximum temperature; T_{opt} = optimum temperature ; r = development rate at optimal temperature ; D = no. of degrees above the base temperature over which thermal inhibition becomes predominant; m = empirical constant; l = empirical constant which forces the curve to intercept the y-axis at a value below zero; R_m = maximum development rate; a, b, c, d, e = empirical constant.

Table 2. Mean (± SE) number of days required for development of *Xyleborus glabratus* eggs and pupae at constant temperatures.

	Developmental period in days			
	Eggs		Pupae	
Temperature (°C)	*N*	Mean ± SE	*N*	Mean ± SE
16	30	21.1 ± 0.75 a	35	12.9 ± 0.51 a
20	43	9.5 ± 0.21 b	34	9.1 ± 0.31 b
24	36	6.6 ± 0.30 c	26	5.8 ± 0.20 c
28	41	3.9 ± 0.17 d	26	4.3 ± 0.22 d
32	24	7.3 ± 0.51 c	28	6.4 ± 0.26 c
36	20	10.9 ± 0.75 b		

Means followed by the same letter are not significantly different based on the Tukey–Kramer test for difference of means ($P < 0.05$). *N* = Number of eggs or pupae that developed to the next stage in the life cycle.

in eggs held at 12 °C. Successful progression from egg to the 1st instar occurred from 16 to 36 °C, with the fastest development rate observed at 28 °C (Table 2). Mean development time for eggs ranged from 21.1 ± 0.75 d at 16 °C to 10.9 ± 0.75 d at 36 °C (Table 2). A linear regression model of temperatures ranging from 16 to 28 °C with development rate yielded a lower temperature threshold of 13.8 °C, requiring 52.1 DD for beetles to develop from egg to the larval stage (Table 3).

The model evaluation parameters, fitted coefficients, and evaluation criteria indices for 7 nonlinear models tested for temperature-dependent development of egg to larval stages are presented in Table 4. The estimated optimum temperature for development of egg to larval stage ranged between 32.3 °C (Briere-2 model) and 27.7 °C (Taylor model). In general, all the models gave a good fit with r^2 values above 0.85, except for the modified Lactin model, where the r^2 value was 0.53. The Briere-2, Ratkowsky, polynomial, and Logan models gave better fits than other models based on a greater r^2 value and smaller RSS and AIC values. The Taylor model gave a good fit based on the greater r^2 value and smaller RSS and AIC values, but its estimated lower development thresholds were less than the observed values. The Logan model provided estimates of T_{max} (37.0 °C) and T_{opt} (28.7 °C). The Ratkowsky and Briere-2 models provided estimates of T_0 (14.4 °C) that were closer to the observed values.

PUPAL DEVELOPMENT

Temperature had a significant effect on the development of the pupal stage ($F = 97.5$; df = 4, 144; $P < 0.0001$) (Table 2). No pupal de-

Table 3. Linear regression parameters for in vitro development of eggs and pupae of *Xyleborus glabratus* over a range of constant temperatures (16–28 °C).

	Life stage	
Parameter	Egg	Pupa
Intercept ± SE	−0.264 ± 0.02	−0.163 ± 0.02
Slope ± SE	0.0191 ± 0.01	0.0146 ± 0.01
[a]*P* value	< 0.0001	< 0.0001
[b]T_{min}	13.8 °C	11.1 °C
[c]*K*	52.1 DD	68.2 DD
[d]r^2	0.65	0.62
[e]RSS	0.5165	0.3139
[f]AIC	−849.0	−931.0

[a] *P* value from the test of significance of the regression coefficient
[b] T_{min} = intercept / slope; *T* represents the lower temperature threshold expressed in °C
[c] *K* = 1 / slope; *K* represents the thermal constant expressed in degree-days (DD)
[d] r^2 represents the coefficient of determination
[e] RSS represents the residual sum of squares
[f] AIC represents the Akaike information criterion value

Table 4. Nonlinear regression parameters, fitted coefficients, and evaluation indices of 7 nonlinear models tested for temperature-dependent development of eggs and pupae of *Xyleborus glabratus.*

Model	Parameter	Eggs	Pupae
Briere-1	$a(\times10^{-4})$	1.64	2.10
	T_0	11.3	11.3
	T_m	36.4	33.4
	T_{opt}	31.5	29.5
	r^2	0.86	0.91
	RSS	0.8114	0.3517
	AIC	−788.94	−902.34
Briere-2	$a(\times10^{-4})$	0.06	2.70
	d	0.9968	45.0
	T_0	14.4	8.9
	T_m	37.9	32.0
	T_{opt}	32.3	27.1
	r^2	0.88	0.88
	RSS	0.7446	0.5459
	AIC	−787.83	−834.39
Lactin	*r*	0.0659	0.2251
	D	13.31	4.44
	T_m	43.1	34.3
	T_{opt}	29.8	29.9
	l	−0.5998	0.0842
	r^2	0.53	0.3410
	RSS	0.7519	0.5370
	AIC	−786.36	−836.85
Logan	*r*	0.1561	0.19
	D	6.41	5.04
	T_m	37.0	33.7
	T_{opt}	28.7	28.7
	r^2	0.92	0.93
	RSS	0.8489	0.3177
	AIC	−770.16	−917.59
Taylor	R_m	0.2455	0.2227
	T_{opt}	27.7	27.4
	T_0	5.8	7.2
	r^2	0.89	0.91
	RSS	0.6728	0.3722
	AIC	−805.04	−893.84
Polynomial	$a(\times10^{-6})$	−0.095	−8.73
	$b(\times10^{-6})$	0.16	58.5
	c	0.0012	−0.0125
	d	−0.0169	0.091
	e	−7.3	−5.3
	r^2	0.88	0.92
	RSS	0.7403	0.3136
	AIC	−788.70	−917.54
Ratkowsky	*b*	0.0264	0.018
	T_0	14.4	6.3
	T_m	37.6	32.2
	c	0.14	3.7
	r^2	0.88	0.46
	RSS	0.7571	0.4396
	AIC	−799.3	−866.2

r = rate of development; *T* = treatment temperature ; T_0 = lower temperature threshold; T_m = lethal maximum temperature; T_{opt} = optimum temperature; *r* = development rate at optimal temperature; *D* = no. of degrees above the base temperature over which thermal inhibition becomes predominant; *m* = empirical constant; *l* = empirical constant which forces the curve to intercept the y-axis at a value below zero; *a*, *b*, *c*, *d*, *e* = empirical constant; R_m = maximum development rate; r^2 = coefficient of determination; RSS = residual sum of squares; AIC = Akaike information criterion value.

velopment was observed at 12 and 36 °C. Mean development times for pupae ranged from 6.4 ± 0.26 d at 32 °C to 12.9 ± 0.51 d at 16 °C (Table 2). Development times for the pupal stages decreased from 16 to 28 °C and then increased at 32 °C. In the temperature range from 16 to 28 °C, linear regression yielded a lower temperature threshold of 11.1 °C, with the pupal stage requiring 68.2 DD to develop to the adult stage (Table 3).

All nonlinear models gave a good fit with r^2 values above 0.87 with the exception of the modified Lactin model, which gave a poor fit with an r^2 value of 0.34. All the evaluation parameters, fitted coefficients, and evaluation criteria indices are presented in Table 4. The optimal temperature of development of the pupal to adult stage ranged from 27.4 °C (Taylor model) to 33.4 °C (Briere-1 model). The Briere-1, Logan, and polynomial models gave better fits based on a greater r^2 value and smaller RSS and AIC values. The Taylor model was a good fit based on a greater r^2 value and lower RSS and AIC values, but its estimated lower development thresholds were less than the observed values. The Logan model provided the best estimates of T_{max} (33.7 °C) and T_{opt} (28.7 °C).

LIFE CYCLE AND DEVELOPMENT OF *X. GLABRATUS* IN AVOCADO LOGS AT CONSTANT TEMPERATURES

Xyleborus glabratus successfully completed its life cycle in avocado logs held at temperatures of 24, 28, and 32 °C. There was no development observed at 16 °C. Temperature had a significant effect on the development of egg stage ($F = 10.78$; df = 3, 14; $P = 0.0006$), larval stage ($F = 7.66$; df =3, 16; $P = 0.0021$), pupal stage ($F = 12.76$; df =3, 13; $P = 0.0004$), and teneral adults ($F = 6.33$; df = 2, 14; $P = 0.01$) in avocado logs placed at different constant temperatures ranging from 16 to 32 °C (Table 5). The mean number of days to first occurrence of each developmental stage in avocado logs held at various constant temperatures is presented in Table 5 and Figs. 1 to 4. The largest numbers of eggs, larvae, and teneral adults were encountered at 28 °C, followed by 24, 32, and 20 °C (Table 6). The largest numbers of pupae were observed at 24 °C followed by 28, 32, and 20 °C.

Discussion

The results from the current investigation suggest that duration of life cycle and development time of immature stages is strongly related to temperature. We exposed egg and pupal stages of *X. glabratus* to constant temperatures ranging from 12 to 36 °C. Egg and pupal development were similar, as reported for *Xyleborus fornicatus* Eichhoff (Gadd 1949; Walgama & Zalucki 2007a). For instance, *X. fornicatus* eggs and pupae did not develop at 15 °C; however, *X. fornicatus* eggs and pupae developed when held at 18 to 32 °C (Gadd 1947; Walgama & Zalucki 2007b). Likewise, eggs of *Ips calligraphus* (Germar) (Coleoptera: Curculionidae) developed at 12.5 to 35.0 °C, and pupae developed at 12.5 to 37.0 °C, when exposed to constant temperatures ranging from 10 °C to 37.5 °C (Wagner et al. 1987, 1988). Identical trends of development were observed with *Ips avulsus* (Eichhoff) (Coleoptera: Curculionidae) egg and pupal stages, with development occurring from 15 to 35 °C when observed at 7 constant temperatures ranging between 10 and 35 °C (Wagner et al. 1988). Thus, *X. glabratus* egg and pupal development range temperatures were similar to those of other scolytine species.

One of the objectives was to select the mathematical model that would best explain the temperature-dependent development of *X. glabratus.* We tested 1 linear and 7 nonlinear models on how well they describe the relationships between temperature and the development rates of eggs and pupae. Linear correlation of the development rates of *X. glabratus* eggs and pupae with temperatures between 16 and 28 °C resulted in estimated lower developmental threshold temperatures of 13.8 °C and 11.1 °C for eggs and pupae, respectively. In contrast, the estimated lower developmental threshold temperatures for egg and pupal stages were 15.7 °C and 14.3 °C, respectively, for *X. fornicatus* (Walgama & Zalucki 2007a) and 10.6 °C and 9.9 °C, respectively, for *Ips typographus* (L.) (Coleoptera: Curculionidae) (Wermelinger & Seifert 1998). The lower threshold temperatures estimated by the linear model for the temperature-dependent development of eggs were close to the observed values, but the estimates for the pupal stage were below the lowest temperature tested experimentally. This discrepancy might be due to nonlinear relationships between temperature and development rate near the threshold temperatures (Wagner et al. 1991).

In the present investigation, we evaluated the performance of 7 nonlinear models to describe the development of egg and pupal stages of *X. glabratus*. The Briere-2, Ratkowsky, polynomial, and Logan models gave good fits for the temperature-dependent development of eggs as indicated by greater r^2 and smaller RSS and AIC values, but the Logan model gave estimates that were closest to the actual observations. For temperature-dependent development of the pupal stage, the Briere-1, Logan, and polynomial models each gave a good fit, with the Logan model giving estimates closest to the observed values. The Logan model proved to be the best model based on the evaluation criteria and its closeness of estimated values of parameters to the actual observed values. In contrast, the Lactin model gave the best fit for temperature-dependent development of *X. fornicatus* as compared with other mathematical models tested (Walgama & Zalucki 2007b), whereas the Lactin model proved least fit to describe the temperature-dependent development of the egg and pupal stages of *X. glabratus*. The Briere-1 model gave the best fit for the temperature-dependent development of *E. lignosellus* as indicated by a larger r^2 value and smaller RSS and AIC values (Sandhu et al. 2010). Examples of best fit for development rates include the following: Logan model for *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) (Coop et al. 1993), Briere-2 model for *P. xylostella* (Golizadeh et al. 2007), Lactin 2 model for *Sesamia nonagrioides* (Lefèbvre) (Lepidoptera: Noctuidae) (Fantinou et al. 2003), and

Table 5. Mean (± SE) number of days to first occurrence of each developmental stage of *Xyleborus glabratus* in avocado (*Persea americana*) logs held at constant temperatures. Results are based on the first observation of each developmental stage in avocado logs dissected at 2 d intervals.

	Means ± SE of developmental period in days after gallery initiation			
Temperature (°C)	Eggs	Larvae	Pupae	Adults
20	23 ± 1.0 a	25.6 ± 0.7 a	39.0 ± 1.4 a	
24	14.8 ± 0.6 bc	20.3 ± 1.4 b	26.4 ± 2.1 c	31.6 ± 1.9 ab
28	12.3 ± 0.8 c	16.3 ± 0.9 c	24.8 ± 2.6 c	27.7 ± 0.7 b
32	16.4 ± 0.5 b	18.8 ± 0.8 bc	32.0 ± 5.0 b	35.3 ± 1.3 a

Means followed by the same letter are not significantly different based on the Tukey–Kramer test for difference of means ($P < 0.05$). No development was observed at temperatures where there are no values given.

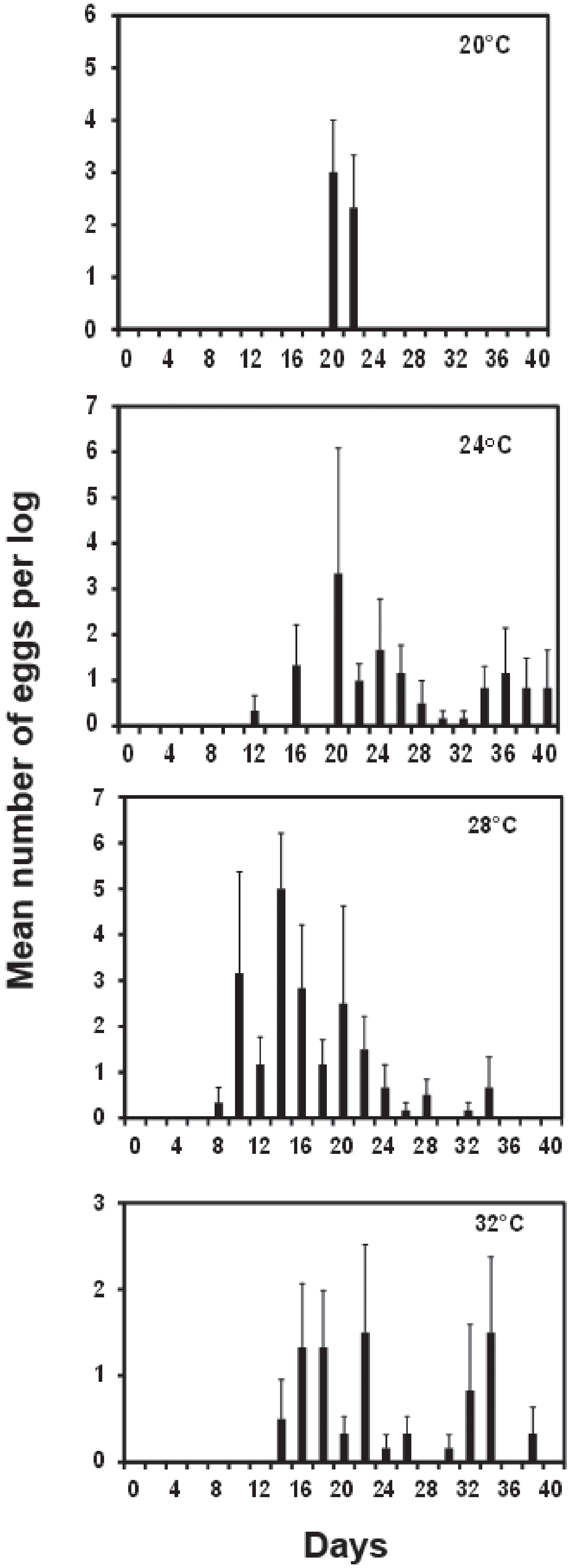

Fig. 1. Mean ± SE number of eggs per 5 galleries per log observed every other day in the avocado logs at 4 constant temperatures.

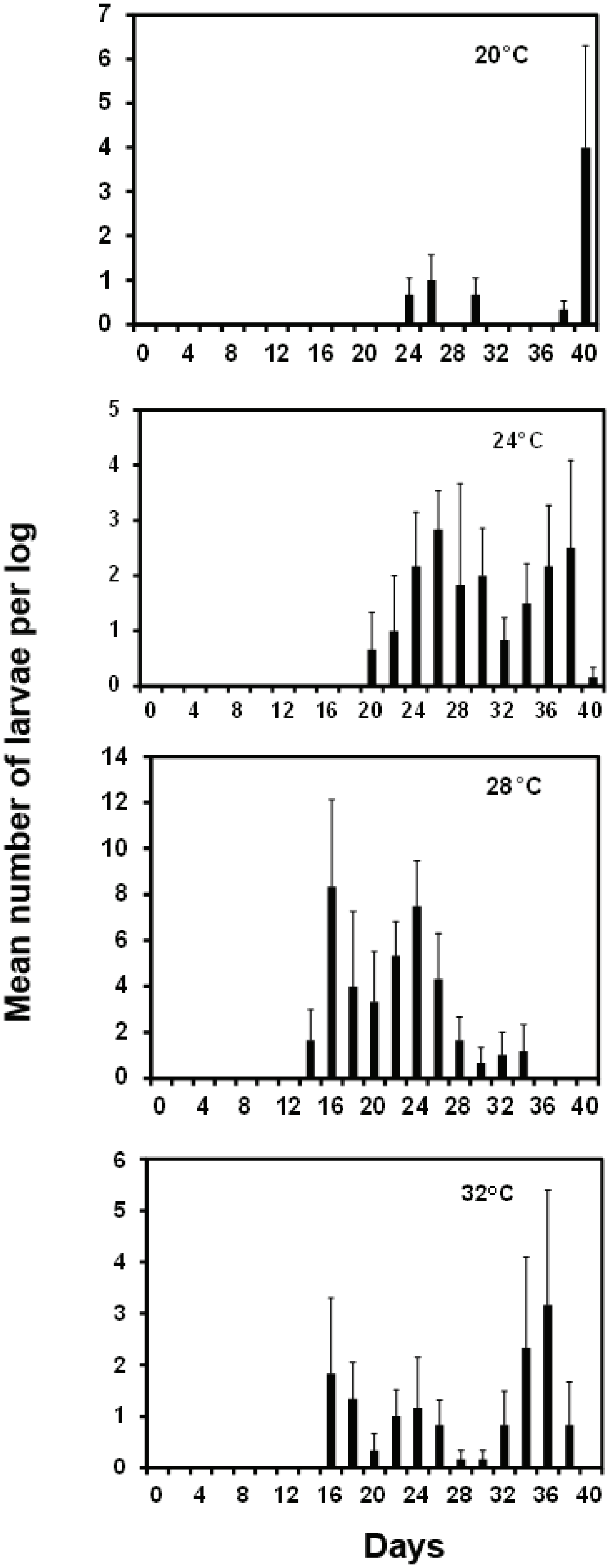

Fig. 2. Mean ± SE number of larvae per 5 galleries per log observed every other day in the avocado logs at 4 constant temperatures.

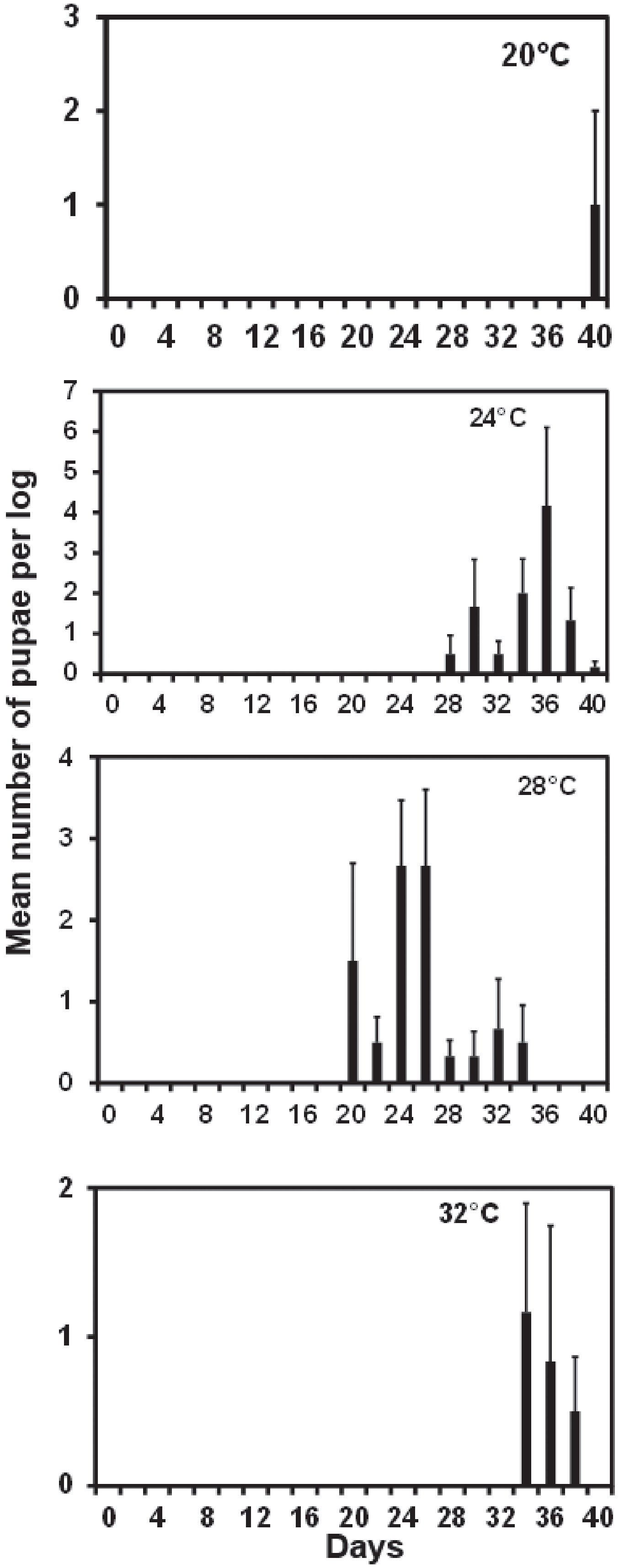

Fig. 3. Mean ± SE number of pupae per 5 galleries per log encountered every other day in the avocado logs at 4 constant temperatures.

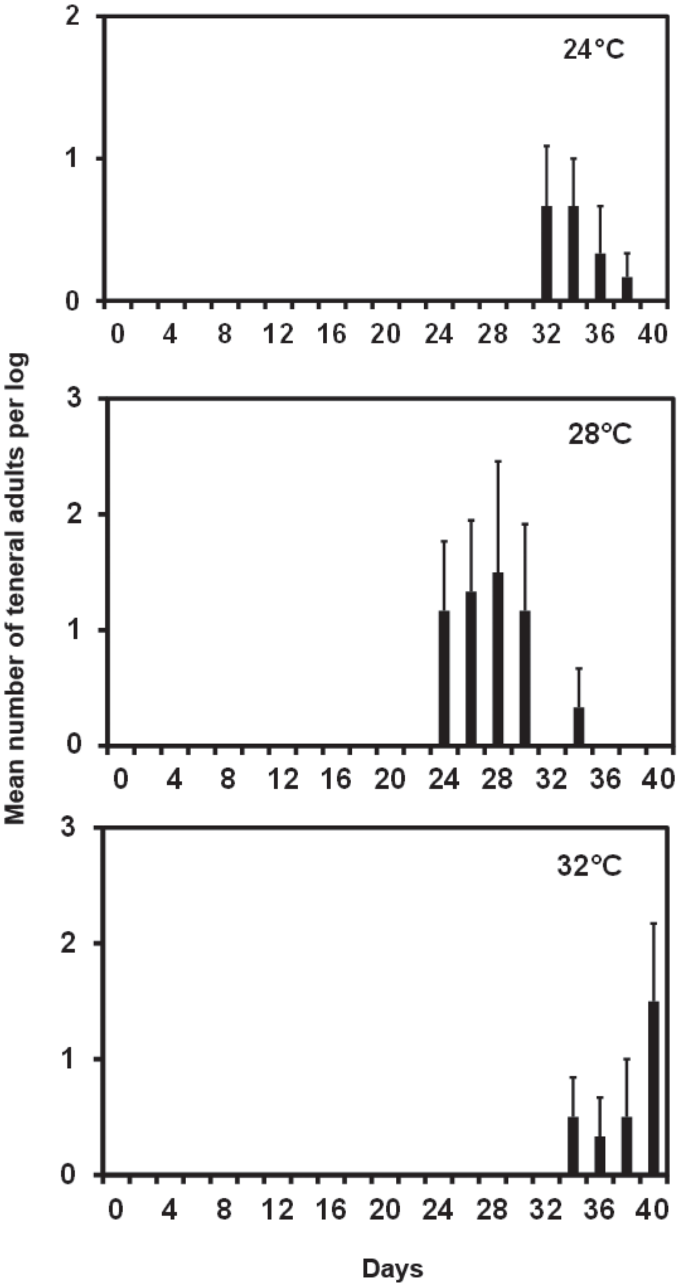

Fig. 4. Mean ± SE number of teneral adults per 5 galleries per log encountered every other day in the avocado logs at 4 constant temperatures.

Briere-1 and Briere-2 models for *C. pomonella* (Aghdam et al. 2009). The variability in the performance of different mathematical models to describe the temperature-dependent development of insects might be due to variability in thermal adaptations of different insect species (Sandhu et al. 2010), but the quality of the data set, especially data near the upper and lower developmental thresholds, also influences model fitting.

Future studies are warranted to study temperature-dependent development of larval stages of *X. glabratus* along with its symbionts at different constant temperatures. Moreover, avocado is not considered the preferred host for *X. glabratus,* and it is important to determine the development of *X. glabratus* on other host plants such as *P. borbonia* and *P. pallustris* that support denser beetle infestations than avocado.

Table 6. Total number of *Xyleborus glabratus* of each developmental stage observed in dissected avocado (*Persea americana*) logs held at constant temperatures. Results are based on observations in logs dissected at 2 d intervals for 40 d after gallery initiation.

	No. observed at each developmental stage			
Temperature (°C)	Eggs	Larvae	Pupae	Teneral adults
20	17	20	3	0
24	80	106	62	11
28	121	251	55	33
32	50	84	15	17

We hypothesize that redbay ambrosia beetle will have more generations per year at lower latitudes compared with higher latitudes. The warm conditions in the southeastern United States and availability of different host trees may be influencing the more rapid range expansion of the redbay ambrosia beetle than predicted by earlier models of Koch & Smith (2008).

Acknowledgments

We gratefully acknowledge Stephen McLean (Entomology and Nematology Department, University of Florida) for help in maintaining the redbay ambrosia beetle colony. We also gratefully acknowledge the Hammock Dunes Club Golf Course, Palm Bay (Brevard County) for allowing us to cut infested redbay and swampbay wood. We gratefully acknowledge the assistance of James Colee (IFAS Statistics, University of Florida). This research was supported by a SCRI grant to Dr. R. C. Ploetz (University of Florida, TREC, Homestead, Florida).

References Cited

Aghdam HR, Fathipour Y, Radjabi G, Rezapanah M. 2009. Temperature-dependent development and temperature thresholds of codling moth (Lepidoptera: Tortricidae) in Iran. Environmental Entomology 38: 885-895.

Brar GS, Capinera JL, McLean S, Kendra PE, Ploetz RC, Peña JE. 2012. Effect of trap size, trap height and age of lure on sampling *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae), and its flight periodicity and seasonality. Florida Entomologist 95: 1003-1011.

Brar GS, Capinera JL, Kendra PE, Peña JE. 2013. Life cycle, development, and culture of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). Florida Entomologist 96: 1158-1167.

Briere JF, Pracros P. 1998. Comparison of temperature-dependent growth models with the development of *Lobesia botrana* (Lepidoptera: Tortricidae). Environmental Entomology 27: 94-101.

Briere JF, Pracros P, Le Roux AY, Pierre JS. 1999. A novel rate model of temperature-dependent development for arthropods. Environmental Entomology 28: 22-29.

Campbell A, Frazer BD, Gilbert N, Gutierrez AP, Mackauer M. 1974. Temperature requirements of some aphids and their parasites. Journal of Applied Ecology 11: 431-438.

Coop LB, Croft BA, Drapek RJ. 1993. Model of corn earworm (Lepidoptera: Noctuidae) development, damage, and crop loss in sweet com. Journal of Economic Entomology 86: 906-916.

Fantinou AA, Perdikis DC, Chatzoglou CS. 2003. Development of immature stages of *Sesamia nonagrioides* (Lepidoptera: Noctuidae) under alternating and constant temperatures. Environmental Entomology 32: 1337-1342.

FDOACS. 2012. Florida Department of Agriculture and Consumer Services Identifies Laurel Wilt Disease in Avocado Production Area of Miami-Dade County. http://www.freshfromflorida.com/newsroom/press/2012/05012012.html (accessed 10 Jul 2013).

Fraedrich SW. 2008. California laurel is susceptible to laurel wilt caused by *Raffaelea lauricola*. Plant Disease 92: 1469.

Fraedrich SW, Harrington TC, Rabaglia RJ, Ulyshen MD, Mayfield AE, Hanula JL, Eicwort JM, Miller DR. 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. Plant Disease 92: 215-224.

Gadd CH. 1947. Observations on the life cycle of *Xyleborus fornicatus* Eichhoff in the artificial culture. Annals of Applied Biology 34: 197-206.

Golizadeh A, Kamali K, Fathipour Y, Abbasipour H. 2007. Temperature-dependent development of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) on two brassicaceous host plants. Insect Science 14: 309-316.

Gramling JM. 2010. Potential effects of laurel wilt of the flora of North America. Southeastern Naturalist 9: 827-836.

Haack RA. 2003. Intercepted Scolytidae (Coleoptera) at U.S. ports of entry. Integrated Pest Management Review 6: 1985-2000.

Hanula JL, Mayfield AE, Fraedrich SW, Rabaglia RJ. 2008. Biology and host associations of the redbay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing redbay (*Persea borbonia*) trees in the southeastern United States. Journal of Economic Entomology 101: 1276-1286.

Hanula JL, Ulysen MD, Horn S. 2011. Effect of trap type, trap position, time of year, and beetle density on captures of the redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae). Journal of Economic Entomology104: 501-508.

Howell JF, Neven LG. 2000. Physiological development time and zero development temperature of the codling moth (Lepidoptera: Tortricidae). Environmental Entomology 29: 766-772.

Hughes M, Brar GS, Ploletz R, Smith JA. 2013. *Persea indica*, a newly recognized host for the laurel wilt pathogen *Raffaelea lauricola*. Plant Health Progress, published 14 Aug 2013 (doi: 10.1094/PHP-2013-0814-02-BR).

Kendra PE, Montgomery WS, Niogret J, Peña JE, Capinera JL, Brar GS, Epsky ND, Heath RR. 2011. Attraction of the redbay ambrosia beetle, *Xyleborus glabratus*, to avocado, lychee, and essential oil lures. Journal of Chemical Ecology 37: 932-942.

Kendra PE, Montgomery WS, Niogret J, Epsky ND. 2013**.** An uncertain future for American Lauraceae: a lethal threat from redbay ambrosia beetle and laurel wilt disease (a review). American Journal of Plant Science 4: 727-738.

Kendra, PE, Montgomery WS, Niogret J, Pruett GE, Mayfield III AE, MacKenzie M, Deyrup MA, Bauchan GR, Ploetz RC, Epsky ND. 2014. North American Lauraceae: terpenoid emissions, relative attraction and boring preferences of redbay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). PLoS ONE 9: e102086 (doi:10.1371/journal.pone.0102086).

Koch FH, Smith WD. 2008. Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) invasion in eastern U.S. forests. Journal of Economic Entomology 37: 442-452.

Kontodimas DC, Eliopoulos PA, Stathas GJ, Economou LP. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria. Environmental Entomology 33: 1-11.

Lactin DJ, Holliday NJ, Johnson DL, Craigen R. 1995. Improved rate model of temperature-dependent development by arthropods. Environmental Entomology 24: 68-75.

Lamb RJ, Gerber GH, Atkinson GF. 1984. Comparison of developmental rate curves applied to egg hatching data of *Entomoscelis americana* Brown (Coleoptera: Chrysomelidae). Environmental Entomology 13: 868-872.

Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK. 1976. An analytical model for description of temperature dependent rate phenomena in arthropods. Environmental Entomology 5: 1133-1140.

Marquardt DV. 1963. An algorithm for least square estimation of nonlinear parameters. Journal of the Society for Industrial and Applied Mathematics 11: 431-441.

Mayfield III AE, Crane JH, Smith JA, Peña JE, Branch CL, Ottoson ED, Hughes M. 2008. Ability of redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) to bore into young avocado (Lauraceae) plants and transmit the laurel wilt pathogen (*Raffaelea* spp.). Florida Entomologist 91: 485-487.

Nielsen AL, Hamilton GC, Matadha D. 2008. Developmental rate estimation and life table analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae). Journal of Economic Entomology 102: 1133-1144.

Peña JE, Carrillo D, Duncan RE, Capinera JL, Brar GS, McLean S, Arpaia ML, Focht E, Smith JA, Hughes M, Kendra PE. 2012. Susceptibility of *Persea* spp. and other Lauraceae to attack by redbay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). Florida Entomologist 95: 783-787.

Ploetz RC, Konkol J. 2013. First report of Gulf licaria, *Licaria triandra*, as a suscept of laurel wilt. Plant Disease 97: 1248.

Ploetz RC, Hulcr J, Wingfield MJ, Beer ZW. 2013. Destructive tree diseases associated with ambrosia and bark beetles: black swan events in tree pathology. Plant Disease 95: 856-872.

Rabaglia R, Duerr D, Acciavatti R, Ragenovich I. 2008. Early detection and rapid response for non-native bark and ambrosia beetles. USDA Forest Service Forest Health Protection, Washington, District of Columbia, USA. 12 pp.

Ratkowsky DA, Lowry RK, McMeekin TA, Stokes AN, Chandler RE. 1983. Model of bacterial culture growth rate throughout the entire biokinetic temperature range. Journal of Bacteriology 154: 1222-1226.

Roy M, Brodeur J, Cloutier C. 2002. Relationship between temperature and development rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). Environmental Entomology 31: 177-187.

Sandhu HS, Nuessly GS, Webb SE, Cherry RH, Gilbert RA. 2010. Temperature-dependent development of lesser cornstalk borer, *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane under laboratory conditions. Environmental Entomology 39: 1012-1020.

Sandhu HS, Nuessly GS, Webb SE, Cherry RH, Gilbert RA. 2013. Temperature-dependent reproductive and life table parameters of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane. Florida Entomologist 96: 380-390.

SAS. 2003. User's Guide. SAS Institute, Cary, North Carolina, USA.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). Biometrika 52: 591-611.

Smith JA, Dreaden TJ, Mayfield III AE, Boone A, Fraedrich SW, Bates C. 2009a. First reports of laurel wilt disease caused by *Raffaelea lauricola* on sassafras in Florida and South Carolina. Plant Disease 93: 1079.

Smith JA, Mount L, Mayfield III AE, Bates CA, Lamborn WA, Fraedrich SW. 2009b. First report of laurel wilt disease caused by *Raffaelea lauricola* on camphor in Florida and Georgia. Plant Disease 93: 198.

Taylor F. 1981. Ecology and evolution of physiological time in insects. The American Naturalist 117: 1-23.

Wagner TL, Hennier PB, Flamm RO, Coulson RN. 1988. Development and mortality of *Ips avulses* (Coleoptera: Scolytidae) at constant temperatures. Environmental Entomology17: 181-191.

Wagner TL, Olson RL, Willers JL. 1991. Modeling arthropod development time. Journal of Agricultural Entomology 8: 251-270.

Wagner TL, Flamm RO, Wu H, Fargo WS, Coulson RN. 1987. Temperature-dependent model of life cycle development of *Ips calligraphus* (Coleoptera: Scolytidae). Environmental Entomology 16: 497-502.

Walgama RS, Zalucki MP. 2007a. Temperature-dependent development of *Xyleborus fornicatus* (Coleoptera: Scolytidae), the shot-hole borer of tea in Sri-Lanka: implications for distribution and abundance. Insect Science 14: 301-308.

Walgama RS, Zalucki MP. 2007b. Evaluation of different models to describe egg and pupal development of *Xyleborus fornicatus* Eichh. (Coleoptera: Scolytidae), the shot-hole borer of tea in Sri Lanka. Insect Science 13: 109-118.

Walker TJ, Gaffney JJ, Kidder AW, Ziffer AB. 1993. Florida Reach-Ins: environmental chambers for entomological research. American Entomologist 3: 177-182.

Wermelinger B, Seifert M. 1998. Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). Journal of Applied Entomology 122: 185-191.