

Thermal Requirements and Development of *Herpetogramma phaeopteralis* (Lepidoptera: Crambidae: Spilomelinae)

NASTARAN TOFANGSAZI,¹ EILEEN A. BUSS,² ROBERT MEAGHER,³ GABRIEL M. MASCARIN,⁴
AND STEVEN P. ARTHURS^{1,5}

J. Econ. Entomol. 105(5): 1573–1580 (2012); DOI: <http://dx.doi.org/10.1603/EC12098>

ABSTRACT The tropical sod webworm, *Herpetogramma phaeopteralis* Guenée is a major turfgrass pest in the southeastern United States. We evaluated larval development on five artificial diets and at six temperatures (15, 20, 25, 30, 32.5, 35 ± 1°C) on St. Augustinegrass (*Stenotaphrum secundatum* (Walter) Kuntze). Only larvae fed St. Augustinegrass and soy-wheat germ diets completed their lifecycles. None of the artificial diets tested (corn-based, soy-wheat germ, corn cob-wheat germ, corn cob-soy flour, or pinto bean) were suitable for rearing this species, because of high mortality and slower developmental time. Total developmental time (oviposition to adult) on *S. secundatum* significantly decreased from 47.8 d at 20°C to 21.1 d at 30°C, and then increased to 32.6 d at 32.5°C. Tropical sod webworm failed to complete larval development at 15 and 35°C. The relationship between temperature and developmental rate was described using linear (common and polynomial) and nonlinear models (Briere-1, Briere-2, and Lactin-2). The estimated lower temperature thresholds using a linear model for eggs, first, second, third, fourth, fifth, and sixth instars, prepupa, pupa, and total development were 10.1, 6.9, 12.3, 10.5, 15.3, 13.9, 9.1, 13.1, 12.0, and 13.1°C, and the thermal constant of these stages were 62.9, 66.2, 38.2, 40.3, 24.9, 32.3, 51.9, 106.4, 109.9, and 370.4 degree-days, respectively. The Briere-1 model provided the best fit with estimated lower, upper, and optimum thresholds for total development of 14.9, 34.3, and 29.4°C, respectively. The developmental requirements of *H. phaeopteralis* can be used to help predict the distribution and seasonal phenology of this pest.

KEY WORDS *Herpetogramma phaeopteralis*, developmental rate, degree-day, nonlinear model, turfgrass

Turfgrass (sod) production is an important industry in the United States, and Florida is one of the main sod producing states cultivating an estimated 37,635 ha and harvesting over 25,495 ha annually (Trenholm and Unruh 2004, Haydu et al. 2006). The tropical sod webworm, *Herpetogramma phaeopteralis* Guenée (Lepidoptera: Crambidae: Spilomelinae) is a destructive pest of warm season turfgrasses in Florida, infesting centipedegrass (*Eremochloa ophiuroides* [Munro] Hackel), Bermuda grass (*Cynodon* spp.), carpetgrass (*Axonopus* spp.), bahiagrass (*Paspalum notatum* Flugge), and St. Augustinegrass (*Stenotaphrum secundatum* (Walter) Kuntze) (Reinert et al. 2009). This pest is especially destructive on newly established sod, lawns, athletic fields, and golf courses (Kerr 1955, Buss and Meagher 2006). *H. phaeopteralis* has been previ-

ously recorded from Florida, Georgia, Louisiana, Texas, Hawaii, Mississippi, Alabama, and the Caribbean islands (Kerr 1955); however, a comprehensive survey for this pest has not been conducted in recent years. St. Augustinegrass, the most common turfgrass planted in home lawns in Florida (Trenholm and Unruh 2004) can be severely defoliated by *H. phaeopteralis*. The first four instars “window feed” on the adaxial side of the grass blade, and their injury is often overlooked (Buss and Meagher 2006). The fifth and sixth instars are defoliators, and produce silk and frass (Kerr 1955). Larval feeding damage reduces turfgrass aesthetics, vigor, photosynthesis, and density. Peak adult emergence is from October to November in southern Florida (Cherry and Wilson 2005). Adult *H. phaeopteralis* may benefit from the presence of nectar sources (Sourakov 2008).

Despite the apparent economic importance of *H. phaeopteralis*, little information on integrated pest management (IPM) programs have been reported. Several insecticides may be used to control this pest, but appropriate timing, risks of resistance and non-target impacts need to be considered (Reinert 1983). Varying levels of resistance to *H. phaeopteralis* has been identified among certain cultivars or hybrids of

¹ Mid Florida Research and Education Center, University of Florida, 2725 Binion Rd., Apopka, FL 32703.

² Entomology and Nematology Department, University of Florida Gainesville, FL 32611.

³ Center for Medical, Agricultural and Veterinary Entomology, USDA-ARS, Gainesville, FL 32608.

⁴ EMBRAPA Arroz e Feijão, Rodovia GO-462, km 12, Zona Rural, C.P. 179, 75375-000, Santo Antônio de Goiás, GO, Brazil.

⁵ Corresponding author, e-mail: spa@ufl.edu.

Table 1. Models evaluated to describe the relationship between temp and developmental rate for immature *H. phaeopteralis* on ‘Palmetto’ St. Augustinegrass, under laboratory conditions

Model	Parameters	Equation	Reference
Linear (common)	2	$Y = a + bX$	Roy et al. (2002)
Briere-1	3	$aT (T - T_0) \times \text{sqrt} (T_L - T)$	Briere et al. (1999)
Briere-2	4	$aT (T - T_0) \times (T_L - T)^{1/m}$	Briere et al. (1999)
Polynomial (second order)	3	$aT^2 + bT + c$	Lamb et al. (1984)
Lactin-2	4	$\exp(\rho T) - \exp[\rho T_L - [(T_L - T)/\Delta]] + \lambda$	Lactin et al. (1995)

In linear, *a*, *b*, and *c* were constants and $T_0 = -a/b$ and degree-days were estimated through $K = 1/b$; where *T* is rearing temp (°C), T_0 is lower threshold, T_L is upper threshold, and T_{opt} is optimum temp. In Lactin-2, Δ is difference between optimal and upper threshold and ρ is rate of increase at optimal thresholds.

Bermuda grass (Reinert and Busey 1983), zoysiagrass, and St. Augustinegrass (Reinert and Engelke, 2001, Reinert et al. 2009). Korndorfer et al. (2004) tested applications of calcium silicate to turfgrass (for anti-biosis), but did not observe any differences in subsequent feeding and development of *H. phaeopteralis* compared with control plants.

It is essential to create laboratory colonies to study the behavior, life history, and feeding habits for this pest. No artificial diets have been published for *H. phaeopteralis*, so our first objective was to evaluate the suitability of various commercial diets. In addition, because insect growth and development rates are closely tied to environmental temperatures (Huffaker et al. 1999), understanding the factors governing *H. phaeopteralis* development and implementing this knowledge into forecast models may facilitate pest management decisions. Therefore, our second objective was to study thermal requirements of *H. phaeopteralis* using linear and nonlinear models.

Materials and Methods

Insect Rearing. A colony of *H. phaeopteralis* was established on St. Augustinegrass ‘Palmetto’ from adults collected from north, central, and south Florida. Larvae were reared in a greenhouse on 15 cm pots of St. Augustinegrass inside rearing cages (60 × 60 × 60 cm) covered with nylon mesh fitted with sleeves for access. Additional pots of grass were provided as needed. To obtain cohorts, newly emerged adults were collected and released into an oviposition cage (26 × 26 × 26 cm) with St. Augustinegrass blades as oviposition sites. Growth chamber conditions were at 25°C, 70% relative humidity (RH), and a photoperiod

of 14:10 (L:D) h. Adults were provided with a 10% honey solution in a snap-cap vial with extruding dental wicks.

Diet Suitability. Five artificial diets were evaluated: 1) a corn-based diet, S.W. Corn Borer F0635 (dry mix) and F0717 (vitamin mix); 2) a soy-wheat germ diet, general purpose diet for Lepidoptera (F9772); 3) a corn cob-wheat germ base diet, European corn borer (*Ostrinia nubilalis* Hübner) diet (F9478B); 4) a corn cob-soy flour base diet, for the sugarcane borer, *Diatraea saccharalis* (F.), U.S. Department of Agriculture (USDA) formula (F9775B), (diets #1–4 were obtained through Bio-Serve, Frenchtown, NJ); and 5) pinto bean diet (Guy et al. 1985; diet ingredients purchased at several locations and prepared at USDA-ARS CMAVE, Gainesville, FL). Diets were prepared according to their directions and dispensed immediately. Agar was added to autoclaved water and boiled for 1 min. Dry mixes and vitamins were added to the agar solution and blended for 2 min. The host plant St. Augustinegrass Palmetto was used as a control.

To study instar-specific survivorship and development, newly emerged neonates were placed individually in 30 ml plastic cups prefilled with 5 ml of diet. Equivalent cups prefilled with 5 ml of water agar containing leaves of St. Augustinegrass blades served as controls. There were 50 replicate larvae per diet. Artificial diets were replaced every 2 wk, whereas St. Augustinegrass was replaced daily. Survival and larval development were monitored every 24 h. Exuviae indicated that the larvae molted and nonfeeding shortened larvae indicated the prepupal stage. This study was conducted in a growth chamber at 25°C, 70% RH, and a photoperiod of 14:10 (L:D) h.

Table 2. Duration (days) of larval, prepupal, and pupal development of *H. phaeopteralis* on five artificial diets and ‘Palmetto’ St. Augustinegrass at 25°C

Diet	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Prepupa	Pupa	Total
St. Augustinegrass	4.0d	3.7c	3.2c	3.8c	3.9b	3.5b	3.6b	10.9b	41.0b
Soy-wheat germ	6.5c	8.1b	8.6b	8.5b	8.8a	7.5a	8.0a	20.7a	69.5a
Sugarcane borer	8.7b	13.0a	14.1a	12.2a	10.7a	8.0a	—	—	—
European corn borer	10.3a	11.4a	18.0a	—	—	—	—	—	—
S. W. corn borer	10.4a	10.8a	10.4ab	10.0b	9.6a	7.4a	9.0a	—	—
<i>F</i>	118.1	54.2	44.2	67.3	49.0	46.5	71.2	137.5	44.2
<i>df</i>	4, 106	4, 92	4, 80	3, 71	3, 63	3, 52	2, 45	1, 34	1, 44
<i>P</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.00001	<0.0001

Means within a column followed by the same letter are not significantly different ($P \leq 0.05$; Tukey’s HSD). —, indicates no survival at that stage. Sample size was 50 larvae per diet.

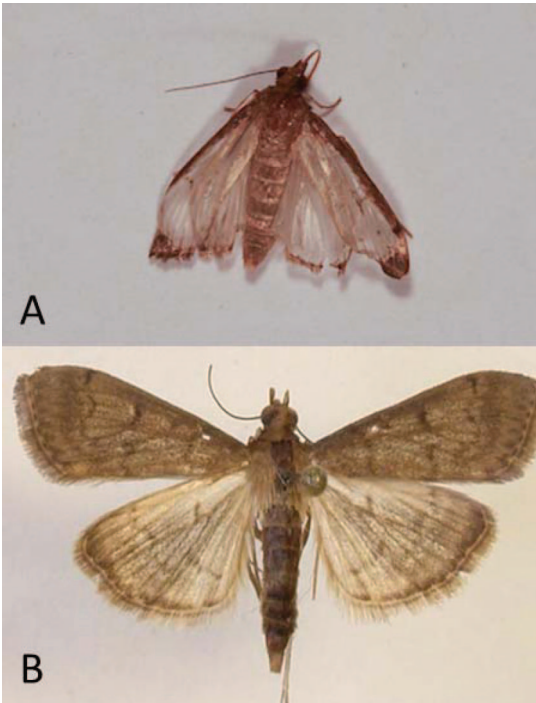


Fig. 1. Abnormal (A) and normal (B) wing of *H. phaeopteralis*. (Photo A by Chris Foosee, photo B by Lyle Buss.). (Online figure in color.)

Temperature-Dependent Development. Day-old neonates were transferred singly to 30 ml plastic cups containing water agar and St. Augustinegrass and were reared at six constant temperatures (15, 20, 25, 30, 32.5, 35 ± 1°C), in growth chambers at 70% RH, and a photoperiod of 14:10 (L:D) h. Larval, prepupal, and pupal survivorship and development were determined as previously described. In addition, ≈100 eggs (within 24 h of oviposition) were also incubated at each assigned temperature. Eggs were checked daily for eclosion.

Developmental Rate and Mathematical Models. The developmental rate (reciprocal of developmental time in days, 1/d) was measured for each immature stage exposed to different temperatures. Two linear (common and second order polynomial) and three nonlinear (Briere-1, Briere-2, and Lactin-2) models were used to explain the relationship between tem-

perature and *H. phaeopteralis* development (Table 1). Thermal requirements were determined for all immature stages (eggs, first to sixth instar larvae, prepupae, and pupae) and overall immature stages by regressing developmental rates against temperature. The parameters of interest were lower (T_0), and upper thresholds (T_L), optimum temperature (T_{opt}), and thermal constant (K). These models were selected based on previous findings (Briere and Pracros 1998, Briere et al. 1999, Aghdam et al. 2009, Sandhu et al. 2010). The Briere-1, Briere-2 and Lactin-2 models provide estimates of all thermal parameters, except for thermal constant (K), whereas the linear model estimates only T_0 and K . To estimate developmental thresholds and other empirical constants, we used iterative analysis at six temperatures (15–35°C) for eggs and five temperatures (15–32.5°C) for the remaining stages, because *H. phaeopteralis* failed to complete development at the highest temperature. The optimum temperature for the Briere-1 and Briere-2 models was calculated using the expression:

$$T_{opt} = \left[(2mT_L) + (m + 1)T_0 + \sqrt{4m^2T_L^2 + (m + 1)^2T_0^2 - 4m^2T_0T_L} \right] / (4m + 2),$$

where the constant m equals two (Briere-1) or is estimated by the iterative analysis (Briere-2) (Briere et al. 1999). For the second order polynomial model, T_0 and T_L were obtained by solving the roots of the equation, while the T_{opt} came from the first derivative of $dR(T)/dT = 0$. For nonlinear models, developmental rate curves were fitted based on the Levenberg-Marquardt algorithm using the PROC NLIN command (Statistical Analysis System [SAS] Institute 2008). For the prepupal stage in Briere-2, we used the Newton-Raphson algorithm because the parameters were not highly correlated (>0.8 or <-0.8). For Lactin-2, parameter estimates were derived by simulation method where developmental rate (1/d) was 0 for T_0 and T_L (identifying upper and lower thresholds intersecting the x-axis), whereas T_{opt} was obtained when developmental rate was maximized (Jandricic et al. 2010). Linear models were fitted using PROC REG (SAS Institute 2008).

Models were validated through R^2 (coefficient of determination), RSS (residual sum of squares), and AIC (Akaike information criterion) (Aghdam et al.

Table 3. Percentage stage survivorship and successful adult emergence (eclosion) of *H. phaeopteralis* reared on five artificial diets and ‘Palmetto’ St. Augustinegrass at 25°C

Diet	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Prepupa	Pupa	Total
St. Augustinegrass	97.9	100	100	97.91	100	95.7	97.7	93.1	83.6
Soy-wheat germ	100	100	90.0	94.4	100	82.3	92.8	30.7	10.0
Sugarcane borer	95.0	84.2	93.7	46.6	57.1	50.0	0	0	0
European corn borer	95.0	47.3	11.1	0	0	0	0	0	0
S. W. corn borer	90.0	94.4	94.1	87.5	71.4	50.0	20.0	0	0
Pinto bean	0	0	0	0	0	0	0	0	0

Sample size was 50 larvae per diet.

Table 4. Developmental time (days) of immature stages of *H. phaeopteralis* at six constant temperatures reared on ‘Palmetto’ St. Augustinegrass

Temp. (°C)	Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Prepupa	Pupa	Total
15	29.6a	—	—	—	—	—	—	—	—	—
20	6.5b	4.7a	4.3a	3.9a	4.0a	4.2a	4.4a	5.6a	11.4a	47.8a
25	4.1c	4.1b	3.8b	3.2b	3.8ab	3.9ab	3.6b	4.6b	10.9a	41.0b
30	3.2d	2.7c	2.0d	2.0d	1.5c	1.8d	2.4d	3.7c	5.3b	21.1d
32.5	3.4e	3.4b	2.6c	2.5cd	3.2b	3.0c	2.9c	4.3cb	6.3b	32.6c
35	3.4e	4.2b	2.6c	2.6c	3.7ab	3.4cb	—	—	—	—
F	60.9	46.5	111.0	48.0	63.3	72.3	101.0	34.9	122.7	121.6
df	5, 35	4, 155	4, 145	4, 142	4, 135	4, 125	3, 115	3, 113	3, 109	3, 107
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means within a column followed by the same letter are not significantly different ($P \geq 0.05$; Tukey’s HSD). Sample size was 50 larvae per temp.

2009, Sandhu et al. 2010). The RSS was derived from analysis of variance (ANOVA), where lower values indicate a better fit. Better models have lower AIC values, which was computed as $AIC = n \ln(SSE/n) + 2p$, where n is the number of observations, p is the number of parameters in the model, and SSE is the sum of the squared error (Sandhu et al. 2010).

Results

Diet Suitability. Larval diets significantly affected the duration of development for all immature stages (Table 2). *H. phaeopteralis* did not survive beyond the first instar on the pinto bean diet. Only larvae reared on St. Augustinegrass and soy-wheat germ diets successfully developed to pupae. However, the adults that emerged from soy-wheat germ diets had aberrant wing pattern (Fig. 1). Total development time and individual instars of *H. phaeopteralis* developed significantly faster on St. Augustinegrass (41.0 ± 0.9 d; instar range 3.2–10.9 d) compared with soy-wheat germ diet (69.5 ± 2.9 d; range 6.5–20.7 d). Development was also significantly slower on the sugarcane borer, S. W. Corn borer and European corn borer diets, and none of the individuals successfully pupated. Total survival to the adult stage was 83.6% on St. Augustinegrass and 10.0% on the soy-wheat germ diet (Table 3). The lowest survivorship on the soy-wheat germ diet was recorded at the pupal stage (30.7%) and only 50.0% of these moths successfully emerged from the pupal case. Larvae reared on the S. W. corn borer diet, sugarcane borer diet and European corn borer diet failed to survive after the prepupal, sixth and third instars, respectively.

Temperature Dependent Development. *H. phaeopteralis* successfully completed its life cycle between 20 and 32.5°C although developmental time varied significantly across rearing temperatures (Table 4). The number of days required for eggs to hatch ranged from 29.6 d at 15°C to 3.2 d at 30°C. For larvae, the first instar required the longest time to develop at all temperatures. The pupal stage required the longest development period, ranging from 5.3 d at 30°C to 11.4 d at 20°C. Longevity significantly decreased from 47.8 d at 20°C to 21.1 d at 30°C and then increased to 32.6 d at 32.5°C. Larvae failed to complete development at 15 and 35°C during the first and fifth instar, respectively (Table 5). The cumulative survivorship was highest at 30°C, followed by 25, 20, and 32.5°C.

Developmental Rate and Mathematical Models. The lower developmental thresholds (T_0) and degree-days values (K) were estimated by the common linear model over the linear response range (excluding 32.5°C) (Table 6). The estimated lower temperature thresholds varied from 6.9°C (first instar) to 15.3°C (fourth instar). The R^2 values for Briere-1, Briere-2, second order-polynomial, and Lactin-2 for total development were 0.9, 0.4, 0.9, and 0.9, respectively (Table 7). The polynomial second order model attained a good fit for the data considering the small value of AIC for eggs (-50.6), larval stage (-40.3), prepupae (-35.3), pupae (-33.6), and the total development (-44.5), but the upper developmental threshold for immature stages (42.1–65.9°C) were higher than observed in the laboratory (Table 7). The Briere-1 and Lactin-2 models provided a good fit for immature stages and total development. Overall we consider the

Table 5. Larval, prepupal, and pupal survival (%) of *H. phaeopteralis* reared at six different constant temperatures on ‘Palmetto’ St. Augustinegrass

Temperature (°C)	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Prepupa	Pupa	Total
15	2.5	0	0	0	0	0	0	0	0
20	92.1	94.2	100	100	96.9	96.8	96.7	100	78.9
25	97.9	100	100	97.9	100	95.7	97.7	93.1	83.6
30	97.5	94.8	100	100	97.2	100	97.2	100	87.5
32.5	82.5	90.9	80.0	87.5	95.1	90.0	88.8	93.7	37.5
35	92.5	83.3	83.3	76.0	36.8	0	0	0	0

Sample size was 50 larvae per temp.

Table 6. Estimates of linear regression parameters, min. temp threshold (T_0), and thermal constant (K) for *H. phaeopteralis* on ‘Palmetto’ St. Augustinegrass under laboratory conditions

Stage	T_0 (°C)	T_u (degree-days)	Linear equation	R^2	AIC
Egg	10.1	62.9	$Y = 0.016x - 0.06$	0.9	-20.8
First instar	6.9	66.2	$Y = 0.015x - 0.10$	0.9	-19.3
Second instar	12.3	38.2	$Y = 0.026x - 0.32$	0.8	-14.4
Third instar	10.5	40.3	$Y = 0.024x - 0.26$	0.9	-16.2
Fourth instar	15.3	24.9	$Y = 0.040x - 0.61$	0.8	-10.7
Fifth instar	13.9	32.3	$Y = 0.031x - 0.43$	0.8	-12.5
Sixth instar	9.1	51.9	$Y = 0.019x - 0.18$	0.9	-19.4
Seventh instar	13.1	106.4	$Y = 0.009x - 0.01$	0.9	-29.7
Pupa	12.0	109.9	$Y = 0.009x - 0.11$	0.8	-19.5
Eggs to adult	13.1	370.4	$Y = 0.003x - 0.04$	0.8	-28.3

Briere-1 model superior by providing a closer match to values observed in the laboratory. The predicted value of the developmental rate as a function of temperature is presented (Fig. 2).

Discussion

This is the first attempt to describe the development of *H. phaeopteralis* mathematically. Previously, Kerr (1955) described the development of *H. phaeopteralis* as having seven larval instars that need ~25 d at 25.5°C to reach pupation, while we observed six instars requiring 22 d at 25°C and a prepupal stage (5 d) before

pupation. The T_0 , T_{opt} , and T_L estimated by the Briere-1 model for all immature stages and total development better reflected the measured parameters than the Briere-2, Lactin-2, and polynomial models. The polynomial and Lactin-2 models overestimated and underestimated the lethal threshold (47.5 and 32°C), respectively. The estimated R^2 values by Briere-2 were low (0.4). Sandhu et al. (2010) reported that the Briere-1 model provided the best fit for the lesser cornstalk borer, *Elasmopalpus lignosellus* Zeller (Lepidoptera: Pyralidae), stating that T_0 , T_{opt} , and T_L for total development of immature stages were 9.3, 31.4, and 37.9°C, respectively. Although these thresh-

Table 7. Estimated coefficients, thermal constants, and goodness of fit for linear and nonlinear models of *H. phaeopteralis* reared on ‘Palmetto’ St. Augustinegrass

Model	Parameter	Eggs	Larvae	Prepupae	Pupae	Total development
Briere-1	a	0.0002	0.00008	0.0003	0.0001	0.00004
	T_0	11.6	14.6	13.5	13.9	14.9
	T_L	38.2	34.4	34.4	37.3	34.2
	T_{opt}	32.0	29.4	29.3	31.7	29.4
	R^2	0.9	0.9	0.9	0.9	0.9
	RSS	0.0009	0.0004	0.0003	0.0002	0.0002
	AIC	-46.44	-41.6	-30.7	-33.4	-46.1
Briere-2	a	0.000005	0.00014	0.0003	0.0003	0.00009
	m	0.6	9.2	1.1	37.2	52.0
	T_0	13.4	12.6	18.7	11.5	12.2
	T_L	50.1	32.5	32.5	32.5	32.5
	T_{opt}	31.8	31.3	26.7	32.2	32.3
	R^2	0.9	0.8	0.08	0.05	0.4
	AIC	-51.8	-41.2	-12.2	-32.1	-47.2
Polynomial second order	A	-0.0009	-0.0003	-0.001	-0.0003	-0.0001
	B	0.06	0.02	0.08	0.02	0.009
	T_0	14.1	14.9	14.9	14.7	15.0
	T_L	51.7	46.0	42.2	65.9	47.5
	T_{opt}	32.9	30.5	28.5	40.3	31.3
	R^2	0.9	0.9	0.7	0.9	0.9
	AIC	-50.6	-40.3	-35.3	-33.6	-44.5
Lactin-2	P	0.033	0.005	0.045	0.008	0.002
	Δ	14.7	0.1	11.3	0.2	0.2
	Lambda	-1.2	-1.1	-1.3	-1.2	-1.0
	T_0	13.5	14.8	14.3	14.5	14.9
	T_L	43.1	32.7	33.5	32.6	32.5
	T_{opt}	32.0	32.0	26.0	31.5	32.0
	R^2	0.9	0.9	0.9	0.9	0.9
	RSS	0.0003	0.0003	0.0034	0.0013	0.00007
	AIC	-51.50	-40.64	-28.49	-33.27	-48.03

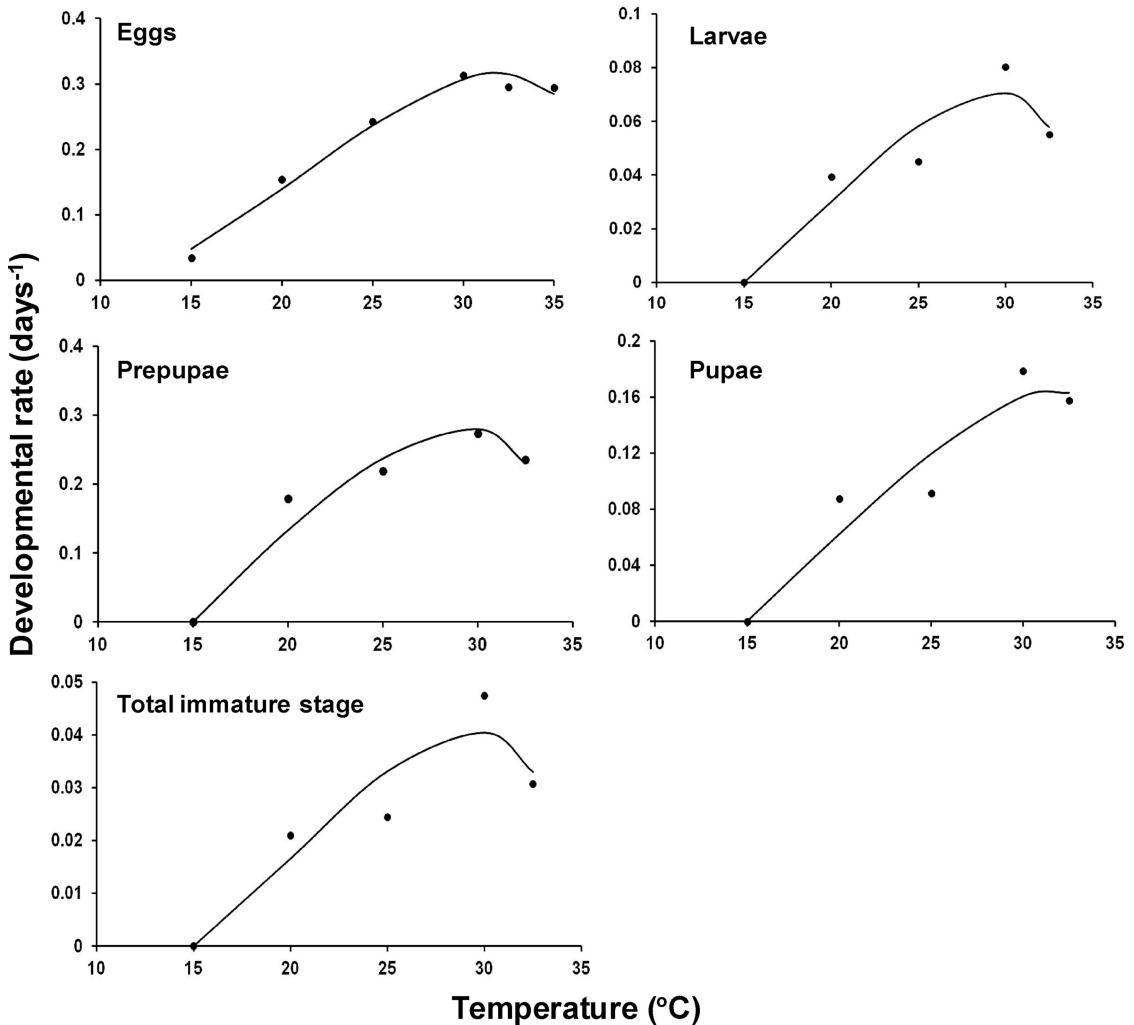


Fig. 2. Temperature-dependent developmental rates (days⁻¹) of immature stages described by the Briere-1 model for *H. phaeopteralis* on 'Palmetto' St. Augustinegrass. Circles indicate observed values, while curves represent the model.

olds are within the results of this study for T_0 (14.9), T_{opt} (29.4), and T_L (34.2) estimated by Briere-1, differences in the host plant and insects will result in different thermal adaptations (Bergant and Trdan 2006). Kerr et al. (1955) noted that adults became inactive at 14°C. Our study demonstrated that the lower thermal threshold for total development is 13.1°C using the linear model and between 12.2 and 15.0°C using the nonlinear models. Jensen and Cameron (2004) concluded that the lower developmental threshold for the grass webworm, *Herpetogramma licarsisalis* (Walker) falls somewhere between 10.8 and 15°C. The optimum temperature for *H. licarsisalis* was reported at or slightly above 31°C based on the limited observations of Tashiro (1976), which is close to the observed (30°C) and estimated optimum temperature for egg-to-adult development by our nonlinear models (29.4–32.3°C). Jensen and Cameron (2004) studied the developmental time of *H. licarsisalis* and found that larvae fed kikuyu grass, *Pennisetum clandestinum*

Hochst. ex Chiov, required 25.0 d at 25°C, 43.4 d at 20°C, 50.4 d at 18°C, and 81.4 d at 15°C to complete the development from egg to adult. These developmental times appear faster than *H. phaeopteralis* at 25 and 20°C on St. Augustinegrass (41.0 and 47.8 d, respectively). In our experiment survivorship declined with decreasing temperature, a trend also reported with *H. licarsisalis* (Jensen and Cameron 2004). It appears that *H. licarsisalis* that successfully developed at 15°C has a lower developmental threshold compared with *H. phaeopteralis* (our study), which may result in different ecological adaptations or host plant associations.

To facilitate our research, we evaluated several existing lepidopteran artificial diets for their usefulness in rearing *H. phaeopteralis*. None of the tested diets was suitable because of high mortality and slower developmental time. Failure to survive on these diets could be because of absence of important nutrients or feeding stimulants (secondary metabolic compounds). Insects often develop better on plant mate-

rials than on artificial diets (Doddall and Ulmer 2004, Shen et al. 2006). The diets based on corn starch were not suitable for rearing *H. phaeopteralis*; similar results were observed in studies with *Lymantria xyliana* (Shen et al. 2006). Our findings suggest that the soy-wheat germ diet, with the highest protein content, was the most suitable compared with other tested diets, in that some larvae successfully pupated and eclosed. Previous studies have also reported that protein source is critical component of insect diets (Schoonhoven et al. 1998, Cohen 2003). For example, *Spodoptera exigua* (Hübner) and *Helicoverpa zea* (Boddie) reared on synthetic diets comprising casein (animal protein) had superior growth compared with those fed soybean powder (vegetable protein) (Duffey et al. 1986). However, emerged adults from soy-wheat germ diet had morphological abnormalities on the wings or scales. Malnourishment leading to wing deformities can be caused by variety of diet-related deficiencies, including various lipids, amino acids, and vitamins as well as mineral deficiency (Cohen 2003). Little is known about identifying nutritional deficiencies in insects by observing a specific set of symptoms (Cohen 2003). Lack of some fatty acids such as linoleic and linolenic acids cause wing deformity in the cabbage looper *Trichoplusia ni* (Hübner) (Grau and Terriere 1971). The diet composition should be adjusted to improve survival and development of *H. phaeopteralis* in future studies.

Our findings provide important information on the developmental biology and thermal characteristics of *H. phaeopteralis*. This information, in conjunction with other ecological data such as fecundity, intrinsic rate of increase, and mortality, will be useful for predicting the potential distribution of this species and conducting pest management strategies such as timing pesticide applications, scheduling sampling intervals, and forecasting occurrence of different life stages in turfgrasses.

Acknowledgments

We are grateful to A. D. Ali (Davey Institute) for suggesting a collection site and Luis F. Aristizabal, James P. Kerrigan, and Robert Leckel for their technical assistance. Nancy Fieleke and Amy Rowley were helpful in pinto bean diet preparation and rearing of this insect. Partial funding was provided by the University of Florida College of Agriculture and Life Sciences.

References Cited

- Aghdam, H. R., Y. Fathipour, G. Radjabi, and M. Rezapannah. 2009. Temperature-dependent development and temperature thresholds of codling moth (Lepidoptera: Tortricidae) in Iran. *Environ. Entomol.* 38: 885–895.
- Bergant, K., and S. Trdan. 2006. How reliable are thermal constants for insect development when estimated from laboratory experiment? *Entomol. Exp. Appl.* 120: 251–256.
- Briere, J. F., and P. Pracros. 1998. Comparison of temperature-dependent growth models with the development of *Lobesia botrana* (Lepidoptera: Tortricidae). *Environ. Entomol.* 27: 94–101.
- Briere, J., P. Pracros, A. Y. le Roux, and J. S. Pierre. 1999. A novel rate model of temperature-dependent development for arthropods. *Environ. Entomol.* 28: 22–29.
- Buss, E. A., and R. Meagher. 2006. Lawn caterpillars. University of Florida, IFAS, EDIS document ENY-352.
- Cherry, R., and A. Wilson. 2005. Flight activity of tropical sod webworms (Lepidoptera: Pyralidae). *Fla. Entomol.* 88: 101–103.
- Cohen, A. C. 2003. Insect diets: science and technology. CRC LLC, Boca Raton, FL.
- Doddall, L. M., and B. J. Ulmer. 2004. Feeding, development, and oviposition of bertha armyworm (Lepidoptera: Noctuidae) on different host plant species. *Environ. Entomol.* 33: 756–764.
- Duffey, S. S., K. A. Bloem, and B. C. Campbell. 1986. Consequences of sequestration of plant natural products in plant-insect-parasitoid interactions, pp. 31–60. In D. J. Boethel and R. D. Eikenbary (eds.), *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. Ellis Horwood, Chichester, United Kingdom.
- Grau, P. A., and L. C., Terriere. 1971. Fatty acid profile of the cabbage looper *Trichoplusia ni* and the effect of diet and rearing conditions. *J. Insect Physiol.* 17: 1637–1649.
- Guy, R. N., N. C. Leppla, J. R. Rye, C. W. Green, S. L. Barette, and K. A. Hollien. 1985. *Trichoplusia ni*, pp. 487–494. In P. Sing and R. F. Moore (eds.), *Handbook of Insect Rearing*, vol. 2. Elsevier, Amsterdam, The Netherlands.
- Haydu, J. J., A. W. Hodges, and C. R. Hall. 2006. Economic impacts of the turfgrass and lawn care industry in the United States. Florida Cooperative Extension Service, IFAS, #FE632. (<http://edis.ifas.ufl.edu>).
- Huffaker, C., A. Berryman, and P. Turchin. 1999. Dynamics and regulation of insect populations, pp. 269–305. In C. B. Huffaker and A. P. Gutierrez (eds.), *Ecological Entomology*, 2nd ed. Wiley, New York.
- Jandricic, S. E., S. P. Wraight, K. C. Bennett, and J. P. Sanderson. 2010. Developmental times and life table statistics of *Aulacorthum solani* (Hemiptera: Aphididae) at six constant temperatures, with recommendations on the application of temperature-dependent development models. *Environ. Entomol.* 39: 1631–1642.
- Jensen, J. G., and C. A. Cameron. 2004. Development and Kikuyu consumption of preimaginal *Herpetogramma licarsialis* (Lepidoptera: Pyralidae) reared at temperatures between 15 and 25°C. *Environ. Entomol.* 33: 1178–1184.
- Kerr, S. 1955. Life history of the tropical sod webworm *Pachyzancla phaeopteralis* Guenée. *Fla. Entomol.* 38: 3–11.
- Korndorfer, A. P., R. Cherry, and R. Nagata. 2004. Effect of calcium silicate on feeding and development of tropical sod webworms (Lepidoptera: Pyralidae). *Fla. Entomol.* 87: 393–395.
- Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen. 1995. Improved rate of temperature-dependent development by arthropods. *Environ. Entomol.* 24: 68–75.
- Lamb, R. J., G. H. Gerber, and G. F. Atkinson. 1984. Comparison of developmental rate curves applied to egg hatching data of *Entomoscelis americana* Brown (Coleoptera: Chrysomelidae). *Environ. Entomol.* 13: 868–872.
- Reinert, J. A. 1983. Field experiments for insecticidal control of sod webworms (Lepidoptera: Pyralidae) in Florida turfgrass. *J. Econ. Entomol.* 76: 150–153.
- Reinert, J. A., and P. Busey. 1983. Resistance of bermudagrass selections to the tropical sod webworm (Lepidoptera: Pyralidae). *Environ. Entomol.* 12: 1844–1845.
- Reinert, J. A., and M. C. Engelke. 2001. Resistance in zoysiagrass, *Zoysia* spp., to the tropical sod webworm, *Her-*

- petogramma phaeopteralis* Guenee. Int. Turfgrass Soc. Res. J. 9: 798–801.
- Reinert, J. A., M. C. Engelke, A. D. Genovesi, A. Chandra, and J. E. McCoy. 2009. Resistance to tropical sod webworm (*Herpetogramma phaeopteralis*) (Lepidoptera: Crambidae) in St. Augustinegrass and zoysiagrass. Intl. Turfgrass Soc. Res. J. 11: 663–673.
- Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and development rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *TetranychusmcDanieli* (Acarina: Tetranychidae). Environ. Entomol. 31: 177–187.
- Sandhu, H. S., G. S. Nuessly, S. E. Webb, R. H. Cherry, and R. A. Gilbert. 2010. Temperature-dependent development of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane under laboratory. Environ. Entomol. 39: 1012–1020.
- Schoonhoven, L. M., T. Jermy, and J.J.A. van Loon. 1998. Insect-plant biology from physiology to evolution. Chapman & Hall, New York.
- Shen, T., C. Tseng, L. Guan, and S. Hwang. 2006. Performance of *Lymantria xyliana* (Lepidoptera: Lymantriidae) on artificial and host plant diets. J. Econ. Entomol. 99: 714–721.
- Sourakov, A. 2008. Trophic interactions involving *Herpetogramma phaeopteralis* (Lepidoptera: Pyralidae) and *Passiflora incarnata* (Passifloraceae). Fla. Entomol. 91: 136–138.
- (SAS) Statistical Analysis System. 2008. SAS/STAT, release 9.2 user's guide. SAS Institute, Cary, NC.
- Tashiro, H. 1976. Biology of the grass webworm, *Herpetogramma licarsisalis* (Lepidoptera: Pyraustidae) in Hawaii. Ann. Entomol. Soc. Am. 69: 797–803.
- Trenholm, L. E., and J. B. Unruh. 2004. Florida lawn handbook, 3rd ed. University of Florida Press, Gainesville, FL.

Received 8 March 2012; accepted 28 June 2012.
