

## ECOLOGY, BEHAVIOR AND BIONOMICS

### Development and Survival of the Diamondback Moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) as a Function of Temperature: Effect on the Number of Generations in Tropical and Subtropical Regions

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#### Keywords

Degree-day, development rate, lower development threshold, thermal requirement, upper development threshold

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#### Abstract

The diamondback moth, *Plutella xylostella* (L.), is the most important pest of brassicaceous crops worldwide. Since temperature is the major abiotic factor influencing insect development and thermal requirements may vary among insect populations, it is important to know the effect of temperature on development and survival of a subtropical strain of *P. xylostella*. Development and survival of the diamondback moth was evaluated under seven constant temperatures ranging from 10°C to 35°C. Development was completed between 10°C and 32.5°C, but at 35°C all individuals died in the larval stage. Data were fitted to one linear and five nonlinear models. Considering as criteria the goodness of fit and the ability to estimate parameters of biological significance, the models Briere-1 and Briere-2 were the most adequate to describe the relationship between temperature and development of *P. xylostella*. The linear model demonstrated that *P. xylostella* required 312.5 degree-days above a lower threshold of 6.3°C to complete development. The degree-day model showed that the number of diamondback moth generations in the tropical region of Brazil is nearly twice the number in the subtropical region of the country. This result explains, at least in part, the higher population levels of this species in the tropical region of Brazil, and also demonstrates that *P. xylostella* is tolerant to a wide range of temperatures (6.1-32.5°C). Therefore, temperature cannot be considered a limiting factor for the occurrence of diamondback moth throughout the year in most regions of Brazil.

#### Introduction

The diamondback moth, *Plutella xylostella* (L.), is the most destructive pest of brassicaceous plants worldwide (Talekar & Shelton 1993). High population levels can cause losses in yield up to 90% (Verkerk & Wright 1996) resulting in an estimated 1 billion US dollars to promote its annual management (Talekar & Shelton 1993). The high incidence of the diamondback moth is partially explained by the absence of effective natural enemies (Lim 1986), as well as by its high capacity to develop

resistance to insecticides (Talekar & Shelton 1993).

Studies on the factors that affect field density and population dynamics are fundamental for the development of management strategies to control *P. xylostella*. Temperature is recognized as the most important environmental factor influencing development and survival of insects (Hallman & Denlinger 1998). Although the relationship between temperature and development of *P. xylostella* has been studied in other countries (Sarnthoy *et al* 1989, Shirai 2000, Liu *et al* 2002, Mohandass & Zalucki 2004, Golizadeh *et al* 2007), the thermal requirements

may vary among different populations (Lee & Elliot 1998, Gomi *et al* 2003) mainly due to geographic differences in climate according to a gradient of latitude (Honék 1996, Addo-Bediako *et al* 2000, Chen & Kang 2004). Honék (1996) showed that in subtropical and temperate zones the lower development threshold decreases with increasing geographical latitude.

The incidence levels of *P. xylostella* on brassicaceous crops in the subtropical region of Brazil (unpublished data) are not as severe as those reported for tropical areas and other countries (Martínez-Castillo *et al* 2002, Guilloux *et al* 2003, Campos *et al* 2006). Thus, this study was conducted to evaluate the upper and lower temperature thresholds for development and survival of a subtropical population of *P. xylostella*, in order to investigate the differences in the population dynamics of the pest in comparison to its incidence levels in the tropical region of Brazil.

## Material and Methods

### Laboratory rearing of *P. xylostella*

A colony of *P. xylostella* was established with larvae and pupae collected in commercial crops of broccoli (*Brassica oleracea* cv. *italica*) and cauliflower (*B. oleracea* cv. *botrytis*). The collection area is located in Colombo, Paraná State, in the subtropical region of Southern Brazil (25°17' S; 49°13' W), a transitional zone between tropical and temperate climates, characterized by cold and dry winters and rainy and moderate temperatures in summer.

Larvae of *P. xylostella* were reared on broccolis leaves until pupation in 18 cm diameter Petri dishes containing 50 neonate larvae. Pupae were individually kept in 2 cm diameter by 4 cm high polyethylene tubes until adult emergence. Adults were kept in 10 cm diameter by 20 cm high polyethylene cages. A 5 x 5 cm leaf piece of broccoli placed between two superposed lids was used as a stimulant for oviposition. The lower lid had a 4 x 4 cm slit in the center to allow adults to reach the leaf inside the cage. The internal surface of the lower lid was lined with sulfite paper, where the eggs were laid around the exposed broccoli leaf. Every three days the paper containing the eggs was removed and the broccoli leaf on the lid was changed. Adults were fed with 10% honey diluted in water, provided in a cotton ball soaked in the solution. The colony was maintained in a climatic chamber at 20 ± 1°C, 70 ± 10% RH and 12:12 L:D photoperiod.

### Development and survival of *P. xylostella* in relation to temperature

Development time and survival of the diamondback moth

were evaluated at 10, 15, 20, 25, 30, 32.5 and 35 ± 1°C, 70 ± 10% RH and 12:12 L:D photoperiod. Sixty newly hatched larvae were transferred from the laboratory colony to each temperature and individually kept in 2 x 4 cm polyethylene vials lined with paper towel. Larvae were fed on broccoli leaves previously washed in a 1% sodium hypochlorite solution. Food was provided daily as well as the recording of mortality and development time. Eggs obtained from females reared at each temperature were used to evaluate the incubation period. Eggs laid at 32.5°C and 35°C did not hatch; thus in these treatments incubation period was assessed on eggs laid at 20°C and immediately transferred to either 32.5°C or 35°C. For each of these temperatures, 30 replicates each containing 40 eggs were tested.

### Relationship between temperature and development

Based on development time for each immature stage in all temperatures evaluated, the development rate (1/development time) was recorded for each individual. The relationship between temperature and development rate of *P. xylostella* was fitted by one linear and five nonlinear models (Table 1). To correctly estimate the linear regression coefficients, only the linear part of the relationship between temperature and development was computed; thus, the data recorded for 32.5°C and 35°C were not used. Using the parameters estimated by the linear regression, the lower temperature threshold ( $T_0$ ) and thermal constant ( $K$ ) were respectively calculated by means of the x-intercept method ( $T_0 = -a/b$ ), and by the reciprocal of the slopes ( $K = 1/b$ ). In the nonlinear models proposed by Brière *et al* (1999), the optimum temperature ( $T_{opt}$ ) was calculated using the  $T_0$  and upper

Table 1 Mathematical models used to describe the relationship between temperature and development rate of *Plutella xylostella*.

Model	Equation	Reference
Linear regression	$D(T) = a + bT$	Roy <i>et al</i> (2002)
Brière-1	$D(T) = aT(T - T_0)(T_{max} - T)^{1/2}$	Brière <i>et al</i> (1999)
Brière-2	$D(T) = aT(T - T_0)(T_{max} - T)^{1/m}$	Brière <i>et al</i> (1999)
Taylor	$D(T) = R_m^{-0.5[(T - T_{opt})/T_0]^2}$	Taylor (1981)
Lactin-1	$D(T) = e^{(\rho T)} - e^{(\rho T_{max} - (T_{max} - T)/\Delta)}$	Lactin <i>et al</i> (1995)
Polynomial	$D(T) = a(T)^4 + b(T)^3 + c(T)^2 + d(T) + e$	Lamb <i>et al</i> (1984)

In linear regression, parameters  $a$  and  $b$  are equation constants and  $T$  is the temperature.

In Brière-1 and Brière-2 models,  $a$  and  $m$  are equation constants,  $T_0$  and  $T_{max}$  are respectively the lower and upper temperature threshold.

In the Taylor model,  $R_m$  is the maximum development rate.

In Lactin-1 model,  $\rho$  and  $\Delta$  are equation constants.

In Polynomial model,  $a$ ,  $b$ ,  $c$ ,  $d$  and  $e$  are equation constants.

temperature threshold ( $T_{max}$ ) estimated by the model, according to the equation:

$$T_{opt} = \frac{[2mT_{max} + (m + 1)T_0] + \sqrt{4m^2T_{max}^2 + (m + 1)^2T_0^2 - 4m^2T_0T_{max}}}{4m + 2}$$

The evaluation of each mathematical model was based on its ability to describe the data accurately. The commonly used statistics for this purpose are the coefficient of determination ( $r^2$ ) and residual sums of square (RSS) (Roy *et al* 2002), that indicates better fits with higher and lower values, respectively (Aghdam *et al* 2009). The Akaike information criterion (AIC) was also used as an additional parameter to evaluate the goodness-of-fit of the mathematical models tested. The AIC was calculated using the equation:

$$AIC = n \ln(SSE/x) + 2p$$

where  $n$  is the number of treatments, SSE is the sum of the squared error, and  $p$  is the number of parameters in the model. Smaller AIC values were considered as an indicative of better fit (Sandhu *et al* 2010). All parameters employed in the regression models were estimated with the software Table Curve 2D (Systat Inc 2002).

#### Number of generations

The number of diamondback moth generations was used as a parameter to assess the role of temperature on population dynamics of the pest. The number of generations was calculated using the cumulative degree-days, according to the single sine method. This method uses daily minimum and maximum temperatures to produce a sine curve over a 24h period, and then estimates degree-days for that day by calculating the area above the threshold and below the curve (Herms 2004). The minimum and maximum daily temperature of different regions of Brazil were obtained from "Instituto Nacional de Meteorologia (INMET)", considering only the months between June and November, which is the period of diamondback moth occurrence in Brazil (Guilloux *et al* 2003, Campos *et al* 2006).

#### Statistical analysis

The effect of temperature on development time of the immature stages was evaluated by analysis of variance (ANOVA). When differences were detected, Tukey's HSD test ( $P < 0.05$ ) was applied to classify the means. Differences in survival rates were compared by Chi-square test ( $P < 0.05$ ). Additionally survival curves were constructed for each temperature and compared using the survival function of Kaplan-Meier estimation (Kaplan & Meier 1958). All analyses were performed using the software Statistica 6.0 (Statsoft Inc 2001).

## Results

### Development time

*Plutella xylostella* completed development from egg to adult in all temperatures evaluated, except at 35°C, which was lethal to the larvae (Table 1). The duration of the immature stages and the time required to complete the cycle from egg to adult were significantly affected by temperature (Table 2). In general, the development time of the immature stages decreased linearly with the increase of temperature between 10°C and 30°C. Above 30°C, the development rate was clearly reduced, indicating that the optimum temperature is close to this value.

### Survival

The lowest and highest temperatures evaluated had a deleterious effect on the survival of *P. xylostella*. Larval survival at 10°C (80.0%), 30°C (76.7%) and 32.5°C (81.7%) was significantly lower ( $\chi^2 = 6.12$ ,  $P < 0.05$ ) than at 15°C (95.0%), 20°C (96.7%) and 25°C (95.0%). Similarly, when *P. xylostella* was maintained at 10, 30 and 32.5°C, the percentage of survival from egg to adult was lower (80.0, 76.7 and 71.7%, respectively) than at 15°C (93.3%), 20°C (96.7%) and 25°C (95.0%) ( $\chi^2 = 9.02$ ,  $P < 0.01$ ). In contrast, no significant differences in mortality were recorded during pupal stage. The survival curves obtained by Kaplan-Meier's estimation showed significant differences according to the temperature ( $\chi^2 = 232.26$   $P < 0.001$ ), and an increase in temperature resulted in a decrease in survival time (Fig 1).

### Model evaluation

When data from 32.5°C and 35°C were excluded from the analysis, the linear regression suitably described the

Table 2 Development time in days (mean  $\pm$  SE) of the immature stages of *Plutella xylostella* in seven constant temperatures.

Temp. (°C)	Egg	Larva	Pupa	Cycle
10	16.0 $\pm$ 0.22a	34.3 $\pm$ 0.71a	22.3 $\pm$ 0.60a	72.6 $\pm$ 0.81a
15	8.3 $\pm$ 0.09b	20.0 $\pm$ 0.26b	11.1 $\pm$ 0.22b	39.3 $\pm$ 0.31b
20	4.5 $\pm$ 0.10c	13.2 $\pm$ 0.12c	6.6 $\pm$ 0.13c	24.3 $\pm$ 0.18c
25	3.0 $\pm$ 0.05d	8.6 $\pm$ 0.13d	4.1 $\pm$ 0.08d	15.7 $\pm$ 0.13d
30	2.3 $\pm$ 0.06e	7.3 $\pm$ 0.13e	3.6 $\pm$ 0.08d	13.2 $\pm$ 0.12e
32.5	3.0 $\pm$ 0.02d	7.0 $\pm$ 0.09e	3.6 $\pm$ 0.07d	13.4 $\pm$ 0.13e
35	3.0 $\pm$ 0.03d	-	-	-
F value	2893.92	1124.53	667.84	3825.41
P	< 0.001	< 0.001	< 0.001	< 0.001

Means followed by different letters are significantly different according to ANOVA, Tukey's HSD test ( $P < 0.05$ ).

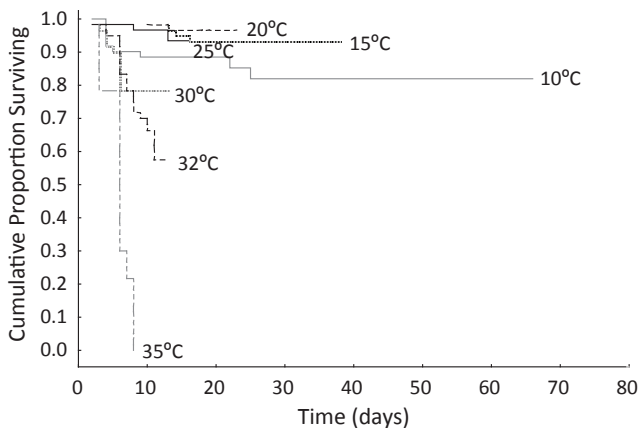


Fig 1 Survival curves of the immature stages of *Plutella xylostella* at seven constant temperatures.

relationship between temperature and development rate of *P. xylostella*, as corroborated by the high  $r^2$  and low RSS and AIC (Table 3). According to the linear regression, the diamondback moth required 312.5 degree-days above the lower threshold of 6.3°C to complete development from egg to adult stage (Table 3).

The mathematical models evaluated provided a good

Table 3 Estimated parameters ( $a$  and  $b$ ) for linear regression, lower threshold temperature ( $T_0$ ) and thermal constant ( $K$ ) in degree-days for the immature stages of *Plutella xylostella*.

Stage	$a$	$b$	$K$	$T_0$ (°C)	$r^2$	RSS ( $\times 10^{-3}$ )	AIC
Egg	-0.1483	0.0191	50.99	7.74	0.98	91.66	-38.34
Larva	-0.0272	0.0054	185.18	5.03	0.99	7.95	-49.89
Pupa	-0.0855	0.0124	80.64	6.89	0.98	38.4	-40.24
Cycle	-0.0203	0.0032	312.50	6.34	0.99	2.63	-55.96

RSS is the residual sums of square, AIC is the Akaike information criterion.

fit to describe the relationship between temperature and development rate of the different life stages of *P. xylostella* (Fig 2, Table 4). The models Brière-1, Brière-2, Lactin-1 and Polynomial showed  $r^2$  higher than 0.93, and low RSS and AIC values (Table 4). In contrast, Taylor's model did not adequately fit the data, especially for larval stage and total development, as indicated by the low  $r^2$  values.

*Number of generations at different localities of Brazil*

In general, the number of diamondback moth generations

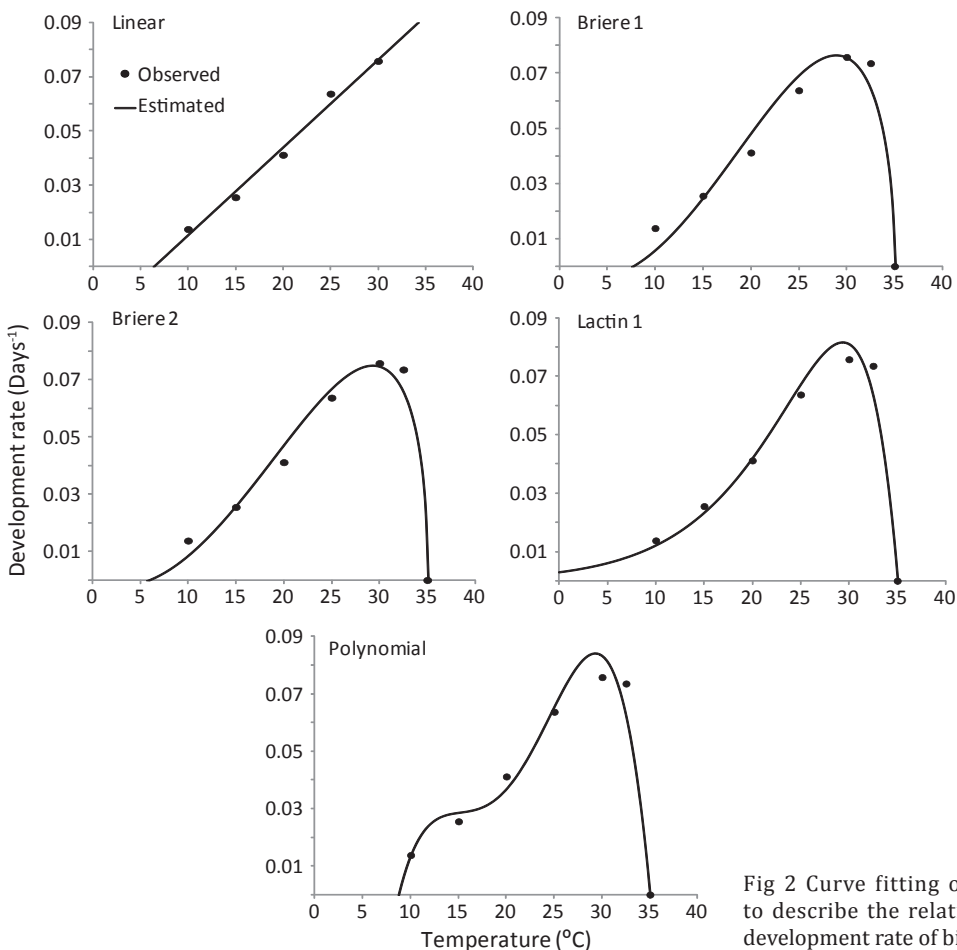


Fig 2 Curve fitting of five mathematical models used to describe the relationship between temperature and development rate of biological cycle of *Plutella xylostella*.

Table 4 Fitted coefficients and evaluation indices of five nonlinear models used to describe the relationship between temperature and developmental rate of *Plutella xylostella* immature stages.

Model	Parameter	Egg	Larva	Pupa	Cycle
Brière-1	$a$ ( $\times 10^{-4}$ )	1.89	0.91	1.23	0.51
	$T_0$	5.27	7.18	4.56	7.88
	$T_{max}$	37.67	35.00	38.78	35.00
	$T_{opt}$	30.67	28.84	31.29	28.81
	$r^2$	0.95	0.94	0.99	0.96
	RSS ( $\times 10^{-3}$ )	101.52	17.18	49.96	5.26
	AIC	-36.53	-54.52	-51.97	-65.77
Brière 2	$a$ ( $\times 10^{-5}$ )	17.57	9.03	22.73	5.17
	$T_0$	5.59	4.52	2.58	6.06
	$T_{max}$	37.96	35.00	34.84	35.00
	$T_{opt}$	30.94	28.49	28.14	28.68
	$m$	1.88	2.35	3.81	2.92
	$r^2$	0.95	0.96	0.99	0.97
	AIC	-34.55	-55.80	-51.63	-67.52
Taylor	$R_m$ ( $\times 10^{-1}$ )	0.39	1.41	2.81	0.78
	$T_{opt}$	29.52	26.68	31.28	26.76
	$T_0$	9.38	6.45	1.73	6.14
	$r^2$	0.96	0.57	0.99	0.62
	AIC	-37.72	-41.51	-56.17	-50.81
Lactin	$\rho$	0.14	0.17	0.16	0.17
	$T_{max}$	38.02	35.15	36.49	35.10
	$\Delta$	6.95	5.88	6.22	5.70
	$r^2$	0.94	0.94	0.99	0.97
	AIC	-43.09	-45.92	-50.82	-68.36
Polynomial	$a$ ( $\times 10^{-6}$ )	-0.16	-7.66	-1.33	-3.93
	$b$ ( $\times 10^{-4}$ )	-0.74	6.16	0.65	3.13
	$c$ ( $\times 10^{-3}$ )	4.73	-17.54	-0.52	8.83
	$d$ ( $\times 10^{-1}$ )	-0.72	2.14	0.01	1.07
	$e$	0.39	-0.90	0.03	-0.45
	$r^2$	0.96	0.94	0.99	0.96
	AIC	-34.07	-51.58	-54.34	-62.39

In linear regression, parameters  $a$  and  $b$  are equation constants and  $T$  is the temperature.

In Brière1 and Brière-2 models,  $a$  and  $m$  are equation constants,  $T_0$  and  $T_{max}$  are respectively the lower and upper temperature threshold.

In the Taylor model,  $R_m$  is the maximum development rate.

In Lactin-1 model,  $\rho$  and  $\Delta$  are equation constants.

Model,  $a$ ,  $b$ ,  $c$ ,  $d$  and  $e$  are equation constants.

increased with decreasing latitude (Table 5). The highest number of generations was estimated for the state of Pernambuco, Northeastern Brazil (11.0), which was nearly twice the number of generations (5.8) estimated for Colombo, state of Paraná in Southern Brazil.

## Discussion

Temperature is the most important abiotic factor affecting insect growth, development rate and survival (Hallman & Denlinger 1998). The diamondback moth develops between 10°C and 32.5°C, but did not survive at the constant temperature of 35°C. Other studies performed with this species reported similar results (Liu *et al* 2002, Golizadeh *et al* 2007), although individuals of some tropical populations were able to complete development at 35°C, with a high mortality rate (Shirai 2000). Survival of *P. xylostella* was also affected by the extreme temperatures evaluated in the study. Diamondback moth mortality followed the pattern described by Liu *et al* (1995), represented by a “U” shaped curve, with highest mortality at 10°C followed by a reduction in mortality as the temperature increased between 15°C and 25°C, and by another increase between 30°C and 35°C.

The influence of temperature on development and survival of the diamondback moth may affect the population dynamics of the pest. Such influence can be quantified by calculating the number of generations for localities with different climatic conditions, based on parameters estimated by the linear model. In this study we demonstrated that a higher number of diamondback moth generations are expected for warmer regions of Brazil. This result confirms the field information, which demonstrate that the abundance of diamondback moth attacking brassicaceous crops in the tropical region of Brazil (Guilloux *et al* 2003) and other countries (Martínez-Castillo *et al* 2002, Ahmad *et al* 2009) is higher if compared with those recorded in the subtropical region (Marchioro 2011). These differences in the number of generations may be even greater if there are strains adapted to local climatic conditions in tropics of Brazil.

Predicting the development time of an insect pest in relation to temperature can be an important tool for pest management (Roy *et al* 2002). In this context, the selection of mathematical models that suitably describe this relationship is essential. The relationship between temperature and development in insects tends to be nonlinear over the full range of tolerable temperature (Logan *et al* 1976, Lactin *et al* 1995). In the present study, the linear regression provided a good fit to describe the data, but only when the linear part of the relationship between temperature and development was considered (10-30°C). The development time of *P. xylostella* from

Table 5 Estimated number of generations of *Plutella xylostella* in different regions of Brazil between June-November.

City - State	Latitude	Minimum temperature (°C)	Maximum temperature (°C)	Cumulative degree-days (CDD)	N.º of generations
Porto Alegre/RS	30° 01' 59" S	13.9 ± 0.57	21.9 ± 0.35	2079.1	6.7
Colombo/PR	25° 17' 30" S	11.3 ± 0.25	20.9 ± 0.33	1801.8	5.8
Maringá/PR	23° 25' 31" S	16.1 ± 0.28	27.2 ± 0.31	2811.5	9.0
Sorocaba/SP	23° 30' 06" S	14.6 ± 0.22	26.7 ± 0.29	2618.2	8.4
Viçosa/MG	20° 45' 14" S	13.9 ± 0.27	25.8 ± 0.24	2475.2	7.9
Brasília/DF	15° 46' 47" S	16.3 ± 0.18	27.6 ± 0.22	2866.0	9.2
Ituaçu/BA	13° 48' 48" S	17.4 ± 0.20	29.8 ± 0.26	3166.6	10.1
Recife/PE	08° 03' 14" S	21.7 ± 0.11	28.5 ± 0.10	3441.4	11.0

egg to adult was longer in temperatures above 30°C, demonstrating that the optimum temperature was exceeded. If the linear regression was used over the full range of tolerable temperature by *P. xylostella*, the results would have been inaccurate, and in this case nonlinear models would be more adequate.

The performance of nonlinear models varies according to the species under study, and in some cases the results can be quite different. The model proposed by Logan *et al* (1976) was suitable for some species (Coop *et al* 1993, Roy *et al* 2002, Fantinou *et al* 2003, Bonato *et al* 2007), whereas for other species better results were obtained using the model of Lactin *et al* (1995) (Kontodimas *et al* 2004, Castillo *et al* 2006) and Briere *et al* (1999) (Roy *et al* 2002, Aghdam *et al* 2009). In our study, the nonlinear models Brière-1, Brière-2, Lactin-1 and Polynomial best described the relationship between temperature and *P. xylostella* development, and can be used to predict development time.

Along with the statistics, another parameter that can be used to select a model is its capacity to estimate parameters of biological significance, such as  $T_0$ ,  $T_{opt}$  and  $T_{max}$  (Roy *et al* 2002). Despite the high number of parameters, the polynomial model did not estimate parameters of biological interest. The Lactin-1 model estimates  $T_{max}$ , but because it predicts positive development rates even at 0°C, this model could not accurately estimate the  $T_0$ . In contrast, Brière 1 and 2 models estimate  $T_0$  and  $T_{max}$ , and based on these parameters allows the calculation of  $T_{opt}$ . Therefore, considering both the statistical criteria and the ability to estimate parameters of biological significance, the models proposed by Briere *et al* (1999) can be considered the most appropriate for *P. xylostella* development time prediction.

The estimated  $T_0$  through the nonlinear models showed subtle differences in comparison to the values obtained by linear regression. Studies performed with other species have shown similar results when comparing the  $T_0$  estimated by linear and nonlinear models (Herrera *et al* 2005, Golizadeh *et al* 2007, Jalali *et al* 2009). This

difference is due to the fact that the linear regression uses only the linear part of the points to calculate the lower temperature threshold, whereas nonlinear models also uses the observed points above the  $T_{opt}$ .

Studies conducted with populations from different geographical areas have shown slight variation in development time, lower threshold and thermal constant of *P. xylostella*. These differences can be attributed to multiple factors such as experimental conditions, host-plant quality and thermal adaptations to different geographical areas. Larval food can affect development time and survival of the diamondback moth (Hamilton *et al* 2005, Ayalew *et al* 2006, Thuler *et al* 2007), and can explain at least in part the differences reported in the literature. Another explanation is the existence of differences among populations from distinct geographical localities due to acclimatization. According to Honék (1996), the lower thermal limits reduces as latitude increases.

Although some studies have demonstrated variations in thermal response of insects along a gradient of latitude (Addo-Bediako *et al* 2000, Kimura 2004), the available information for *P. xylostella* is conflicting. For example, in a study with three populations of this species from geographically isolated localities of Japan, differences in the development rate among the populations were reported (Umeya & Yamada 1973). On the other hand, in a study comparing Japanese and Thai populations of the diamondback moth no difference in development time was recorded (Sarnthoy *et al* 1989). This view was confirmed in a study with nine populations of *P. xylostella* from tropical and subtropical regions of Asia (Shirai 2000). In this study, the author emphasized that it is unlikely that clear geographical differences in thermal response would be generated in a highly mobile species like *P. xylostella*. However, as pointed out by Mohandass & Zalucki (2004), the populations evaluated by Shirai (2000) were kept under laboratory conditions for a long time and the possibility of acclimatization of the strains to local conditions was not evaluated.

The minimum temperature tested in the work of Sarnthoy *et al* (1989) was 17°C, and 15°C in Shirai (2000), which were higher than the lowest one tested in the present study (10°C). According to Mohandass & Zalucki (2004), the inclusion of lower temperature regimes in such experiments would give an indication of the differences in development rate among strains from temperate zones against those from tropical and subtropical zones. In fact, the development time registered (72.6 days) at a temperature closer to the lower thermal limit evaluated in our study (10°C) was lower than the 88.8 days (Liu *et al* 2002), 85.1 and 81.2 days (Golizadeh *et al* 2007) reported in other studies at 10°C.

Another way to evaluate differences among populations in thermal response is through comparison of parameters such as lower temperature threshold and thermal constant. According to Trudgill (1995), species with low  $T_o$  develop faster at low temperatures, while warm adapted species develop faster at high temperatures. Therefore higher  $T_o$  and lower  $K$  are expected for populations of tropical regions, whereas in subtropical and temperate regions a lower  $T_o$  and higher  $K$  is expected (Trudgill & Perry 1994). The comparison of  $T_o$  and  $K$  estimated for diamondback moth populations from subtropics and temperate regions with those estimated for tropical populations clearly show this pattern. The parameters estimated for a tropical population from Indonesia (Latitude 3° S) were 8.1°C and 232.5 DD, respectively (Shirai 2000). In contrast,  $T_o$  and  $K$  estimated for populations of China (Liu *et al* 2002, latitude 30° N), Iran (Golizadeh *et al* 2007, latitude 35° N), Japan (Shirai 2000, latitude 43° N) and Brazil (present study, latitude 25° S), were respectively: 7.4°C and 268.2 DD, 7.0°C and 263.7 DD, 6.7°C and 285.7 DD and 6.3°C and 312.5 DD.

Considering the lower and upper temperature thresholds estimated by the nonlinear models and the capacity of *P. xylostella* to survive at temperatures below 0°C for up to two months (Gu 2009), it is unlikely that temperature limits the occurrence of the diamondback moth throughout the year in most regions of Brazil. Nevertheless, studies carried out in different regions of Brazil have shown that *P. xylostella* occurs in high levels only between June and November (Guilloux *et al* 2003, Campos *et al* 2006, Marchioro 2011), period in which temperatures are lower. The results indicate that local factors other than temperature must be considered, such as rainfall intensity and levels of parasitism. To avoid these unfavorable conditions, the moths might be adapted to abandon the habitat as soon as they emerge from the pupae (Campos *et al* 2006).

The results obtained in this study show that temperature play an important role on development and survival of the diamondback moth, and that mathematical models can be used to describe the relationship between temperature and development rate. Differences in

temperature between tropical and subtropical regions affect the number of generations of the diamondback moth, and may be responsible for the differences in population levels recorded between these regions.

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