Modelling reproduction of *Plutella xylostella* L. (Lepidoptera: Plutellidae): climate change may modify pest incidence levels

C.A. Marchioro and L.A. Foerster*

Department of Zoology, Universidade Federal do Paraná PO Box 19.020, 81531-990 Curitiba, PR, Brazil

Abstract

Temperature is considered to be an important abiotic factor influencing insect reproduction. Despite the importance of *Plutella xylostella* L. (Lepidoptera: Plutellidae) as a pest of brassicaceous crops worldwide, the effects of temperature on its reproduction are not well understood. We evaluated the effect of constant temperatures ranging from 10 to 32.5°C on the reproduction of *P. xylostella* and developed an oviposition model for the species. The model combined temperature-dependent parameters of total fecundity, age-specific oviposition rate and age-specific survival. Additionally, we modelled population growth as a function of temperature. The estimated parameters allowed us to discuss the possible consequences of global warming on *P. xylostella* distribution. Temperature affected the length of pre-oviposition after adult emergence, oviposition period, longevity, total fecundity and egg viability. The model predicted that both daily egg production and length of oviposition period decreased at temperatures below 15°C and above 25°C. Population growth increased linearly with temperature in a range from 10°C to 25°C; however, the model predicted a reduction in population growth at temperatures above 28.6°C. Data suggested that temperature plays a critical role in *P. xylostella* reproduction, and subtle differences in average temperature could have an impact on its population growth. This is especially important in the context of global climate change, which in turn could alter the distribution and abundance of the pest in some regions of the world.

Keywords: Diamondback moth, oviposition model, population growth, global warming, temperature

Introduction

The reproduction and abundance of insects are affected by the interaction between intrinsic life history traits and extrinsic factors, such as food quality, temperature, photoperiod and moisture (Awmack & Leather, 2002; Malaquias *et al.*, 2010).

Among the abiotic factors, temperature may be the most important (Hentz *et al.*, 1998; Sagarra *et al.*, 2000) because it directly affects reproductive parameters, such as the duration of oviposition period, total fecundity and egg viability (Kim & Lee, 2003; Son & Lewis, 2005; Ali & Rizvi, 2008).

The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is the most important pest of brassicaceous crops worldwide (Talekar & Shelton, 1993). It has a cosmopolitan distribution, occurring in regions with distinct climates ranging from the cold Himalayan Mountains (Mohan *et al.*, 2009) to the dry heat of Ethiopia (Ayalew & Ogol, 2006).

---

*Author for correspondence
Fax: 55 041 32662042
E-mail: foerster@ufpr.br

Several studies investigated the influence of temperature on the development of *P. xylostella* (Shirai, 2000; Liu *et al*., 2002; Golizadeh *et al*., 2007); however, the impact of temperature on reproduction has received little attention. Apart from the study of Golizadeh *et al*. (2009), which investigated the effect of temperature on life table parameters of *P. xylostella*, no studies have provided quantitative information on age-specific survivorship and fecundity at different temperatures (Sarnthoy *et al*., 1989; Wakisaka *et al*., 1992; Shirai, 2000), which are important factors influencing population growth (Birth, 1948).

Understanding the effect of temperature on an insect's reproductive parameters is critical for predicting the timing of oviposition and other events related to insect population growth and pest status (Son & Lewis, 2005). Such knowledge can also be useful in predicting the impact of global climate change on the abundance of various pest insects by estimating the lower and upper temperature thresholds for insect population growth. In this context, mathematical models are important analytical tools to predict and understand the population dynamics of a species (Sporleder *et al*., 2004). Oviposition models can be developed based on temperature-dependent components, such as total fecundity, age-specific oviposition rate and age-specific survival. Such an approach, using simple mathematical models to describe these reproductive parameters as a function of temperature, was undertaken in the example of black vine weevil, *Otiorhynchus sulcatus* (Son & Lewis, 2005). In this study, the influence of temperature on reproduction and population growth of *P. xylostella* was evaluated in the laboratory; and, based on these data, an oviposition model was developed that may be used to predict both the timing and intensity of egg laying in the field.

Materials and methods

Laboratory rearing of *P. xylostella*

A colony of *P. xylostella* was established in the laboratory with *ca*. 200 larvae and pupae collected in commercial crops of broccoli (*Brassica oleracea* cv. *italica*) and cauliflower (*B. oleracea* cv. *botrytis*). Every week, 50 field-collected larvae were added to the laboratory colony to maintain the genetic diversity of the stock. The collection was made in the county of Colombo, in the state of Paraná, southern Brazil (25°17′S; 49°13′W). This is a transitional zone between the tropical and temperate climates characterised by cold and dry winters, and moderately warm and wet summers.

Larvae were reared on broccoli leaves until pupation in Petri dishes (18 cm diameter, 2 cm height). Newly hatched larvae were reared in groups of approximately 60 individuals; and, as they grew bigger, the number of individuals per dish was reduced. Pupae were kept in groups of five in polyethylene tubes (2 cm in diameter, 4 cm high) until adult emergence. Adults were reared in cylindrical polyethylene cages (10 cm in diameter, 20 cm high) and fed with 10% honey solution in a cotton ball. Females of *P. xylostella* laid eggs only in the presence of a host plant, and therefore a piece of broccoli leaf was used as a stimulant. This broccoli leaf (5 × 5 cm) was placed between two superposed lids, and the lower lid had an opening (4 × 4 cm) in the centre to allow adults to contact with the leaf inside the cage. The internal surface of the lower lid was lined with sulfite paper, and eggs were laid around the exposed broccoli leaf. Every three days the paper containing

eggs was removed and the broccoli leaf was changed. The colony was maintained in a climatic chamber (FANEM® Ltd, model 347 CDG) at 20 ± 1°C and a photoperiod of 12:12 h (light:dark).

Experimental procedure

The reproduction of *P. xylostella* was evaluated in environmental chambers regulated at constant temperatures of 10, 15, 20, 25, 30 and 32.5 ± 0.5°C, and a photoperiod of 12:12 h (light:dark). Insects were reared from the first instar through adult emergence at each temperature. Twenty males and 20 females were paired, and each pair was kept in a cylindrical polyethylene cage (10 cm diameter, 10 cm high) lined with absorbent paper towel. Pieces of broccoli leaf were used to induce ovipositing behaviour, as described above. Adults were fed with 10% honey solution in a cotton ball placed on a round plastic lid (2 cm in diameter) at the base of the cage. Food was changed, and the number of eggs laid and adult longevity were recorded daily for each insect pair. Egg viability was assessed using eggs laid by females reared throughout the adult stage at each temperature. However, because none of the eggs deposited by females reared at 32.5°C gave rise to hatchlings, we tested whether the time of exposure to this temperature influenced hatchability. For this purpose, viability was assessed on eggs that were laid at 20°C and immediately transferred to 32.5°C. In this test, 30 replicates of 40 eggs were used. The following parameters of adult life history were measured: pre-oviposition and oviposition periods, longevity, survival, fecundity and egg viability.

Reproduction model

Pre-oviposition and oviposition period and longevity model

These parameters were modelled as a function of temperature using the three-parameter polynomial equation:

$$Y(T) = a + b(T) + c(T)^2$$

where Y is the mean pre-oviposition period, oviposition period or longevity at temperature, T (°C); and a, b and c are parameters to be estimated.

Normalized age

Cumulative probability distributions of oviposition and survival rate are displaced in time because of the strong influence of temperature on adult longevity. The timing of each measured distribution can be normalized, allowing the use of a single temperature-independent curve to describe the distributions at all temperatures (Wagner *et al*., 1984). The cumulative oviposition and survival rates distributions were normalized by dividing the adult age by the mean longevity. This procedure was repeated for each temperature, and the values were plotted within the same graph (Skinner *et al*., 2004).

Total fecundity and age-specific oviposition rate model

The relationship between total fecundity and temperature was described by the Gaussian equation (Taylor, 1981):

$$f(T) = F_{max} \exp\left[-1/2((T - T_{max})/k)^2\right],$$

Table 1. Mean length of pre-oviposition and oviposition periods, longevity, fecundity and fertility of *Plutella xylostella* at six constant temperatures.

Temp. (°C)	Pre-oviposition period (±SEM)	Oviposition period (±SEM)	Longevity (±SEM)		Fecundity (eggs/female) (±SEM)	Egg viability (%) (±SEM)
			Male	Female		
10	5.1±0.99a	30.4±2.07a	75.5±4.90Aa	50.1±3.11Ba	196.5±20.11b	72.1±5.24a
15	3.6±0.66ab	19.4±1.69b	68.9±9.08Aa	42.6±5.56Ba	287.8±26.18a	71.7±6.11a
20	2.1±0.38bc	17.1±1.25b	62.6±5.14Aa	27.4±1.87Bb	333.3±31.32a	64.3±5.30a
25	1.1±0.17c	12.9±1.04bc	40.9±3.36Ab	18.1±1.79Bc	266.1±14.19ab	73.4±6.44a
30	1.7±0.38c	7.2±0.89cd	22.4±3.30Ac	11.4±0.96Bc	186.6±15.82b	59.3±7.39a
32.5	2.5±0.36abc	10.0±1.61d	20.3±2.35Ac	12.2±1.90Bc	79.6±16.61c	00.0±00.00b

Means followed by the same lower case letter in rows and upper case letters in columns are not significantly different from each other according to ANOVA, Tukey's HSD test (*P* > 0.05).

where $F(T)$ is the total number of eggs laid per female during its lifetime in a given temperature, T; F_{max} is the maximum reproductive capacity; T_{max} is the temperature at which maximum reproduction is achieved; and k is a parameter to be estimated.

Age-specific cumulative oviposition rate is the proportion of the total lifetime reproductive potential during a period of time (Kim & Lee, 2003). The four-parameter Weibull cumulative function was used to describe the cumulative oviposition rate against the normalized age:

$$p(Px) = a[1 - \exp(-(x + c(\ln 2)^{1/d} - b)/c)^d]$$

where $P(x)$ is the cumulative oviposition rate at the normalized age x, b is the normalized age at 50% cumulative oviposition, a, c and d are fitted parameters.

Age-specific survival rate

The age-specific survival rate is the proportion of individuals alive at a given age (Kim & Lee, 2003). A sigmoid function was used to describe the age specific survival distribution of *P. xylostella* females, according to the equation:

$$s(Px) = a/[1 + \exp(-(x - b/c)]$$

where $S(x)$ is percentage of live females at the normalized age x; b is the normalized age at 50% survival; and a and c are fitted parameters.

Daily egg production

The daily egg production can be described by the product of the temperature-dependent total fecundity [$f(T)$], age-specific cumulative oviposition rate [$p(Px_i)$], and the age-specific survival rate [$s(Px_i)$]. According to Kim & Lee (2003), the number of eggs laid by a female during the interval between x_i and x_{i+1} is calculated as:

$$f(T)[p(Px_{i+1}) - p(Px_i)][s(Px_i) + s(Px_{i+1})/2]$$

Life table calculations

Life tables were constructed for each temperature, except for 32.5°C, at which all the eggs failed to hatch. The reproductive parameters calculated were the net reproductive rate (R_0), the rate of increase (r_m), the finite rate of increase (λ) and the mean generation time (T), according to Carey (1993). To obtain the sex ratio (females/males+females) at each

temperature, 60 newly hatched larvae were reared on broccoli leaves until adult emergence. The sex ratios used in the construction of life tables were 0.45, 0.55, 0.43, 0.50 and 0.53 at 10, 15, 20, 25 and 30°C, respectively. The relationship between net reproductive rate and temperature was described by the Gaussian model. The model proposed by Briere *et al.* (1999) was used to describe the relationship between temperature and the intrinsic rate of increase. All parameters employed in the mathematical models were estimated with the software Table Curve 2D (Systat Inc., 2002).

Statistical analysis

The effect of temperature on reproductive parameters was evaluated using analysis of variance (ANOVA). To compare longevity between males and females, a factorial ANOVA was performed using sex and temperature as factors. When differences were detected ($P < 0.05$), Tukey's HSD test was applied to classify the means. The Kaplan-Meier analysis was performed to compare survival rates of males and females between temperatures (Kaplan & Meier, 1958). The analyses were performed with the software Statistica (Statsoft Inc., 2001).

Results

Pre-oviposition and oviposition periods and longevity

The lengths of pre-oviposition ($F_{(5,105)} = 5.99$, $P < 0.001$) and oviposition periods ($F_{(5,115)} = 31.81$, $P < 0.001$) were significantly affected by temperature. These traits decrease linearly with an increase in temperature in a range from 10° to 30°C (table 1). Adult longevity was significantly affected by temperature ($F_{(5,205)} = 39.94$; $P < 0.001$), sex ($F_{(1,205)} = 23212.77$; $P < 0.001$) and the interaction between these two factors ($F_{(5,205)} = 861.64$; $P < 0.001$). Males lived longer than females at all temperatures evaluated (table 1). The three-parameter polynomial function provided a good fit to describe the relationship between temperature and pre-oviposition period (table 2, fig. 1A), oviposition period (table 2, fig. 1B) and female longevity (table 2, fig. 1C).

Total fecundity

Total fecundity of *P. xylostella* was significantly influenced by temperature ($F_{(5,105)} = 14.91$, $P < 0.001$), and the maximum fecundity observed was 333.3 eggs at 20°C. At temperatures below and above 20°C, fecundity decreased and, at 32.5°C,

Table 2. Estimated parameters for the model employed to describe the relationship between temperature and adult life history traits of *Plutella xylostella*.

Models type	Parameters[1]	Estimate	SEM	r^2
Preoviposition model	*a*	11.891	1.278	0.961
	b	−0.818	0.131	
	c	0.016	0.003	
Oviposition period model	*a*	50.786	7.838	0.955
	b	−2.498	0.804	
	c	0.037	0.001	
Longevity model	*a*	83.508	10.716	0.985
	b	−1.794	1.098	
	c	−0.011	0.002	

[1] *a*, *b* and *c* are fitted parameters; r^2, coefficient of determination.

only 79 eggs were laid on average (table 1). The relationship between temperature and total fecundity was suitably described by the Gaussian model (table 3, fig. 2A), which predicted a maximum reproductive output of 332.5 eggs per female at an optimum temperature of 19.3°C.

The variation in cumulative egg production among different temperatures was reduced using the normalized age, and is well described by the four-parameter Weibull function (table 3, fig. 2B). According to the Weilbull function, 50% of the eggs were laid at 0.24 normalized age. Egg viability was also affected by temperature ($F_{(5, 105)} = 18.49$, $P < 0.001$) and, at 32.5°C, all eggs laid were infertile (table 1). However, when eggs were laid at 20°C and immediately transferred to 32.5°C, 62% of them hatched. No significant differences were detected in hatchability at the other temperatures.

Survival of diamondback moth adults

The Kaplan-Meier survival analysis showed that temperature affected the survival of both females ($\chi^2_{(5)} = 70.24$, $P < 0.001$) and males ($\chi^2_{(5)} = 70.64$, $P < 0.001$). The survival curve exhibited low rates of mortality at early and late ages, and a linear decrease in survival during mid-ages (fig. 2C). According to the sigmoid function, 50% mortality was reached at normalized age of 0.90 (table 3).

Daily egg production

The predicted reproductive density curve in relation to temperature and female cohort age showed that both egg production and oviposition period decreased at temperatures below 15°C and above 25°C. At the extreme temperatures, the daily egg production was drastically reduced (fig. 3).

Life table parameters

The finite rate of increase (λ) was greater at higher temperatures (table 4), whereas the mean generation time (*T*) decreased as temperature increased. The net reproductive rate (R_0) increased between 10°C and 15°C and, above this range, decreased linearly with an increase in temperature. The relationship between R_0 and temperature was well described by the Gaussian model (table 5, fig. 4A), which estimated the highest R_0 of 74.6 at 18.4°C. The intrinsic rate of increase (r_m) increased proportionally with temperature in a range from 10°C to 25°C. This pattern was well described by the nonlinear model, which estimates lower and upper limits of
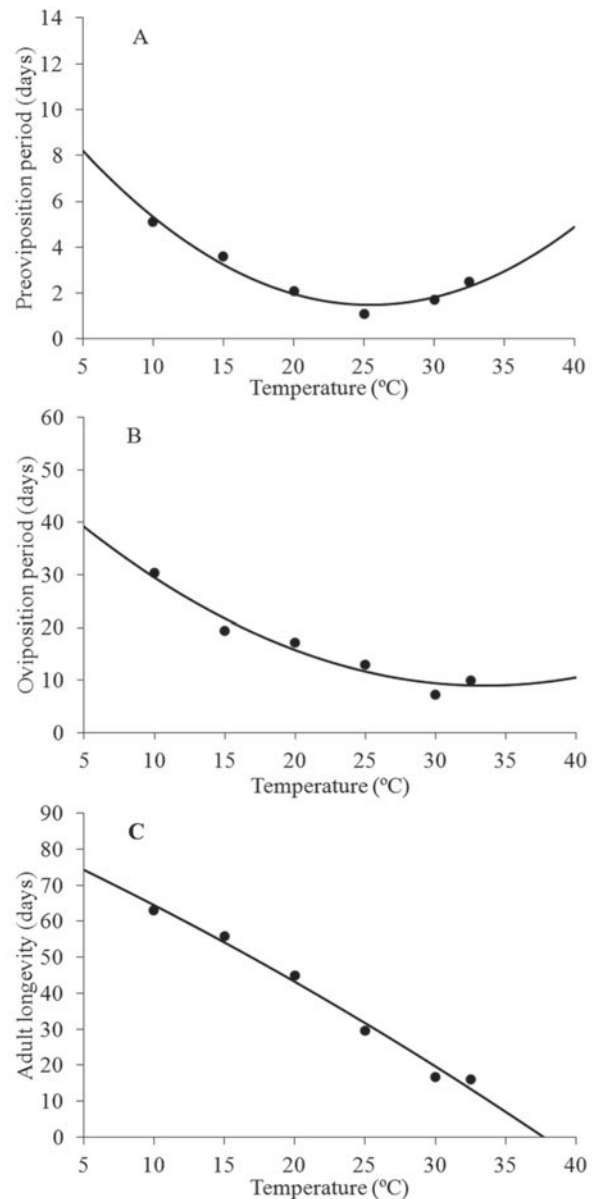

Fig. 1. (A) Temperature-dependent pre-oviposition period (B) oviposition period and (C) longevity of *Plutella xylostella* (●, observed; ——, estimated).

2.6°C and 35.4°C, respectively, and an optimum temperature of 28.6°C (table 5, fig. 4B).

Discussion

The effect of temperature on insect development has been studied extensively, but comparatively little is known about its influence on reproduction. The diamondback moth is a good example of this. In this study, we evaluated the effects of constant temperatures on reproduction of *P. xylostella*. Although insects rarely live in a stable environment without temperature fluctuation in the field, the results of studies

Table 3. Estimated parameters for temperature-dependent models of *Plutella xylostella* reproduction.

Models type	Parameters	Estimate	SEM	r^2
Total fecundity model[1]	F_{max}	332.515	17.545	0.958
	T_{max}	19.299	0.561	
	k	8.804	0.677	
Age-specific cumulative oviposition rate model[2]	a	102.239	2.480	0.966
	b	0.242	0.006	
	c	0.228	0.016	
	d	1.199	0.142	
Age-specific survival rate model[3]	a	98.718	4.867	0.894
	b	0.904	0.030	
	c	−0.237	0.021	

r^2, coefficient of determination; [1]F_{max} is the maximum reproductive capacity; T_{max} is the temperature at which maximum egg production is achieved; k is a fitted parameter.
[2] b is the normalized age at 50% cumulative oviposition; a, c and d are fitted parameters.
[3] b is the normalized age at 50% survival; a and c are fitted parameters.

under constant temperatures are still useful in understanding the population dynamics of various insects (Summers *et al.*, 1984).

The results show that temperature plays a critical role in the reproduction of *P. xylostella*, as indicated by its effect on various reproductive parameters. The diamondback moth is able to survive and reproduce in a wide range of temperatures, unsurprising given its cosmopolitan distribution including regions of different climatic conditions. However, fecundity and egg viability are negatively affected by the extreme temperatures evaluated. Mean fecundity was particularly low at 10, 30 and 32.5°C. Furthermore, all eggs laid by females reared throughout the immature and adult stages at 32.5°C failed to hatch. At this temperature, eggs gave rise to hatchlings only when they were laid at 20°C and then transferred to 32.5°C, indicating that the exposure time to temperatures below or above the optimum range is an important factor influencing hatchability.

Only a few studies have investigated the effect of temperature on reproduction of *P. xylostella* (Sarnthoy *et al.*, 1989; Wakisaka *et al.*, 1992; Shirai, 2000; Golizadeh *et al.*, 2009), and two of these provided some information about fecundity and other reproductive parameters in a wide range of temperatures (Shirai, 2000; Golizadeh *et al.*, 2009). The results obtained in our study showed some differences and similarities when compared with those studies. Wakisaka *et al.* (1992) recorded an inverse relationship between temperature and fecundity between 25 and 33°C. As found in our study, Sarnthoy *et al.* (1989) observed a bell-shaped relationship between the two variables, with the highest egg production at 23°C. However, Shirai (2000), using nine populations of *P. xylostella*, reported that fecundity decreased as temperature increased within a range from 15°C to 35°C. Likewise, Golizadeh *et al.* (2009) investigated the influence of temperature on reproduction of *P. xylostella* and obtained results quite different from those of the present study, especially at low temperatures. Female longevity (30 days on cauliflower and 24 days on cabbage) and oviposition period (18 days on cauliflower and 13 days on cabbage) reported by the authors at 10°C were almost half of the values recorded in our study (table 1).
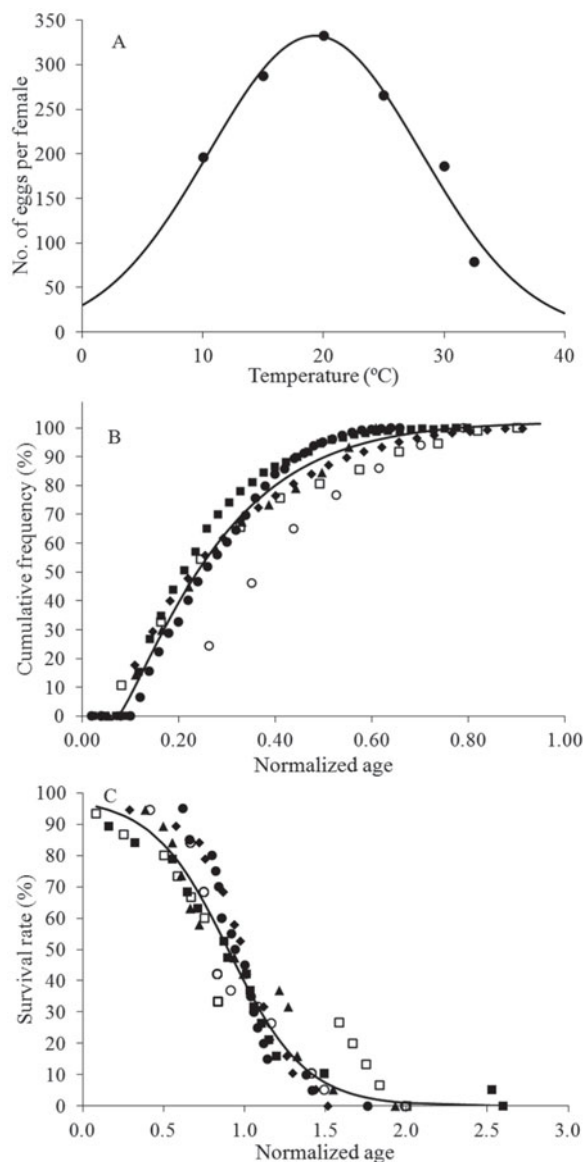

Fig. 2. (A) Temperature-dependent total fecundity curve (●, observed; ——, predicted), (B) age-specific cumulative oviposition rate (●, 10°C; ■, 15°C; ♦, 20°C; ▲, 25°C; ○, 30°C; □, 32.5°C; ——, predicted) and (C) age-specific survival rate of *Plutella xylostella* (●, 10°C; ■, 15°C; ♦, 20°C; ▲, 25°C; ○, 30°C; □, 32.5°C; ——, predicted).

Comparison between studies should be conducted carefully because differences in experimental methods, such as larval food, temperature schedule and geographical origin of the insect, can affect biological parameters. It is known that larval host plants also influence reproduction of *P. xylostella* (Ayalew *et al.*, 2006), which may explain, at least in part, the differences among studies. Furthermore, in the present study, individuals were maintained in the tested temperatures from egg hatching; whereas, in the experiment of Shirai (2000), all larvae were reared at 26°C before adults were tested at different temperatures. Thermal tolerance of insects may vary among different geographical populations (Honék, 1996;

Table 4. Estimated life table parameters of *Plutella xylostella* at five constant temperatures.

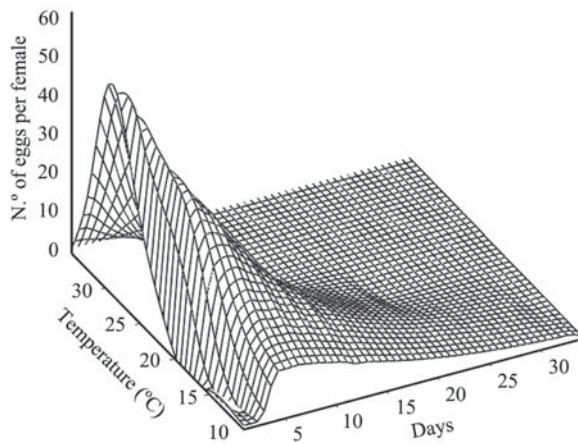| Temp. (°C)	Net reproductive rate (R_0)	Finite rate of increase (λ)	Intrinsic rate of increase (r_m)	Generation time (T)
10	43.64	1.05	0.05	77.54
15	74.94	1.11	0.10	41.64
20	66.37	1.17	0.16	26.18
25	60.43	1.26	0.23	17.83
30	25.97	1.26	0.23	13.90

Table 5. Estimated parameters for the models employed to describe the relationship between temperature and life table parameters of *Plutella xylostella*.

Models type	Parameters	Estimate	SEM	r^2
Net reproductive rate (R_0)	R_{max}	74.59	5.900	0.922
	T_{max}	18.35	0.824	
	k	8.41	1.082	
	a ($\times 10^{-4}$)	1.23	0.196	0.994
Intrinsic rate of increase (r_m)	T_0	2.57	2.024	
	T_L	35.44	1.226	
	T_{opt}	28.62	–	

r^2, coefficient of determination; R_{max}, maximum net reproductive rate; T_{max}, temperature at which maximum net reproductive rate is achieved; k, fitted parameter; a, fitted parameter; T_0 and T_L, lower and upper temperature thresholds for intrinsic rate of increase; T_{opt}, temperature at which maximum intrinsic rate of increase is achieved.
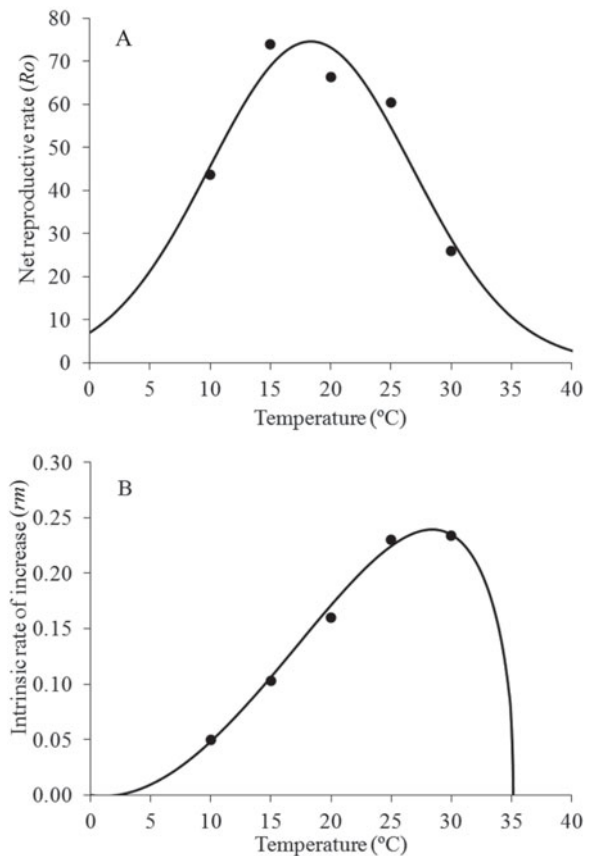

Fig. 3. Predicted oviposition density curves of *Plutella xylostella* in relation to adult age and temperature.

Fig. 4. Temperature-dependent net reproductive rate (R_0, A) and intrinsic rate of increase (r_m, B) of *Plutella xylostella* (●, observed; ——, estimated).

Addo-Bediako et al., 2000; Kimura, 2004), indicating that life history parameters may be adapted to the prevailing climatic conditions of the habitat of each population.

Models are important analytical tools for predicting, evaluating and understanding the dynamics of populations under a variety of environmental conditions and management practices (Sporleder et al., 2004). Our oviposition model allows the estimation of the daily egg production of *P. xylostella* in the field and shows that high egg production is expected at temperatures between 15°C and 25°C, with a significant reduction at temperatures below and above this range. This model can be incorporated into a population dynamics model and help to predict *P. xylostella* seasonal abundance. Comparison of the model outputs with field observations will provide a better understanding of the egg production of *P. xylostella* and indicate whether modifications will be necessary to improve the model (Kim & Lee, 2003).

Other life history parameters, such as survival and development time of immature stages, influence insect population dynamics and are also important in determining the effects of temperature on population growth in the field. This effect can be quantified by the intrinsic rate of increase (r_m), considered a key demographic parameter in the prediction of population growth potential under a given environmental conditions (Andrewartha & Birch, 1954). The r_m estimated for each evaluated temperature demonstrates that a difference of 5°C in mean temperature can have a great impact on *P. xylostella* population growth. This might explain the situation in the counties of Brasilia and Colombo, Midwest

and southern Brazil, respectively. Field surveys carried out in Brasilia, with an annual average temperature of 21.4°C, reported a population peak of 110 *P. xylostella* larvae per plant (Guilloux et al., 2003), a value significantly higher than the peak of five larvae per plant found in southern Brazil, where the mean temperature is 16.5°C (Marchioro, 2011). The insects were collected on cabbage in Brasilia and on broccoli in

Colombo, and in both areas other vegetable crops are grown along the year. In Brasilia and Colombo, a similar parasitism rate of *ca*. 23% was recorded.

The quantification of the impact of temperature on population growth is important in the context of global climate change. The third Intergovernmental Panel on Climate Change (IPCC) report predicted that global average surface temperature would further increase by 1.4 ± 5.8°C by 2100 (Climate Change Impact Review Group, 1996; Houghton *et al.*, 2001). Increases of this magnitude in global average temperature can modify the pattern of distribution and abundance of *P. xylostella* worldwide. Using mathematical models, we estimated the lower and upper temperature thresholds, as well as the optimum temperature for population growth of the diamondback moth. The model allows a prediction of potential range limits of occurrence of *P. xylostella* imposed by temperatures. If global warming continues, it is possible that in the next decades *P. xylostella* might become less common in some regions where it is presently abundant (e.g. midwest Brazil) and become more abundant in others (e.g. southeastern Brazil).

In conclusion, our study demonstrates that temperature has a significant impact on reproduction of *P. xylostella* and provides quantitative information on age-specific survivorship and fecundity at different constant temperatures. Based on these data, our oviposition model may facilitate prediction of egg production at different temperatures in the field. This might lead to localised pest control recommendations based on meteorological data. Further studies should investigate reproduction under alternating temperatures, because our results showed that females of *P. xylostella* are able to lay viable eggs at unfavourable temperatures if they have grown at favourable temperatures as immature stages. Ultimately, studies using bioclimatic models could prove useful to predict changes in the distribution and abundance of *P. xylostella*, and other major pests, in the context of global climate change.

Acknowledgements

References

Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London* **267**, 739–745.

Ali, A. & Rizvi, P.Q. (2008) Effect of varying temperature on the survival and fecundity of *Coccinela sptempunctata* (Coleoptera: Coccinelidae) fed on *Lipaphis erysimi* (Hemiptera: Aphididae). *Journal of Entomology* **5**, 133–137.

Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. Chicago, IL, USA, University of Chicago Press.

Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**, 817–844.

Ayalew, G. & Ogol, C.K.P.O. (2006) Occurrence of the diamondback moth (*Plutella xylostella* L.) and its parasitoids in Ethiopia: influence of geographical region and agronomic traits. *Journal of Applied Entomology* **130**, 343–348.

Ayalew, G., Löhr, B., Ogol, C.K.P.O. & Baumgärtner, J. (2006) Suitability of cultivated and wild crucifers for the development of diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae). *Journal of Entomology* **3**, 82–88.

Birth, L.C. (1948) The intrinsic rate of natural increase in insect population. *Journal of Animal Ecology* **17**, 15–26.

Briere, J.F., Pracos, P., Le Roux, A.Y. & Pierre, J.S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology* **28**, 22–29.

Carey, J.R. (1993) *Applied Demography for Biologists*. New York, USA, Oxford University Press.

Climate Change Impacts Review Group (1996) *Review of the Potential Effects of Climate Change in the United Kingdom*. London, UK, HMSO.

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.

Golizadeh, A., Kamali, K., Fathipour, Y. & Abbasipour, H. (2009) Effect of temperature on life table parameters of *Plutella xylostella* (Lepidoptera: Plutellidae) on two Brassicaceous host plants. *Journal of Asia-Pacific Entomology* **12**, 207–212.

Guilloux, T., Monnerat, M., Castelo-Branco, M., Kirk, A. & Bordat, D. (2003) Population dynamics of *Plutella xylostella* (Lep., Yponomeutidae) and its parasitoids in the region of Brasilia. *Journal of Applies Entomology* **127**, 299–292.

Hentz, M.G., Ellsworth, P.G., Naranjo, S.E. & Watson, T.F. (1998) Development, longevity, and fecundity of *Chelonus* sp. nr. *curvimaculatus* (Hymenoptera: Braconidae), an egg-larval parasitoid of pink bollworm (Lepidoptera: Gelechiidae). *Environmental Entomology* **27**, 443–449.

Honék, A. (1996) Geographical variation in thermal requirements for insect development. *European Journal of Entomology* **93**, 303–312.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Xiaosu, D., Maskell, K. & Johnson, C.A. (2001) *Climate Change 2001: The Scientific Basis*. Cambridge, UK, Cambridge University Press.

Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457–481.

Kim, D.S. & Lee, J.H. (2003) Oviposition model of *Carposina sasakii* (Lepidoptera: Carposinidae). *Ecological Modelling* **162**, 145–153.

Kimura, M.T. (2004) Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia* **140**, 442–449.

Liu, S.S., Chen, F.Z. & Zalucki, M.P. (2002) Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. *Environmental Entomology* **31**, 221–231.

Malaquias, J.B., Ramalho, F.S., Fernandes, F.S., Nascimento Júnior, J.L., Correia, E.T. & Zanuncio, J.C. (2010) Effects of photoperiod on reproduction and longevity of *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Annals of the Entomological Society of America* **103**, 603–610.

Marchioro, C.A. (2011) Flutuação populacional de *Plutella xylostella* (L., 1758) (Lepidoptera: Yponomeutidae) e de seus parasitóides larvais no Sudeste do Paraná: biologia em

plantas silvestres e cultivadas e exigências térmicas. PhD thesis, Universidade Federal do Paraná, Curitiba, Paraná.

Mohan, M., Sushil, S.N., Selvakumar, G., Bhatt, J.C., Gujarb, G.T. & Gupta, H.S. (2009) Differential toxicity of *Bacillus thuringiensis* strains and their crystal toxins against high-altitude Himalayan populations of diamondbackmoth, *Plutella xylostella* L. *Pest Management Science* **65**, 27–33.

Sagarra, L.A., Vincent, C., Peters, N.F. & Stewart, R.K. (2000) Effect of host density, temperature, and photoperiod on the fitness of *Anagyrus kamali*, a parasitoid of the hibiscus mealybug *Maconellicoccus hirsutus*. *Entomologia Experimentalis et Applicata* **96**, 141–147.

Sarnthoy, O., Keinmeesuke, P., Sinchaisri, N. & Nakasuji, F. (1989) Development and reproductive rate of the diamondback moth *Plutella xylostella* from Thailand. *Applied Entomology and Zoology* **24**, 202–208.

Shirai, Y. (2000) Temperature tolerance of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae) in tropical and temperate regions of Asia. *Bulletin of Entomological Research* **90**, 357–364.

Skinner, L.C., Ragsdale, D.W., Hansen, R.W., Chandler, M.A. & Moon, R.D. (2004) Temperature-dependent development of overwintering *Aphthona lacertosa* and *A. nigriscutis* (Coleoptera: Chrysomelidae): two flea beetles introduced for the biological control of leagy spurge, *Euphorbia esula*. *Environmental Entomology* **33**, 147–154.

Son, Y. & Lewis, E.E. (2005) Effects of temperature on the reproductive life history of the black wine weevil, *Otiorhynchus sulcatus*. *Entomologia Experimentalis et Applicata* **114**, 15–24.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004) A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae). *Environmental Entomology* **33**, 477–486.

Statsoft Inc. (2001) Statistica for Windows. Tulsa, OK, USA, Statsoft Inc.

Summers, C.G., Coviello, R.L. & Gutierrez, A.P. (1984) Influence of constant temperatures on the development and reproduction of *Acyrthosiphon kondoi* (Homoptera: Aphididae). *Environmental Entomology* **13**, 236–242.

Systat Inc. (2002) Table Curve 2D. Chicago, IL, USA, Systat Software Inc.

Talekar, N.S. & Shelton, A.M. (1993) Biology, ecology, and management of the diamondback moth. *Annual Review of Entomology* **38**, 275–301.

Taylor, F. (1981) Ecology and evolution of physiological time in insects. *American Naturalist* **117**, 1–23.

Wagner, T.L., Wu, H.I., Sharpe, P.J.H. & Coulson, R.N. (1984) Modelling distributions of insect development times: a literature review and application of the Weibull function. *Annals of the Entomological Society of America* **77**, 475–487.

Wakisaka, S., Tsukuda, R. & Nakasuji, F. (1992) Effects of natural enemies, rainfall, temperature and host plants on survival and reproduction of the diamondback moth. pp. 15–26 in *Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop*. Asian Vegetable Research and Development Center, Shanhua, China, 10–14 December 1990, Taiwan.