Journal of Asia-Pacific Entomology 17 (2014) 349–354

Contents lists available at ScienceDirect

Journal of Asia-Pacific Entomology

journal homepage: www.elsevier.com/locate/jape

Development response of *Spodoptera exigua* to eight constant temperatures: Linear and nonlinear modeling

Azadeh Karimi-Malati, Yaghoub Fathipour *, Ali Asghar Talebi

Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P. O. Box 14115-336, Tehran, Iran

ARTICLE INFO

Article history:
Received 5 November 2013
Revised 21 February 2014
Accepted 7 March 2014
Available online 15 March 2014

Keywords:
Spodoptera exigua
Beet armyworm
Thermal model
Intrinsic optimum temperature
Thermal constant

ABSTRACT

Temperature-dependent development of *Spodoptera exigua* (Hübner) were evaluated at eight constant temperatures of 12, 15, 20, 25, 30, 33, 34 and 36 °C with a variation of 0.5 °C on sugar beet leaves. No development occurred at 12 °C and 36 °C. Total developmental time varied from 120.50 days at 15 °C to 14.50 days at 33 °C. As temperature increased from 15 °C to 33 °C, developmental rate (1/developmental time) of *S. exigua* increased but declined at 34 °C. The lower temperature threshold (T_{min}) was estimated to be 12.98 °C and 12.45 °C, and the thermal constant (K) was 294.99 DD and 311.76 DD, using the traditional and Ikemoto–Takai linear models, respectively. The slopes of the Ikemoto–Takai linear model for different immature stages were different, violating the assumption of rate isomorphy. Data were fitted to three nonlinear models to predict the developmental rate and estimate the critical temperatures. The T_{min} values estimated by Lactin-2 (12.90 °C) and SSI (13.35 °C) were higher than the value estimated by Briere-2 (8.67 °C). The estimated fastest development temperatures (T_{fast}) by the Briere-2, Lactin-2 and SSI models for overall immature stages development of *S. exigua* were 33.4 °C, 33.9 °C and 32.4 °C, respectively. The intrinsic optimum temperature (T_{Φ}) estimated from the SSI model was 28.5 °C, in which the probability of enzyme being in its native state is maximal. The upper temperature threshold (T_{max}) values estimated by these three nonlinear models varied from 34.00 °C to 34.69 °C. These findings on thermal requirements can be used to predict the occurrence, number of generations and population dynamics of *S. exigua.*

Introduction

Understanding the factors affecting poikilotherm development is useful to estimate their survival, reproduction, movement, potential distribution, abundance and hence their population dynamics (Campbell et al., 1974; Zahiri et al., 2010). This knowledge may assist in determination of number of generations and forecasting life history. In fact, predicting the seasonal occurrence of ectotherms such as insects is essential for the timing of treatments and samples (Wagner et al., 1984; Ranjbar-Aghdam et al., 2009). These predictions are practical especially about explosive pests, which are difficult to be controlled.

The beet armyworm, *Spodoptera exigua* (Hübner) has been long considered as a major pest of many agricultural areas in vegetable, field and ornamentals (Taylor and Riley, 2008). Successful management of this pest is complicated by its broad host range, migratory dispersal, lack of understanding the distribution of overwintering regions, relatively brief developmental time, high reproductive capacity and rapidly evolving resistance to conventional pesticides (Hogg and Gutierrez, 1980; Ali and Gaylor, 1992). These problems, coupled with an increasing public concern over the environmental consequences of usage of conventional insecticides, point to the need to develop environmentally sound pest control strategies.

Prediction is one such strategy that can be an important component of an integrated pest management (IPM) system. Understanding dormant stages and regions of pests, which are affected by thermal constrains, will facilitate finding their local population source and establishing a forecasting system. Predicting the seasonal occurrence of serious agricultural pests such as *S. exigua* is essential for its accurate scheduling of census samples and control tactics. Temperature is the most important abiotic factor on insect life history and the thermal requirements of development are often used as a basis for predictions (Wagner et al., 1984; Haghani et al., 2007a,b). Insect development occurs only between an upper and a lower temperature threshold. There is no development at temperatures below the lower threshold or above the upper threshold. A variety of functions or models have been proposed to describe the relationship between temperature and arthropod development (Sharpe and DeMichele, 1977; Lactin et al., 1995; Briere et al., 1999). Although a linear relationship between developmental rate and temperature is valid, it can be measured only at moderate temperatures. Lower developmental threshold and thermal constant can be estimated from the linear approximation. This relationship is curvilinear near extremes and several nonlinear models provide value estimates of lower and upper temperature thresholds, fastest development temperature

---

* Corresponding author. Tel.: +98 21 48292301; fax: +98 21 48292200.
E-mail address: fathi@modares.ac.ir (Y. Fathipour).

http://dx.doi.org/10.1016/j.aspen.2014.03.002

and intrinsic optimum temperature for development of a given stage (Wagner et al., 1984; Ranjbar-Aghdam et al., 2009; Shi et al., 2012). Amarasekare and Savage (2012) stated that the temperature, at which the intrinsic rate of increase (*r*) is maximal, should be considered as the optimal temperature but Shi et al. (2013) emphasized that both population size and body size are important in fitness of ectotherms.

Data on temperature-dependent development of *S. exigua* reported in the aforementioned literature suggest wide variations with regard to geographical region, method of experiments, statistical analyses and host plants (Butler, 1966; Fye and McAda, 1972; Hogg and Gutierrez, 1980; Ali and Gaylor, 1992). Butler (1966) presented information on the developmental time of *S. exigua* at constant and fluctuating temperatures. Fye and McAda (1972) reported development of *S. exigua* on artificial diet at four constant temperatures. Hogg and Gutierrez (1980) found threshold temperatures for the pest using temperature ranges of 15.6 °C to 32.2 °C for the eggs. Our study determined developmental rates of egg, larval and pupal stages at eight constant temperatures on sugar beet leaves. Two linear and three nonlinear models were used for describing the relationship between temperature and developmental rate and estimating accurate optimal temperature and temperature thresholds of *S. exigua.* Using the data obtained in this study, the rate isomorphy was tested for this species. This information should be useful for the development of detailed simulation models that could predict phenology of *S. exigua* under field conditions. Forecast models enable effective timing of interventions and increases efficacy and success of control measures.

Materials and methods

Rearing methods and experimental conditions

The individuals of *S. exigua* were originally collected from sugar beet fields of Mashhad, Khorasan Razavi province, Iran during March 2009. The colony was reared for two generations before using in the experiments in a growth chamber (27 ± 0.5 °C, $65 \pm 5\%$ RH and a photoperiod of 16 L: 8 D h), provided with fresh sugar beet leaves (cultivar Renger). To obtain the same aged eggs, adult male and female moths (10–22 pairs) were kept inside the oviposition containers (12 cm in diameter and 8 cm in height). After mating and oviposition, the containers were transferred to the growth chambers at eight constant temperatures of 12, 15, 20, 25, 30, 33, 34 and 36 °C with a variation of 0.5 °C. One hundred to 300 freshly laid eggs (<10 h old) were incubated at the same temperature at which they had been laid. All eggs were checked daily for eclosion. The newly hatched larvae were transferred individually to the plastic containers (5 cm diameter and 8 cm height). The plastic containers were covered by mesh cloth for ventilation. Freshly cut sugar beet leaves were supplied daily. The larvae were monitored in their development, and the instars were regularly recorded. The exuviae of head capsule were used to discriminate the larval molting. Larval maturation was considered complete when they began making cocoons in 1 cm height soil provided in their own rearing containers. The cocooned larvae were checked daily and the emerged adults recorded daily. Developmental time of eggs, larvae, pupa and total immature stages were measured based on regular observations with 24-h intervals.

Developmental rate and mathematical models

The relationship between temperature and developmental rate is described by a logistic curve when development rate is expressed as the reciprocal of developmental time. In fact, development is completed when the sum of daily developmental rate values equals 1 (Curry et al., 1978). Therefore, the traditional (Campbell et al., 1974) and Ikemoto–Takai (Ikemoto and Takai, 2000) linear and three nonlinear descriptive models were used to determine relationship between temperature and developmental rate of *S. eixgua*. The linear models are commonly used to determine thermal constant and lower temperature threshold. In linear models, only the developmental rate included in the linear part of developmental curve was used. To obtain the correct calculation of thermal constant and lower temperature threshold, the developmental rate for egg, larva, pupa and whole immature stage of *S. exigua* at 34 °C was omitted. The traditional and Ikemoto–Takai linear formula are shown in the following equations, respectively:

$$\frac{1}{D} = -\frac{T_{\min}}{K} + \frac{T}{K}$$

$$DT = K + T_{\min} D$$

where *D* indicates the duration of development (days), *T*, ambient temperature, $T_{\min}$, the lower temperature threshold and *K* is the thermal constant. The latter function was proposed by Ikemoto and Takai (2000). This equation is derived from the traditional linear model to obtain more reliable estimates of the parameters.

According to Ikemoto–Takai model, the slopes of the linear equations represented the $T_{\min}$ for different stages. Rate isomorphy hypothesis stated that the proportion of developmental time in each stage is unaffected by temperature (van Rijn et al., 1995); consequently equality among the $T_{\min}$ values for different stages indicates rate isomorphy. No formal statistical method for testing isomorphy was offered by van Rijn et al. (1995) but Kuang et al. (2012) tested five analytical methods for the rate isomorphy, in which analysis of covariance to compare the slopes of the linear equations was used as method 2. Using ANCOVA in this study, difference among $T_{\min}$ values for different stages of *S. exigua* based on the Ikemoto–Takai linear equation was tested.

The relationship between temperature and developmental rate is not linear near the threshold and development may continue below this point and similarly for the upper lethal limit. To describe the developmental rate more realistically and over a wider temperature range, three nonlinear models have been applied. Briere-2 and Lactin-2 were chosen because they are the most commonly used for that purpose. These nonlinear formulations are:

$$\frac{1}{D} = \mathrm{a} \times T(T - T_{\min}) \times (T_{\max} - T)^{\frac{1}{d}} (\text{Briere-2})$$

$$\frac{1}{D} = \exp(\mathrm{p} \times T) - \exp\left(\mathrm{p} \times T_{\max} - \left(\frac{T_{\max} - T}{\Delta T}\right)\right) + \lambda (\text{Lactin-2})$$

where *d*, *a*, *p*, $T_{\max}$, ΔT and λ are fitted coefficients (Lactin et al., 1995; Briere et al., 1999).

A modified function of Sharpe and DeMichele (1977) and Schoolfield et al. (1981) by Ikemoto (2005) (SSI) was also used because the temperature dependence of arthropods and other poikilotherms is well expressed by this thermodynamic model based on enzymatic reactions (Sharpe and DeMichele, 1977; Schoolfield et al., 1981). The SSI thermodynamic model is able to estimate the intrinsic optimum temperature as the most important thermal parameter for physiological, ecological and evolutional processes of ectotherms (Ikemoto et al., 2013; Shi et al., 2013). SSI model is as follows:

$$\frac{1}{D} = \frac{\rho_\Phi \dfrac{T}{T_\Phi} \exp\left[\dfrac{\Delta H_A}{R} \times \left(\dfrac{1}{T_\Phi} - \dfrac{1}{T}\right)\right]}{1 + \exp\left[\dfrac{\Delta H_L}{R} \times \left(\dfrac{1}{T_L} - \dfrac{1}{T}\right)\right] + \exp\left[\dfrac{\Delta H_H}{R} \times \left(\dfrac{1}{T_H} - \dfrac{1}{T}\right)\right]}$$

where ρ_Φ is the mean developmental rate at T_Φ ($1/d$), T_Φ is the intrinsic optimum temperature at which the probability of an enzyme being in the active state is maximal. ΔH_A, ΔH_L and ΔH_H are the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal/mol), the change in enthalpy associated with low temperature inactivation of the enzyme (cal/mol) and the change in enthalpy associated with high temperature inactivation of the enzyme (cal/mol), respectively, *R* is the gas constant (1.987 cal/deg/mol), T_L is the temperature at which the enzyme is 1/2 active and 1/2 low temperature inactive (in