



Temperature-dependent development of diapausing larvae of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae)



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ABSTRACT

Temperature-dependent development rate, percent diapause induction (hibernation at low temperature and aestivation at high temperature), and survival of diapausing larvae of *Chilo partellus* (Swinhoe, 1885) were examined on 13 constant temperatures ranging from 8 to 40 °C. Development of hibernating and aestivating larvae occurred from 10 to 25 °C and 27–38 °C, respectively. However, no development occurred at 8 °C and 40 °C. To determine actual thermal conditions that affect development and trigger both kind of diapause (hibernation and aestivation), various thermal parameters were estimated by fitting the development rate data to two linear (Ordinary equation and Ikemoto & Takai) models and thirteen non-linear models. The lower thermal thresholds (T_{min}) for development of diapausing larvae of *C. partellus* were calculated as 9.60 °C and 10.29 °C using the ordinary linear model and Ikemoto & Takai model, respectively. Similarly, the thermal constants (K) estimated using the ordinary linear model was 333.33 degree-days and that estimated with Ikemoto & Takai model was 338.92 degree-days. Among the non-linear models, Lactin-2 followed by Lactin-1 were found to be the best as these models estimated the critical temperatures (T_{min} , T_{max} and T_{opt}) similar to those of observed values. Conclusively, the Ikemoto & Takai linear model and Lactin-2 followed by Lactin-1 non-linear models are useful and efficient for describing temperature-dependent development and estimating the temperature thresholds of diapausing larvae of *C. partellus*. Our findings provided fundamental information for estimation of thermal requirement and temperature based development models for diapausing larvae of *C. partellus*. This information will be highly useful for predicting the occurrence, seasonal emergence, number of generations and population dynamics of *C. partellus*.

1. Introduction

Spotted stem borer, *Chilo partellus* (Swinhoe, 1885) (Lepidoptera: Crambidae) is one of the most destructive pest causing 18–25% loss in maize and sorghum in Asia (Dhaliwal et al., 2015). One aspect of *C. partellus* biology that is relevant to understanding its population dynamics and geographic distribution, is the diapause strategy (Ofomata et al., 1999; Kfir et al., 2002). It enters facultative diapause as mature larvae inside the old stems or stubbles which usually occur under drought conditions and maturity of host plants (Scheltes, 1978; Dhillon et al., 2017). When dry conditions of host plants synchronize with cold season, *C. partellus* enters winter diapause (hibernation) in North India (Dhillon et al., 2017). Similarly when dry conditions synchronize with warm season it enters summer diapause (aestivation) in southern India (Trehan and Butani, 1949). Genetic determination of locally adapted life-history traits like diapause and polyphenism are important to understand bio-ecology and population dynamics of insects in response to abiotic and biotic factors (Söderlind and Nylin, 2011). Diapause is a

genetically determined stage of suppressed development which is expressed by unfavorable environmental factors (Tauber et al., 1986). Among the environmental factors, temperature plays an important and critical role in development biology of insects. The relationship between temperature and rate of development is crucial, as it influences insect phenology, distribution and abundance (Sharpe and DeMichele, 1977; Zahiri et al., 2010; Padmavathi et al., 2013; Arbab et al., 2016).

Temperature-dependent development rate models using physiological time data have been developed for many insect species to predict emergence of adults from the diapausing generations (Howell and Neven, 2000; Aghdam et al., 2009). Several phenological models have been developed to determine the development rate of an insect. These models have practical implications to predict the important events in the life cycle of insects as well as to devise an appropriate control strategy (Brière et al., 1999; Kontodimas et al., 2004). These phenological models are based on temperature-dependent development rate and governed by either linear or non-linear relationships (Howell and Neven, 2000; Arbab et al., 2016). Linear approximation allows the

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estimation of lower thermal thresholds (T_{min}) and thermal constants (K) within a limited range of temperature, and is extensively used in predicting insect population dynamics (Jarosik et al., 2002). However, non-linear models have not been routinely used because of their complexity, but describe stage-specific lower, upper and optimal thermal thresholds across temperature ranges, appropriately (Howell and Neven, 2000; Kontodimas et al., 2004; Arbab et al., 2006; Soderlind and Nylin, 2011).

Importance of predicting seasonal occurrence of insect has led to development of many mathematical models describing temperature-dependent development rates (Wagner et al., 1984). Utilization of temperature-dependent development data and its application in phenological models has long been known as an important tool for management of insect pests. These models have traditionally been used to predict seasonal emergence, density and survival of insect pests under field conditions, and helpful in optimization of pesticide use for their control (Herrera et al., 2005). Evaluation of these models are based on specific criteria such as fit to data, number and biological values of the fitted coefficients, number of measurable parameters, and the accuracy in the estimation of thresholds (Kontodimas et al., 2004).

The literature on effect of wide range of temperatures on the development of diapausing larvae of *C. partellus* is completely lacking. Nevertheless, to the best of our knowledge, no phenological model is available to predict seasonal emergence of *C. partellus* from diapause experiencing populations. Therefore, aim of this study was to develop knowledge on thermal characteristics and optimize temperature thresholds for development of hibernating and aestivating larvae of *C. partellus* using linear and non-linear temperature-dependent development rate models.

2. Materials and methods

2.1. Insect rearing and experimental conditions

Larvae of *C. partellus* were collected during February 2014 from experimental field of Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India (Latitude: 28°38'23" N, Longitude: 77° 09'27"E, and height above mean sea level: 228.61 m). Larval culture was maintained on artificial diet (Sharma et al., 1992) under laboratory conditions at 27 ± 1 °C, $65 \pm 5\%$ relative humidity, and 12 h photoperiod. Adults emerged from the culture were released in oviposition cages and provided with cotton swab soaked in water. The oviposition cages were covered with wax-paper from outside to serve as an oviposition substrate. The wax-papers were changed daily and kept at 27 ± 1 °C and photoperiod 12:12 (L: D) for hatching. After hatching the neonates were transferred to plastic container (1000 ml capacity) at 27 ± 1 °C, 12 L:12D and $65 \pm 5\%$ RH in Biological Oxygen Demand (BOD) incubator. The 4th instar stage was used in further experimentation.

2.2. Constant temperatures and diapause cycle

To determine critical thermal conditions that affect development and trigger both kind of diapause (hibernation and aestivation), we used 4th instar larvae from above mentioned laboratory culture and exposed them to thirteen constant temperature regimes i.e., 8°, 10°, 15°, 18°, 20°, 22°, 25°, 27°, 30°, 32°, 35°, 38° and 40 °C, 12 L:12D, $65 \pm 5\%$ R.H. together with dry diet (~20% moisture contents). Earlier studies reported that lower than optimum temperature (27 °C) together with dry diet induce hibernation (Dhillon et al., 2017), while higher than the optimum temperature induce aestivation (Mukesh K. Dhillon, unpublished) in *C. partellus*. The optimum temperature defined in previous studies by Dhillon et al. (2017) was 27 °C, at which the larvae completed timely development with highest rate of survival and adult emergence. Hibernating and aestivating larvae do not show any difference in morphological features, therefore collectively designated as

diapausing larvae (Dhillon and Hasan, 2017). The terms hibernation and aestivation were used only to indicate the range of temperature on which diapause was induced.

This experiment was set up with 50 newly molted 4th instar *C. partellus* larvae released on dry artificial diet in plastic jars (1000 ml capacity). After larval inoculation, the experimental jars were immediately transferred to the above mentioned constant temperature regimes in BOD incubator. Observations were made daily on any sign of diapause induction and larval mortality. When exposed larvae showed any kind of transitional morph (an intermediate between diapausing and non diapausing larvae as described by Dhillon et al., 2017), were considered as diapausing and calculations were carried out on percent larvae underwent in hibernation and aestivation at respective temperature regimes. The duration from exposure to appearance of transitional morph were also recorded. These larvae were allow to remain in diapause upto 45 days, which afterwards provided with fresh artificial diet with sufficient moisture and placed back to 27 °C, 12L:12D and $65 \pm 5\%$ RH to terminate the diapause, and the data were used to calculate the percentage of larvae terminating diapause at respective temperature regimes. The time from appearance of transitional morph to the formation of pupa was considered as diapause duration and these data were used in analysis of temperature-dependent development rate models. Moreover, 2nd order polynomial regressions were performed to model the trends of percent diapause induction and larval survival with respect to test temperatures.

2.3. Development rate models

Fifteen development rate models viz., two linear and 13 non-linear models were chosen to describe the relationship between temperature (T) and development rate (d), which is reciprocal of development time (D). Moreover, two procedures were used to estimate biological parameters (i.e., threshold temperatures and K) from these models. These were: (i) Two linear regression models were used to determine thermal constant (K) and lower thermal threshold (T_{min}). In order to obtain correct calculation of T_{min} and K , the data on 8 °C and 40 °C were omitted in this model, as no development was recorded at these temperatures. (ii) Thirteen widely used non-linear models were chosen because the estimates of these models have biological significance by estimating the lower (T_{min}), optimum (T_{opt}) and high temperature (T_{max}) thresholds (Table 1). These bioclimatic parameters were either directly estimated by the fitted model or obtained mathematically using SPSS v. 15.0 statistical package (SPSS Inc. Chicago, IL, US). The models that estimate all of the temperature thresholds and optimal temperature are Lactin-1, Lactin-2 and Sharpe-Schoolfield-Ikemoto (SSI) model. Most non-linear models are able to estimate two or more parameters.

The performance of linear and non-linear mathematical models was judged based on the following criteria:

- (1) Higher values of coefficient of determination (R^2) indicate a good fit.
- (2) Lower value of residual sum of square (RSS) indicate a good fit.
- (3) The adjusted coefficient of determination (R_{adj}^2): This criteria is also parameter independent and can be calculated as: $R_{adj}^2 = 1 - (n-1/n-k) \cdot (1 - R^2)$, where n is the number of observations, k = number of model parameters + 1, and R^2 is the coefficient of determination. A higher value of R_{adj}^2 indicates better fit without overfitting.
- (4) Corrected Akaike information criteria (AIC_c): AIC_c is estimated as $AIC_c = -2L + 2k + [(2k(k+1))/(n-k-1)]$, where, n = number of observations, k = number of model + 1 (added 1 represents the model error term) parameters and L is a maximized log-likelihood value (Akaike, 1974). L can be obtained as $L = -(N/2) \cdot \ln(RSS/N)$. The model having smallest value of AIC_c is considered best (Anderson, 2008).
- (5) Akaike weights (W_j) criteria: The candidate models can be compared by their Akaike weights (Akaike, 1974). The tested model

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