A Laboratory Study on the Modeling of Temperature-Dependent Development and Antioxidant System of *Chilo suppressalis* (Lepidoptera: Crambidae)

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**Abstract**

The developmental rates of *Chilo suppressalis* (Walker; Lepidoptera: Crambidae) were investigated at different constant temperatures of 11, 18, 22, 24, 26, 30, 32, 34, and 36°C to find out temperature thresholds, thermal requirements and larval antioxidant responses. The time to complete immature stages separately reduced by raising the rearing temperature except for eggs which showed no significant differences at 30–34°C. Data analysis by traditional and Ikemoto–Takai linear models determined *T*~*min*~ of 10.0 and 9.92°C as well as thermal constants of 840.34 and 848.0 DD for the overall immature stages. The models including Analytis, Briere-2, Lactin-2, and Sharpe–Schoolfield–Ikemoto (SSI) calculated *T*~*min*~ values of 9.15, 9.57, 10.0, and 11.37°C for overall immature stages while *T*~*fast*~ was found to be 33.8, 33.3, 33.7, and 33.0°C, respectively. *T*~*max*~ was calculated as 35.12, 34.66, 34.56, 36.84, 34.11, and 35.15°C for Analytis, Briere-2, Lactin-2, SSI, Logan-6, and Logan-10. *Topt* using SSI was calculated as 24.42°C for total developmental time. The larvae exposure to 34°C in the short-term period demonstrated the highest activities of catalase, peroxidase, and superoxide dismutase compared to control (24°C). Activities of ascorbate peroxidase and glucose-6-phosphate hydrogenase also increased at 34°C in the short-term period for all preparations. The larvae exposed to 34°C in short-term period showed the highest amounts of Malondialdehyde and oxidized and reduced thiols (RSSR/RSH) ratio compared to control. These results may be useful to explain potentially ecological performance of *C. suppressalis* as the major pest of rice in Iran.

**Key words:** rice striped stem borer, temperature, development, antioxidant system

The rice striped stem borer, *Chilo suppressalis* (Walker; Lepidoptera: Crambidae) is a pest of economic importance causing annually significant yield losses in Asia, southern America and northern Africa (Lu et al. 2015). The larvae intensively feed on rice stems and cause ‘dead-heart’ and ‘white head’ of rice seedlings as the two common symptoms of damage (Zibaee et al. 2009). Over the years, different control tactics by releasing parasitoid wasps, pheromone traps using attract-kill process and sanitation have been developed to suppress population outbreaks of *C. suppressalis* but only spraying by synthetic insecticides have earned proper results (Cheng et al. 2010). Such a spraying, mainly by diazinon, have had its costs on development of insecticide-resistance and environmental pollutions (Zibaee et al. 2009).

Insects are the poikilothermous organisms which depend on temperature for different biological performances like development, survival, reproduction, mortality and sex ratio (Jia et al. 2011, Moallem et al. 2017). Hence, determination of temperature requirements is considered as a tool to predict population dynamic of insects like estimation of occurrence or prevalence, size of emerged population from overwintering generation, egg eclosion, larval and pupal development and generation time (Sharpe and De Michele 1977, Honek 1996, Briere et al. 1999, Herms 2004, Moallem et al. 2017). Appropriate temperature is necessary to insect development but it may be an environmental stress in extreme ranges which decrease insect survival mainly immature stages while middle-extremes induce production of free radicals damaging tissues (Lopez-Martinez et al. 2008, Zhang et al. 2015). Free radicals are the uncharged, highly active and short-lived molecules which impair normal physiology by cell damage, inhibition of DNA replication and mutation (Zhang et al. 2015). Hence, the antioxidant system of organisms has been developed to protect cells against free radicals (e.g., Reactive Oxygen Species) by preventing damages to DNA, proteins and reduction of lipid peroxidation level (Dubovskiy et al. 2008). Such a system recruits different enzymes like ascorbate peroxidases.
(APOX), superoxide dismutases (SOD), catalases (CAT), peroxidases (POX), glutathione-S-transferase (GST), glutathione peroxidase (GPOX), glucose-6-phosphate dehydrogenase (GPDH) in addition to some non-enzymatic antioxidants as ascorbic acid, malondialdehyde (MDA), thiol and α-tocopherol (Felton and Summers 1995, Dubovskiy et al. 2008).

As an important pest, it is useful to find thermal requirements of *C. suppressalis* and determine potential antioxidant responses to high temperatures as it is exposed during summer. Hence, the present study initially was designed to determine developmental responses of *C. suppressalis* at the eight constant temperatures of 11, 18, 22, 24, 26, 30, 32, 34, and 36°C by estimating of thermal requirements by linear and non-linear models. Then, the larvae were exposed to an optimal (control) and high temperature in short- and long-term periods to find out antioxidant responses. These findings will be useful to forecast distribution and abundance of *C. suppressalis* regarding environmental conditions in the paddy fields.

**Materials and Methods**

**Thermal Experiments**

One-day old eggs of *C. suppressalis* received from a laboratory stock at Rice Research Institute of Iran (Amol, Mazandaran province) in July 2016. The stock population was reared for at least five generations to have a unified cohort of individuals at 26 ± 1°C, 85% of relative humidity and 16:8 (L:D) h of photoperiod. The larvae were fed on the Haemi seedlings of rice in all generations. Depending on thermal treatment, 600 to 1,000 eggs (24 h old) were transferred to the test tubes, coated with wet cotton and put in growth chambers at nine constant temperatures of 11, 18, 22, 24, 26, 30, 32, 34, and 36°C with 70 ± 5% of relative humidity and photoperiod of 16:8 (L:D) h. Once the color of eggs was changed to grey, the fresh stems (Hashemi variety) were provided in the breeding tubes. Thereafter, stems containing neonate larvae were split, a group of 10 larvae were transferred to the new stems and exposed to each temperature regime as indicated above. As soon as the larvae reached to the third instar, each larva was placed in different breeding tubes and reared individually. The size of head capsule was used to discriminate the larval molting. Developmental period of the larvae and food quality were checked 3–4 times per week. The old cutting stems were replaced by the fresh cutting 3–4 times a week which the whole process took 3–4 h in a day although a short time of about 15–20 min was spent to handle the embryonic and pupal stages. Every 24 h, the laboratory conditions were checked and rearing containers were cleaned to remove larval feces and exuviae. At the end of larval period, pupae were transferred to the new tubes and checked until the emergence of adults. The sex of adult moths was determined based on Ebert (1973) (Females have yellow to brown forewings while the forewings of males are grey. More precisely, male genitalia are bifurcate symmetrical with bowed arms of equally long without subapical teeth. Female genitalia contain heavily sclerotized ostial pouch which slightly has demarcated from ducus bursae.). A daily monitoring was carried out recording the duration of egg development and the total number of immature stages of *C. suppressalis*.

**Thermal Models**

The development rate of *C. suppressalis* was calculated by the reciprocal of temperature-dependent development of egg, larval, pupal, and total immature stage. All the thermal experiments were the modification of previous reports of Moallem et al. (2017) on *Glyphodes pyloalis* (Walker; Lepidoptera: Crambidae). The relationship between temperature and developmental rate described using traditional and Ikemoto–Takai linear models. The formulas are as follows, respectively (Ikemoto and Takai 2000):

\[
\frac{1}{D} = \frac{T_{\text{max}} - T}{K} 
\]

\[
DT = K + T_{\text{max}}D 
\]

where *D* is the duration of development (days), *T* is the ambient temperature, *T_{\text{max}}* is the lower temperature threshold, and *K* is the thermal constant (Degree Day, DD).

Because the traditional linear model may result a lower *T_{\text{max}}* and a larger *K*, Ikemoto and Takai (2000) derived equation 2 from the traditional linear model to get more reliable values because the relationship between exposed temperatures and developmental rate is curvilinear near lower and upper temperature thresholds. In the followings, four nonlinear models including Analytis, Briere–2, Lactin–2, Logan 6, Logan 10 and Sharpe–Schoolfield–Ikemoto (SSI) were calculated using formulas as below (Lactin et al. 1995, Briere et al. 1999, Shi et al. 2011):

\[
\frac{1}{D} = a \times (T - T_{\text{max}}) \times (T_{\text{max}} - T)^y 
\]

\[
\frac{1}{D} = a \times T(T - T_{\text{max}}) \times (T_{\text{max}} - T)^1 
\]

\[
\frac{1}{D} = \exp(P \times T) - \exp\left(P \times T_{\text{max}} - \left(\frac{T_{\text{max}} - T}{\Delta T}\right)\right) + \lambda 
\]

\[
\frac{1}{D} = \psi \times \exp\left(P \times T\right) - \exp\left(P \times T_{\text{max}} - \left(\frac{T_{\text{max}} - T}{d}\right)\right) 
\]

\[
\frac{1}{D} = \alpha \times \left(1 + K \times \exp(-P \times T)\right)^{-1} - \exp\left(-\frac{T_{\text{max}} - T}{d}\right) 
\]

\[
\frac{1}{D} = \frac{\rho_a T_{\text{opt}} \times \exp\left(\frac{\Delta H_a}{R} \times \frac{1}{T_{\text{opt}}} \times \frac{1}{T}\right)}{1 + \exp\left(\frac{\Delta H_a}{R} \times \frac{1}{T_{\text{opt}}} \times \frac{1}{T}\right)} 
\]

where *T_{\text{max}}* is the lower temperature threshold, *T_{\text{opt}}* is the upper temperature threshold; *a, d, λ, n, P, and K* are the fitted coefficients (Analytis 1981, Briere et al. 1999, Roy et al. 2002, Kontodimas et al. 2004). The SSI model estimates the intrinsic optimal temperature (*T_{opt}*) led to the highest population size with the least mortality (Ikemoto 2005, 2008; Shi et al. 2011). This parameter differs from *T_{fast}*, which *T_{fast*} denotes the temperature that causes fastest development time per given period (Moallem et al. 2017). So, *PΦ* is the mean developmental rate at *T_{opt}*/(1/d), *T_{opt}* is the intrinsic optimal temperature which the enzyme represents the highest activity, *ΔH_a*, *ΔH_{ai}*, and *ΔH_{ij}* are the enthalpy to activate the reaction that is catalyzed by the enzyme (cal/mol), *R* is the gas constant (1.987 cal/deg/mol), *T_1* is the temperature at which the enzyme is 1/2 active and 1/2 low temperature inactive, and *T_{ij}* is the temperature at which the enzyme is 1/2 active and 1/2 high temperature inactive (both in Kelvin degrees).

**Critical Temperatures Estimation**

The lower temperature threshold (*T_{min}*) is the least temperature showing no development in life stages. The standard error (SE) of *T_{min}*, calculated from the linear models as follows:
\[ SE_{bm} = \frac{r}{b} \times \sqrt{\frac{S^2}{N \times r} + \left( \frac{SE_b}{b} \right)^2} \]  
where \( S^2 \) is the residual mean square of \( r \), \( r \) is the sample mean, and \( N \) is the sample size (Campbell et al. 1974, Kontodimas et al. 2004). The upper temperature threshold (\( T_{max} \)) is the temperature in which the insect is unable to survive for significant period (Kontodimas et al. 2004). \( T_{max} \) was estimated by the nonlinear models. The fastest development temperature (\( T_{fast} \)) defines as the temperature showing the highest developmental rate. The thermal constant (\( K \)) was estimated by the linear equation and the related \( SE \) was determined using the following equation (Campbell et al. 1974, Kontodimas et al. 2004).

\[ SE_k = \frac{SE_b}{b^2} \]  
Where \( b \) is the slope and \( SE_b \) is the standard error of regression line slope (Campbell et al. 1974, Kontodimas et al. 2004).

**Thermal Stress**

The larvae were divided into different groups to determine antioxidant responses due to thermal stress. The first group was the larvae reared on optimal (24°C, also referred as control) and stress temperature (34°C, determined based on the thermal experiments) from first to fifth larval instars (24 h old) to show long-term effects of thermal stress. The second group were the larvae reared on optimal temperature but those were exposed to temperature stress (34°C) for 24 h when fifth instars were emerged to show short-term effects of thermal stress. Three replicates containing 60 larvae were used in short- and long-term experiments and the antioxidant system were evaluated in hemocytes, midgut, fat body, and total body of C. suppressalis larvae (Cui et al. 2011).

**Determination of Antioxidant System**

**Sample Preparations**

The larvae of C. suppressalis exposed to optimal (Control) and extreme temperatures in both short- and long-term exposures were randomly selected and dissected in saline solution (NaCl, 10 mM). The samples including fat body (w/v in distilled water), midgut (w/v in distilled water) and total body (w/v in distilled water) were homogenized in test tubes and centrifuged at 20,000 × g for 20 min at 4°C (Dubovskiy et al. 2008). For hemocyte preparation, initially the collected hemolymph was added into anticoagulant solution containing 0.01 M ethylenediamine tetracetic acid, 0.1 M glucose, 0.062 M NaCl, 0.026 M citric acid, (pH = 4.6) as described by de Azambuja et al. (1991). Then, the sample was centrifuged at 20,000 × g for 20 min at 4°C and the obtained supernatant was removed and distilled water was added to pellets containing hemocytes. This new mixture was homogenized by a hand pestle and re-centrifuged in the same condition. The new supernatant was used for biochemical assays using hemolymph sample. For all samples, supernatants were collected and stored at −20°C to onset of the biochemical experiments (less than a week).

**CAT Assay (EC 1.11.1.6)**

A method described by Wang et al. (2001) was used to assay CAT activity in the control and thermal stressed larvae. The reaction mixture consisted 100 µl of sample and 500 µl of hydrogen peroxide (1%) which incubated for 10 min at 28°C for 10 min prior to read the absorbance at 240 nm.

**SOD Assay (EC 1.15.1.1)**

Initially, xanthine oxide solution was prepared by 10 mg of bovine albumin and 100 µl of xanthine oxidase (5.87 units/ml) dissolved in 2 ml of phosphate buffer (0.1 M, pH 7). Then, 100 µl of the solution was added to 500 µl of a mixture containing 70 µM of NBT (Nitro blue tetrazolium) and 125 µM of xanthine which have been dissolved in PBS. The incubation was initiated in darkness for 20 min at 28°C once 100 µl of sample was added to the whole mixture. Finally, absorbance was read at 560 nm and the activity was reported as ΔA 560 nm/min/mg protein (McCord and Fridovich 1969).

**POX Assay (EC 1.11.1)**

Briefly, 100 µl of sample was added to 500 µl of pyrogallol solution (0.05 M pyrogallol in 0.1 M phosphate buffer [pH 7.0]) and 500 µl of H2O2 (1%). Thereafter, changes in absorbance were monitored for 2 min every 30 s at 430 nm (Addy and Goodman 1972).

**APOX Assay (EC 1.11.1.11)**

The enzyme activity was determined by adding 100 µl of sample into a solution containing 67 mM potassium phosphate buffer (pH 7) and 2.5 mM of ascorbic acid (250 µl). Thereafter, 200 µl of H2O2 (30 mM) was added and absorbance was read at 290 nm for 5 min (Asada 1984).

**GPDH (EC 1.1.1.49)**

Briefly, 100 µl of sample was added into a solution containing 100 µl Tris-HCl buffer (100 mM, pH 8.2), 0.2 mM NADP and 0.1 M of MgCl2. Then, 100 µl of glucose-6-phosphate (6 mM) was added and absorbance was read at 340 nm to determined enzymatic (Balinsky and Bernstein 1963).

**MDA Assay**

A solution containing 100 µl of trichloroacetic acid (20%) and 100 µl of sample was prepared and centrifuged at 15,000 × g for 10 min at 4°C. Then, supernatant was carefully separated and poured into 100 µl of 2-thiobarbituric acid solution (TBA, 0.8%). The incubation was prolonged for 60 min at 100°C and the absorbance was read at 535 nm. A molar extinction coefficient of 1.56 × 105 M−1 cm−1 was considered to calculate MDA concentration per mg protein (Bar-Or et al. 2001).

**Oxidized and Reduced Thiols Assay**

A method described by Khramtsov et al. (1997) was used to find the concentrations of oxidized (RSSR) and reduced (RSH) thiols in the control and thermal stressed larvae. RSH was provided by decomposing RSSRs using hydrochloric acid (1M) for 20 min. The prepared mixture was neutralized by sodium hydroxide. Then, 50 µl of sample was added into 500 µl of 0.1 % 5,5-dithiobis-(2-nitrobenzoic acid) DNTB solution (Prepared in PBS, 0.1 M, pH 7) and incubated at 37°C for 10 min. The absorbance of both preparations was read at 405 nm.

**Protein Assay**

The protein content of samples was assayed by the method of Lowry et al. (1951) which recruits reaction of Cu²⁺, produced by the oxidation of peptide bonds with Folin–Ciocalteu reagent. Briefly, 20 µl of sample was added to 100 µl of reagent and incubated for 30 min prior to read the absorbance at 545 nm (Recommended by Ziest Chem. Co., Tehran-Iran).
Statistical Analysis

Data of temperature-dependent development was checked for normality using Kolmogorov–Smirnov test. A one-way analysis of variance ANOVA (PROC GLM, SAS Institute 2007) was run to analyze the effect of temperature on developmental periods of *C. suppressalis* via Tukey Honestly Significant Difference HSD multiple comparison (*P* ≤ 0.01). MINITAB version 16.0 and JMP, version 7.0 provided by SAS institute were used to analyze linear and non-linear models of development, respectively while SSI model was analyzed by R software (Shi et al. 2011). Finally, the data of antioxidant assay was analyzed using Tukey Honestly Significant Difference (HSD) multiple comparison (*P* ≤ 0.05).

Results

Developmental Rate

Rice striped stem borer was able to complete all immature stages in the given temperatures while no egg hatch was observed in the temperatures of 11 and 36°C following 30 and 15 d of storage in the growth chambers which led to considering death of eggs in those temperatures following distinct time storage (Table 1). The length of embryonic period (from egg to the emergence of first instar larvae) showed a significant difference at the given temperatures as it linearly decreased along with temperature elevation. Also, there were significant differences between developmental periods of the larvae at the studied temperatures (*P* < 0.05, Tukey).

Model Evaluations

The developmental rate of *C. suppressalis* increased linearly from 18 to 32°C while but other temperature values were outside the linear segment of the growth curve so those were excluded from the linear regression. The estimated lower temperature thresholds (*T*<sub>min</sub>) were 11.25, 8.60, 12.82, and 10.0°C for eggs, larvae, pupae and overall immature stages using the traditional linear model. These values were calculated as 12.30, 8.35, 13.0, 9.92°C for the given stages based on Ikemoto-Takai model (Table 2). The thermal constants (*K*) for eggs, larvae, pupae and overall immature stages were found to be 78.13, 666.67, 111.48, and 848. 34 DD from traditional model as well as 71.7, 679.0, 110.0, 848.0 DD from Ikemoto-Takai model (Table 2). Moreover, Fig. 1 shows the effects of temperature on developmental rate of overall immature stages in *C. suppressalis*.

The six nonlinear models including Analytis, Briere-2, Lactin-2, Logan-6, Logan-10, and SSI were fitted to calculate the developmental rate of egg, larval, pupal, and overall immature stages in Table 1. Developmental time (means ± SE) and survival in the immature stages of *Chilo suppressalis* at seven constant temperatures

| Temperature (°C) | Stage | 18 | 22 | 24 | 26 | 30 | 32 | 34 |
|------------------|-------|----|----|----|----|----|----|----|
| Egg              | 13.00 ± 0.00a | 7.00 ± 0.00b | 5.00 ± 0.00c | 5.00 ± 0.00c | 4.00 ± 0.00d | 4.00 ± 0.00d | 4.00 ± 0.00d |
| No (s)           | 124 (25%) | 230 (71.73%) | 124 (83.2%) | 208 (78.36%) | 169 (75.73%) | 298 (70.8%) | 478 (41.84%) |
| Larva            | 69.33 ± 1.16a | 49.03 ± 0.68b | 41.94 ± 0.68c | 41.26 ± 0.42c | 30.07 ± 0.46c | 28.65 ± 0.51d | 31.53 ± 1.5e |
| No (s)           | 82 (51.51%) | 165 (54.87%) | 104 (68.26%) | 163 (72.39%) | 128 (60.15%) | 211 (38.38%) | 200 (7.5%) |
| Pupa             | 21.74 ± 0.4a | 12.64 ± 0.15b | 9.50 ± 0.23c | 7.96 ± 0.07d | 6.63 ± 0.09e | 6.60 ± 0.19f |
| No (s)           | 42 (71.11%) | 90 (95.29%) | 71 (95.77%) | 118 (95.76%) | 77 (96%) | 81 (91.3%) | 15 (86.6%) |
| Immature stage   | 105.13 ± 1.17a | 68.69 ± 0.63b | 56.36 ± 0.63c | 54.26 ± 0.5c | 42.52 ± 0.5d | 37.75 ± 0.5e | 39.50 ± 0.65e |
| No (s)           | 124 (25%) | 230 (37.39%) | 124 (54.8%) | 208 (54.32%) | 169 (45.30%) | 298 (24.83%) | 478 (2.71%) |

No, sample size; s, survival (%). Means within rows followed by the same letters are not significantly different (*P* < 0.05, Tukey).

Table 2. Lower temperature threshold (*T*<sub>min</sub> ± SE) and thermal constant (*K* ± SE) of immature stages of *Chilo suppressalis* estimated by linear models

| Stage               | Regression | *T*<sub>min</sub> | *K* | *R*<sup>2</sup> | *R*<sup>2</sup><sub>adj</sub> | *P* |
|---------------------|------------|-------------------|-----|--------------|----------------|-----|
| Traditional linear model |            |                  |     |              |                |     |
| Egg                 | 1/D = −0.144 + 0.0128T | 11.25 ± 1.94 | 78.13 ± 12.0 | 97.4% | 96.5% | 0.002 |
| Larva               | 1/D = −0.0129 + 0.00150 T | 8.60 ± 0.32 | 666.67 ± 57.55 | 98.3% | 97.7% | 0.001 |
| Pupa                | 1/D = −0.115 + 0.00897 T | 12.82 ± 0.47 | 111.48 ± 5.25 | 99.3% | 99.1% | 0.000 |
| Immature stage      | 1/D = −0.0119 + 0.00119 T | 10.0 ± 0.42 | 840.34 ± 39.19 | 99.7% | 99.6% | 0.000 |
| Ikemoto–Takai linear model |        |                  |     |              |                |     |
| Egg                 | DT = 71.70 ± 12.3 D | 12.3 ± 0.98 | 71.7 ± 6.90 | 99.1% | 98.8% | 0.000 |
| Larva               | DT = 679.0 ± 8.35 D | 8.35 ± 1.03 | 679.0 ± 47.31 | 95.70% | 94.2% | 0.000 |
| Pupa                | DT = 110.0 ± 13.0 D | 13.0 ± 0.36 | 110.0 ± 4.27 | 99.8% | 99.7% | 0.000 |
| Immature stage      | DT = 848.0 ± 9.92 D | 9.92 ± 0.37 | 848.0 ± 24.24 | 99.6% | 99.5% | 0.000 |
34°C as the stress temperature for short- and long-term periods. Activity of CAT was the highest in the larvae exposed to the short-term period of 34°C. Also, the enzyme had the higher activity than control in all larval preparations (total, hemolymph, fat body, gut) (Fig. 3). No significant differences of POX activity were observed in hemolymph and gut preparations of control and 34°C exposed larvae but the enzymatic activity was the highest in the larvae exposed to 34°C in both periods compared to control (Fig. 3). Total body, fat body and gut preparations of the larvae exposed to 34°C in short-term period showed the highest activity of SOD compared to control and long-term exposure. Although control larvae had the lowest activity of SOD compared to thermal stressed larvae but no significant differences were observed between short- and long-term exposures to 34°C (Fig. 3).

The activity of APOX was the highest in the *C. suppressalis* larvae exposed to 34°C in the short-term period for all preparations compared to control and log-term exposure (Fig. 4). Similar trend was observed in the activity of GPDH but no significant differences were found in the enzymatic activities between control and long-term exposed larvae (Fig. 4). The larvae exposed to 34°C in short-term period had the highest amount of MDA compared to control and long-term exposed larvae as the similar results on RSSR/RSH ratio (Fig. 5).

### Discussion

In agricultural entomology, the appropriate control techniques are primarily dependent on a thorough understanding of pest phenology, prediction of growth, and the relationship between temperature and development. On the other hand, pest monitoring is a pivotal component of pest management program, which can provide reliable and valuable information for predicting the time and rate of pest damages (Legg et al. 2000, Karimi-Malati et al. 2014). In our study, the two linear models of conventional and Ikemoto-Takai were appropriate to calculate the low temperature thresholds of *C. suppressalis* because of the high values of 97.85, 92.62, 96.45, 94.91, 92.11, and 99.38 for overall immature stages using Analytis, Briere-2, Lactin-2, Logan-6, Logan-10, and SSI models. The lower developmental thresholds (*T*~low~) of 9.15, 9.57, and 10.0°C were found for the overall immature stages of *C. suppressalis* estimated by Analytis, Briere-2, and Lactin-2 models, respectively (Table 3) while the *T*~opt~ value was evaluated as 11.37°C by SSI model. Analytis, Briere-2, Lactin-2, Logan-6, Logan-10 and SSI models calculated the *T*~fast~ values of 33.80, 33.70, 33.70, 33.80, 33.40 and 33.0°C whereas the *T*~opt~ values calculated by SSI model were 23.30, 26.32, 23.63, and 24.42°C for egg, larvae, pupa, and overall immature stages of *C. suppressalis* (Table 3).

**Antioxidant Responses**

Figure 3 shows the activities of CAT, POX, and SOD in the total body and different tissues of *C. suppressalis* larvae exposed to 34°C as the stress temperature for short- and long-term periods. Activity of CAT was the highest in the larvae exposed to the short-term period of 34°C. Also, the enzyme had the higher activity than control in all larval preparations (total, hemolymph, fat body, gut) (Fig. 3). No significant differences of POX activity were observed in hemolymph and gut preparations of control and 34°C exposed larvae but the enzymatic activity was the highest in the larvae exposed to 34°C in both periods compared to control (Fig. 3). Total body, fat body and gut preparations of the larvae exposed to 34°C in short-term period showed the highest activity of SOD compared to control and long-term exposure. Although control larvae had the lowest activity of SOD compared to thermal stressed larvae but no significant differences were observed between short- and long-term exposures to 34°C (Fig. 3).

The activity of APOX was the highest in the *C. suppressalis* larvae exposed to 34°C in the short-term period for all preparations compared to control and log-term exposure (Fig. 4). Similar trend was observed in the activity of GPDH but no significant differences were found in the enzymatic activities between control and long-term exposed larvae (Fig. 4). The larvae exposed to 34°C in short-term period had the highest amount of MDA compared to control and long-term exposed larvae as the similar results on RSSR/RSH ratio (Fig. 5).

**Nonlinear relationship of development rate in different developmental stages of *C. suppressalis* was fitted by several nonlinear models. Many of these models, in addition to low- growth estimates, are able to estimate high temperatures and temperatures in which occurred the fastest growth rates (*T*~fast~). In practice, it is difficult to determine these points because the high mortality rate often occurs at high temperatures and it is therefore based on a relatively small number of insects. In *T*~fast~ although the insect developmental period reaches the shortest possible time, it is inequivalent to the favorable temperature for the insect. At *T*~fast~, the highest developmental rate is associated with a very high mortality rate while at optimal temperatures,
favorable conditions for population growth are associated with the lowest mortality. In fact, the optimum temperature estimated by SSI model was the temperature at which the enzymes had the highest activity. In our study, the amount of minimum temperatures calculated by the SSI model was closer to our results in the laboratory. The maximum thresholds estimated by all the nonlinear models used in this study were able to estimate the high temperature threshold for the whole immature period.

Laboratory observations in the present study indicated that no egg hatch occurred at 36°C. Logan-10, Logan-6, Lactin-2, Briere-2, Analytis, and SSI models succeeded in estimating the high-temperature threshold. As can be deduced from the data in Table 3 and Fig. 2, SSI, Analytis and Lactin-2 models fitted with the data of developmental rate. Hence, it seems that the SSI model can be used to forecast accurately occurrence of the pest life stages in rice fields.

Table 3. Estimated parameters and goodness of the nonlinear models fitting to developmental rates of *C. suppressalis*

| Model  | Parameters | Egg          | Larva        | Pupa          | Immature     |
|--------|------------|--------------|--------------|---------------|--------------|
|        | *A*        | 572.42 × 10⁻⁴| 1.10 × 10⁻³  | 212.80 × 10⁻⁵| 7.49 × 10⁻⁴  |
|        | *Tₐₜₕ*    | 13.09        | 10.53        | 12.01         | 9.15         |
|        | *Tₐₜₕ*    | 36.75        | 35.0         | 35.0          | 35.12        |
|        | *M*        | 1.14         | 1.07         | 1.38          | 1.10         |
|        | *Tₐₜₕ*    | 0.28         | 0.12         | 0.19          | 0.06         |
|        | *P*        | 0.000        | 0.001        | 0.003         | 0.000        |
|        | *R₂*       | 97.83        | 94.91        | 99.09         | 98.28        |
|        | *R₁ₕ*     | 97.40        | 93.64        | 93.12         | 97.85        |
| Briere-2| *A*        | 15.90 × 10⁻⁵| 3.49 × 10⁻⁵  | 23.46 × 10⁻⁵| 3.37 × 10⁻⁵  |
|        | *D*        | 1.94         | 3.21         | 10.0          | 10.0         |
|        | *Tₐₜₕ*    | 11.94        | 11.27        | 12.0          | 9.57         |
|        | *Tₐₜₕ*    | 38.0         | 35.65        | 34.9          | 34.66        |
|        | *M*        | 31.70        | 32.50        | 34.90         | 33.30        |
|        | *P*        | 0.000        | 0.006        | 0.001         | 0.001        |
|        | *R₂*       | 97.52        | 87.49        | 94.76         | 94.10        |
|        | *R₁ₕ*     | 97.03        | 84.37        | 93.45         | 92.62        |
| Lactin-2| *P*        | 992.90 × 10⁻⁵| 1.56 × 10⁻³  | 764.48 × 10⁻⁵| 1.15 × 10⁻³  |
|        | *∆T*       | 0.81         | 0.48         | 1.00          | 0.10         |
|        | *λ*        | -1.10        | -1.02        | -1.10         | -1.01        |
|        | *Tₐₜₕ*    | 36.63        | 36.40        | 37.42         | 34.56        |
|        | *M*        | 9.50         | 9.90         | 12.70         | 10.0         |
|        | *P*        | 0.000        | 0.003        | 0.000         | 0.000        |
|        | *R₂*       | 93.26        | 91.50        | 99.30         | 97.16        |
|        | *R₁ₕ*     | 96.45        | 99.13        | 99.13         | 96.45        |
| Logan-6 | *d*        | 6.48         | 0.05         | 5.65          | 0.05         |
|        | *ψ*        | 713.13 × 10⁻³| 7.51 × 10⁻³  | 1046.38 × 10⁻¹| 4.20 × 10⁻³  |
|        | *P*        | 0.15         | 0.05         | 0.18          | 0.06         |
|        | *Tₐₜₕ*    | 37.96        | 34.10        | 37.58         | 34.11        |
|        | *M*        | 31.50        | 33.80        | 31.90         | 33.80        |
|        | *P*        | 0.000        | 0.001        | 0.000         | 0.000        |
|        | *R₂*       | 93.00        | 93.00        | 98.87         | 95.92        |
|        | *R₁ₕ*     | 94.91        | 95.92        | 94.91         | 94.91        |
| Logan-10| *d*        | 0.40         | 0.14         | 0.05          | 0.30         |
|        | *ψ*        | 71.31 × 10⁻³ | 7.51 × 10⁻³  | 1046.38 × 10⁻¹| 4.20 × 10⁻³  |
|        | *P*        | 0.15         | 0.05         | 0.18          | 0.06         |
|        | *Tₐₜₕ*    | 34.88        | 31.50        | 33.80         | 31.90        |
|        | *M*        | 33.20        | 33.60        | 37.40         | 33.40        |
|        | *P*        | 0.000        | 0.001        | 0.002         | 0.001        |
|        | *R₂*       | 98.18        | 92.98        | 92.11         | 93.68        |
|        | *R₁ₕ*     | 97.81        | 91.23        | 90.14         | 92.11        |
| SSI    | *ρ*ₕ       | 0.15         | 0.03         | 0.10          | 0.02         |
|        | *Tₐₜₕ*    | 23.30        | 26.32        | 23.63         | 24.42        |
|        | *Tₐₜₕ*    | 15.89        | 8.33         | 15.62         | 11.37        |
|        | *M*        | 35.34        | 35.38        | 34.81         | 36.84        |
|        | *ΔHₕ*     | 15286.14     | 11264.81     | 16520.96      | 12595.6      |
|        | *ΔHₕ*     | -124974.0    | -52106.5     | -112074.0     | -61667.7     |
|        | *ΔHₕ*     | 74192.16     | 123182.4     | 524090.6      | 73163.43     |
|        | *Tₐₜₕ*    | 31.80        | 33.60        | 31.80         | 33.0         |
|        | *Xₕ*       | 0.002        | 1.4 × 10⁻⁴   | 0.001         | 7.27 × 10⁻⁵  |
|        | *R₂*       | 98.80        | 98.97        | 98.82         | 99.38        |

The bold values are indicating to attention of reviewers.
SOD is a major antioxidant component against superoxide radicals which catalyzes the breakdown of superoxide anions and transforms them into hydrogen peroxide and oxygen (Zelko et al. 2002). In accordance, the two other enzymes known as catalase (CAT) and peroxidase (POX) destroy hydrogen peroxide in the stressed tissues or organisms (Gaetani et al. 1996, Halliwell 1999). Our results showed that the activities of SOD, POX, and CAT increased in both short- and long-terms exposures of *C. suppressalis* larvae to 34°C than control; however, the levels of increase varied among different tissues. Jia et al. (2011) showed that the activities of CAT and POX significantly increased in *Bacterocera dorsalis* (Hendel; Diptera: Tephritidae) under temperature extremes. Cui et al. (2011) indicated that thermal stress significantly increased the amount of ROS and activities of SOD and CAT in the hemocytes of

**Fig. 2.** Fitting the nonlinear models based on the developmental rates of *Chilo suppressalis*. (a) Analytis, (b) Logan-6, (c) Logan-10, (d) Briere, (e) Lactin-2, (f) SSI (*) observed data. SSI model (O) indicates data points outside the range of the linear model. □ denotes the predicted developmental rates at TL, Topt, and TH.
C. suppressalis larvae. Jena et al. (2013) investigated the effect of temperature stresses in different time periods on Antheraea mylitta (Drury; Lepidoptera: Saturnidae) by exposing the pupae at temperatures of 35 and 40°C for 2, 4, and 6 d. The authors found the higher activity of CAT in all treatments compared to control while the significant increase of SOD activity was observed only after 2 d of exposure. It has been shown that temperature stress (37°C) on Propylaea japonica (Mulsant; Coleoptera: Coccinellidae) increased the activity of POX compared to control (25°C), although no significant effect was found on POX and SOD. Further, the temperatures of 39 and 41°C significantly enhanced the activities of all three enzymes of CAT, POX, and SOD compared to control (Zhang et al. 2015). In our study, increased activities of SOD, CAT, and POX in the short- and long-term exposures may be attributed to the higher production of reactive oxygen species due to temperature stresses of the larvae. SOD causes the conversion of radical superoxide to hydrogen peroxide, which is subsequently metabolized by catalase in peroxisomes and APOX in the cytoplasm, mitochondria,

![Fig. 3. Activities of Catalase, Peroxidase, and SOD in the different tissues of Chilo suppressalis larvae exposed to 24°C (Control) and 34°C (short- and long-term). Values are means ± SE (n = 3). Statistical differences have been marked by the different letters in each sample preparation (Tukey, P ≤ 0.05).](https://academic.oup.com/jinsectscience/article-abstract/18/2/35/4956169)
and chloroplasts. Since hydrogen peroxide is a substrate of catalase and peroxidase, the higher activity of CAT can be deduced from the production of hydrogen peroxide in the treated larvae by temperature or activity of SOD. In addition, due to the activity of SOD, it can be concluded that the short-term and long-term stresses act as an inducer and, by increasing the activity of antioxidant enzymes, prevent the oxidative explosion in larvae to moderate the level of hydrogen peroxide. The significant increase in peroxidase activity of whole body and fat body of the exposed larvae to short- and long-term periods is definitely due to the higher level of ROS. In contrast the lack of significant increase in hemolymph and gut preparations can also be attributed to the low level of ROS present in the tissues to induce the enzyme or to occupy the active site of the enzyme due to excessive concentrations of ROS and subsequent enzymatic inactivation, which requires further investigation. APOX is an enzyme that decomposes hydrogen peroxide by the concurrent oxidation of ascorbate (Asada 1984). While GPDH is an essential enzyme for oxidation-reduction and decontamination of oxidant agents. In the face of increased levels of free radicals due to stresses like temperature, the higher activity of GPDH implies on the higher production of NADPH to neutralize the products of APOX activity (Mardani-Talae et al. 2016). Also, NADPH deactivates electrons to free radicals, thereby reducing their toxic effects (Nation 2008).

The ratio of oxidized- to reduced thiols (RSSR/RSH) is an indicator of oxidative stress following oxidation of free radicals by antioxidant system of organism (Dubovsky et al. 2008). However, the formation of active oxygen species in different tissues can lead to peroxidation of the membrane lipids, which leads to the higher amount of MDA, indicates the destruction and increase of cell membrane permeability (Wang et al. 2001). MDA is a peroxidation product of unsaturated fatty acids in phospholipids, therefore, it should be considered as a reagent to investigate membrane injuries under stress conditions (Rael et al. 2004) hence our results may indicate that thermal stress has been associated with lipid peroxidation in insects like C. suppressalis (An and Choi 2010, Yang et al. 2010).

The results of our study determined the optimal and stress temperatures of C. suppressalis using several mathematical models. Additionally, the antioxidant responses of larvae to thermal stress was investigated in short and long terms by evaluating enzymatic and non-enzymatic compounds within different tissues. The data presented here are new and useful for the knowledge of biology needs and the spread of C. suppressalis in the paddy fields of Iran. The determination of antioxidant capacity could justify population increase during August in Iran’s rice fields. This project will continue with the success of the defense compatibility with the pathogenic fungi and its potential or weakness in rejection of microbial agents.
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