Modeling Temperature-Dependent Development of *Glyphodes pyloalis* (Lepidoptera: Pyralidae)

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Abstract

Development of *Glyphodes pyloalis* Walker was studied under laboratory conditions at constant temperatures of 12, 16, 20, 24, 28, 30, 32, and 36 °C. No development occurred at 36 °C. Although eggs hatched at 12 °C, no larvae were capable of developing to adult stage. At 16 °C, survival rate was low (4%) and prepupal stage lasted 101.68 ± 11.03 d. Larvae completed development through six stadia at 16, 30, and 32 °C. Developmental time of overall immature stages varied from 46.62 d at 20 °C to 22.04 d at 30 °C and increased at 32 °C. The lower temperature thresholds of 10.30 and 11.22 °C, and thermal constants of 429.18 and 401.88 DD were estimated by traditional and Ikemoto–Takai linear models, respectively. The $T_{\text{min}}$ values estimated by Analytis, Briere-2, Lactin-2, and Sharpe–Schoolfield–Ikemoto (SSI) for overall immature stages were 12.40, 12.92, 9.00, and 13.04 °C, respectively. The fastest development temperatures ($T_{\text{f}}$) of 31.1, 31.1, 30.8, and 30.7 °C were estimated for overall immature stages based on Analytis, Briere-2, Lactin-2, and SSI, respectively. The intrinsic optimum temperature ($T_{\text{opt}}$) estimated from the thermodynamic SSI model for total developmental time was 24.63 °C, in which the maximal active state enzymes involved in developmental process. The nonlinear models of Analytis, Lactin-2, Briere-2, and SSI estimated the upper temperature thresholds ($T_{\text{max}}$) at 36.66, 35.97, 38.88, and 34.05 °C, respectively. These findings could be used to predict the population dynamics of *G. pyloalis* for an effective management.

Key words: degree day, *Glyphodes pyloalis*, temperature threshold, thermal model

The lesser mulberry pyralid, *Glyphodes pyloalis* Walker (Lepidoptera: Pyralidae), is a specialist pest on mulberry (*Morus* spp.) and is widely distributed throughout Asia, where the species causes serious damage to sericulture not only by its larval grazing on leaves but also by transmission of some viral diseases infectious to the silkworm (*Watanabe et al. 1988, Madyarov et al. 2006*). On the other hand, *G. pyloalis* becomes a major pest of mulberry as shade trees in urban area (*Kumar et al. 2002*). Recently, this pest has caused severe damage to mulberry plantations in northern Iran especially Guilan province. The leaf area eaten by the first and second instar larvae is negligible, but feeding increases in later instars, and fifth instar larvae feed whole leaf and finally only the ribs remain (*Khosravi and Jalali Sendi 2010*). Since the larvae of the pest defoliate mulberry and finally lead to plant death, some investigations were done to know its biological parameters and control tools. *Khosravi and Jalali Sendi (2010)* studied the demographic parameters of *G. pyloalis* and its behavioral aspects. *Yazdani et al. (2014)* stated that the essential oils of *Thymus vulgaris* L. and *Origanum vulgare* L. were effective for *G. pyloalis* control through disturbance on activity of macromolecules, digestive and detoxifying enzymes. Moreover, the effects of different mulberry varieties on the nutritional indices of *G. pyloalis* larvae (*Oftadeh et al. 2014*), as well as its life table parameters (*Oftadeh et al. 2015*) were determined under laboratory conditions. Furthermore, the influence of abiotic climate factors on incidence and severity (*Ramegowda et al. 2012*) and damage rate of *G. pyloalis* (*Borgohain et al. 2015*) was described to evolve a successful IPM program. According to *Borgohain et al. (2015)*, the evening relative humidity and minimum temperature had significant positive effects on occurrence of *G. pyloalis*.

It should be considered that among the climatic factors, temperature is the most important, as it has profound influence on the development and survival of insects. The insect developmental rate, as poikilothermic organism, is affected by the temperature to which insects are exposed (*Davidson 1944, Campbell et al. 1974*). In fact, temperature is a critical factor that influences pest biology, distribution and abundance, as well as its population dynamics (*Braman et al. 1984, Tobin et al. 2003, Zahiri et al. 2010*). Attempts to quantify the effects of temperature on developmental rate, growth, fecundity and enzyme activities have been carried out by several studies for different insect and mite species (*Kontodimas et al. 2004, Zahiri et al. 2010, Jafari et al. 2012, Karimi-Malati et al. 2014*). In addition, a variety of temperature-driven rate models have been

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proposed to describe the relationship between temperature and insect development (Sharpe and DeMichele 1977; Analytis 1981; Schoolfield et al. 1981; Lactin et al. 1995; Briere et al. 1999; Shi et al. 2011a,b). Several studies revealed that there is no development at temperatures below the lower threshold. While as temperature rises, developmental rates increase up to an optimum temperature, above which they again decrease and eventually cease at their upper threshold (Sharpe and DeMichele 1977, Analytis 1981, Briere et al. 1999). Based on linear models, lower temperature threshold and thermal constant can be estimated at moderate temperatures. However, linear models proved insecure in predicting developmental rate near extreme conditions, therefore, nonlinear models have been proposed to describe developmental rate response curves over the broad range of temperatures (Wagner et al. 1984).

Although different climate factors affecting occurrence and infestation of G. pyloalis were considered (Ramegowda et al. 2012, Borgohain et al. 2015), no information exists on the relationship of its developmental rate and temperature. This study was conducted to assess the developmental rate of G. pyloalis at eight constant temperatures and estimate the temperature thresholds and thermal requirements, which would be useful in developing models for predicting its distribution and abundance. Predicting the seasonal occurrence of G. pyloalis based on climate factors such as temperature is essential for its accurate scheduling of census samples and control tactics. Two linear and four nonlinear models were used for estimating accurate thermal constant and temperature thresholds of G. pyloalis, which would be useful in developing phenological models and constructing an effective pest management program.

Materials and Methods

Rearing Methods

The larvae of G. pyloalis were collected from mulberry trees in Rasht, Guilan province, Iran during 2015. They were reared at laboratory conditions at 25 ± 1 ºC and 70 ± 10% RH, with a photoperiod of 16:8 L:D h on fresh mulberry leaves. To obtain the same aged eggs, female and male moths (15 pairs) were kept inside the oviposition containers (50 × 50 × 50 cm) with a 10% honey solution on cotton wool for feeding and mulberry leaves for oviposition.

Development and Survivorship of Immature Stages

After mating and oviposition, one hundred to 300 (depending thermal treatment) freshly laid eggs (<24 h old) were transferred to plastic boxes (18 × 15 × 7 cm) with wet cotton wool in growth chambers at eight constant temperatures of 12, 16, 20, 24, 28, 30, 32, and 36 ± 1 ºC at 70 ± 10% R.H. and photoperiod of 16:8 L:D h. Changing in shape and color of eggs was monitored daily under the stereomicroscope. Incubation period and hatching rate were recorded.

The newly hatched larvae were placed individually in plastic containers (7 × 8 × 3 cm) with a hole in their lids covered by a fine mesh to provide ventilation. The petioles of mulberry leaves were kept in tubes containing water to keep the cutting leaves as fresh as possible. The leaves were replaced every other day for larvae at 16–24 ºC and daily for those larvae at 28–32 ºC because plant desiccation occurred faster than lower temperatures. The larvae were checked and the instars were regularly recorded using the exuviae of larval head capsules. The matured larvae changed color from green to purple and began making fine cocoons considering prepupal stage. After pupation, they were slipcovered and sexes were determined based on morphological characters of pupal last abdominal segment. After that they were replaced in their fine cocoons. The cocooned pupae were checked and the emerged adults recorded daily. Developmental time of different and overall immature stages was recorded based on regular observations with 24 h intervals.

Thermal Models

The reciprocal of developmental time for different stages of G. pyloalis was calculated to obtain the developmental rate. Two linear, traditional and Ikemoto–Takai models were applied to estimate the temperature-dependent development of egg, larval, prepupal, pupal, and total immature stages of G. pyloalis on mulberry leaves. The traditional and Ikemoto–Takai models are as follows, respectively:

\[
\frac{1}{D} = \frac{T_{\text{min}} - T}{K} + \frac{T}{K} \quad (1)
\]

\[
DT = K + T_{\text{min}}D \quad (2)
\]

where \(D\) is the duration of development (days), \(T\) is the ambient temperature, \(T_{\text{min}}\) is the lower temperature threshold, and \(K\) is the thermal constant (degree day, DD).

The latter function is a new linearized formula was proposed by Ikemoto and Takai (2000). Ikemoto and Takai (2000) particularized some problems regarding the traditional linear model would result in a lower \(T_{\text{min}}\) and larger \(K\), hence, equation (2) is derived from the traditional linear model to obtain more reliable estimates of the parameters.

It should be considered that the relationship between temperatures and developmental rate is curvilinear near lower and upper temperature thresholds. To describe the developmental rate over a wider temperature range, four nonlinear models including Analytis, Briere-2, Lactin-2, and Sharpe-Schoolfield-Ikemoto (SSI) were chosen (Analytis 1981, Lactin et al. 1995, Briere et al. 1999, Shi et al. 2011b). These four mentioned nonlinear formulations are as follows, respectively:

\[
\frac{1}{D} = a \times (T - T_{\text{min}})^{n} \times (T_{\text{max}} - T)^{m} \quad (3)
\]

\[
\frac{1}{D} = a \times T(T - T_{\text{min}}) \times (T_{\text{max}} - T)^{1/d} \quad (4)
\]

\[
\frac{1}{D} = \exp(p \times T) - \exp \left( p \times T_{\text{max}} - \frac{T_{\text{min}} - T}{\Delta T} \right) + \lambda \quad (5)
\]

where \(T_{\text{min}}\) is the lower temperature threshold, \(T_{\text{max}}\) is the upper temperature threshold, \(a, d, n, m, p, \lambda\), and \(\Delta T\) are fitted coefficients (Analytis 1981, Briere et al. 1999, Roy et al. 2002, Kontodimas et al. 2004). In addition, the SSI model was used in this research which is closely related to the impact of temperature on the enzyme. Using SSI model enable researchers to estimate the intrinsic optimum temperature \((T_{\text{opt}})\) in which the population size is maximal with a low mortality (Ikemoto 2005, 2008, Shi et al. 2011b). Ikemoto (2005) and Shi et al. (2011b) demonstrated that the intrinsic optimum temperature \((T_{\text{opt}})\) should represent a temperature at which the mortality of insects is very low, and that the net reproduction rate is generally highest. In fact, \(T_{\text{opt}}\) is different from \(T_{\text{las}}\) that makes insects develop fastest within shortest duration:

\[
\rho_{b} = \frac{T_{\text{opt}}}{T_{\text{opt}}} \times \exp(\Delta H_{A}/R \times ((1/T_{\text{opt}}) - (1/T))) \quad (6)
\]

where \(\rho_{b}\) is the mean developmental rate at \(T_{\text{opt}}\) (1/d), \(T_{\text{opt}}\) is the intrinsic optimum temperature at which the probability of an enzyme being in the active state is maximal. \(\Delta H_{A}\), \(\Delta H_{C}\), and \(\Delta H_{T}\) 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), \( T_e \) is the temperature at which the enzyme is 1/2 active and
1/2 low temperature inactive, and \( T_{HI} \) is the temperature at which
the enzyme is 1/2 active and 1/2 high temperature inactive (Both in
Kelvin degrees).

Since running the SSI model through Ikemoto (2008) takes 3 h
for an average personal computer, a modified mentioned program
was proposed by Shi et al. (2011b) to speed up the estimation of
model parameters.

**Critical Temperatures and Parameter Estimation**

Critical temperatures and thermal requirement of *G. pyloalis*
were estimated by above-mentioned models.

The lower temperature threshold (\( T_{min} \)), the temperature below
which different stages did not develop. The standard error (SE) of
\( T_{min} \) calculated from the linear models is

\[
SE_{T_{min}} = \frac{S}{E} \times \sqrt{\frac{S^2}{N} + \left(\frac{SE_a}{E}\right)^2}
\]  

[7]

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 (\( T_{max} \)), the temperature above
which the life cannot be maintained for any significant period
(Kontodimas et al. 2004). This value was estimated only by the non-
linear models.

The fastest development temperature (\( T_{fast} \)), defined as the tem-
perature at which the highest developmental rate was recorded.
However, the fitness of population is usually not maximal because
of the higher mortality at \( T_{fast} \).

| Stage     | Temperature (°C) | 16  | 20  | 24  | 28  | 30  | 32  |
|-----------|-----------------|-----|-----|-----|-----|-----|-----|
| Egg       |                 | 9.75±0.07a | 6.52±0.04b | 4.76±0.04c | 3.71±0.05d | 3.00±0.00e | 3.00±0.00e |
|           | 20 (65.71)      | 150 (70.38) | 107 (83.53) | 80 (87.50) | 106 (77.36) | 84 (61.90) |
| Larva I   |                 | 8.92±0.18a | 4.97±0.09b | 3.15±0.07c | 2.38±0.10d | 2.00±0.00e | 2.45±0.10d |
| no (s)    | 97 (91.75)      | 78 (85.90) | 89 (100) | 59 (100) | 82 (100) | 52 (100) |
| Larva II  |                 | 6.48±0.14a | 3.68±0.10b | 2.41±0.06c | 2.00±0.04d | 1.04±0.03e | 1.84±0.10d |
| no (s)    | 89 (94.38)      | 67 (98.51) | 89 (97.75) | 59 (94.92) | 82 (100) | 52 (100) |
| Larva III |                 | 6.18±0.13a | 4.00±0.12b | 2.15±0.05c | 2.06±0.03cd | 1.76±0.06ed | 1.95±0.10cd |
| no (s)    | 84 (90.48)      | 66 (93.94) | 87 (97.70) | 56 (100) | 82 (95.12) | 52 (98.08) |
| Larva IV  |                 | 6.72±0.17a | 5.53±0.15b | 2.64±0.07c | 2.44±0.07cd | 1.88±0.05e | 2.00±0.08de |
| no (s)    | 76 (85.53)      | 62 (96.77) | 85 (98.82) | 56 (94.64) | 78 (94.87) | 51 (100) |
| Larva V   |                 | 8.22±0.16a | 6.18±0.13b | 3.72±0.08c | 2.87±0.09d | 3.07±0.07ed | 2.74±0.16d |
| no (s)    | 65 (83.08)      | 60 (100) | 84 (96.43) | 53 (98.11) | 74 (93.24) | 51 (86.27) |
| Larva VI  |                 | 8.33±1.33a | –            | –            | –            | 4.50±1.15b | 2.67±0.19b |
| no (s)    | 54 (92.59)      | –            | –            | –            | 69 (98.55) | 44 (86.36) |
| Larva a   |                 | 37.02±0.34a | 24.37±0.31b | 14.06±0.12c | 11.75±0.13d | 10.16±0.18e | 11.89±0.28d |
| no (s)    | 97 (51.55)      | 78 (76.92) | 89 (91.01) | 59 (88.14) | 82 (82.93) | 52 (73.08) |
| Pre pupa b|                 | 101.68±11.03 | 4.64±0.01a | 2.28±0.05b | 1.94±0.03c | 2.11±0.06bc | 2.25±0.19bc |
| no (s)    | 50 (38)         | 60 (83.33) | 81 (96.30) | 52 (100) | 68 (92.65) | 38 (84.21) |
| Pupa b    |                 | 24.67±1.61 | 12.32±0.14a | 8.62±0.07b | 7.08±0.05c | 6.80±0.09c | 6.14±0.08d |
| no (s)    | 19 (31.57)      | 50 (94) | 78 (87.18) | 52 (98.08) | 63 (85.71) | 32 (65.63) |
| Immature b|                 | 134.33±25.19 | 46.62±0.23a | 29.34±0.17b | 24.47±0.17c | 22.04±0.20d | 22.43±0.25d |

Table 1. Developmental time (means ± SE) and survival of *Glyphodes pyloalis* immature stages at constant temperatures

\[ SE_K = \frac{SE_b}{b^2} \]  

[8]

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

\*At 20, 24, and 28 °C larvae completed development in five stadia.

\*\*Comparing the prepupal, pupal, and total developmental times was done without considering of the temperature at 16 °C.

Thermal constant (\( K \)), the amount of thermal energy (DD)
needed to complete development of different stages. The thermal
constant can be estimated only by the linear equation. The SE of \( K \)
was estimated by using the following equation (Campbell et al.
1974, Kontodimas et al. 2004).

**Statistical Analysis**

Normality of distribution was checked with the Kolmogorov–
Smirnov test before comparative analyses were performed. Effect of
temperature on developmental periods of *G. pyloalis* was analyzed
by one-way analysis of variance ANOVA (PROC GLM, SAS
Institute 2007) and means were separated using Tukey Honestly
Significant Difference HSD multiple comparison \((P \leq 0.01)\). The
linear models were analyzed using statistical software MINITAB 16.0
and nonlinear models analyzed using linear and nonlinear platforms
of JMP, v 7.0 (SAS Institute 2007). For estimating the parameters of
the SSI model, a program which runs on R software was used at the
present study (Shi et al. 2011b).

**Results**

**Developmental Time and Mortality**

The mean developmental time of each immature stage of *G. pyloalis*
at six constant temperatures are shown in Table 1. The results of
developmental time and survival rate showed that *G. pyloalis* was
able to complete its life cycle and development at a wide range tem-
perature. In fact, the adults were capable of emergence across a
range of 20–32 °C, whereas few eggs developed to adult stage at
16 °C (with 4% survivorship; only six emerged adults). As far as pre-
pupal stage is concerned, at 16 °C *G. pyloalis* required
101.68 ± 11.03 d to develop to pupal stage maybe due to stop developing (or diapause occurrence) in prepupal stage. For these two reasons, too long duration and low survivorship of prepupal stage both occurred at 16 °C, developmental times of prepupal, pupal, and total immature stages were ignored and comparing the mean duration of above-mentioned stages (prepupal, pupal, and total developmental times) was done without considering of the temperature at 16 °C (Table 1).

According to our results, eggs could hatch after 17.72 ± 0.86 d at 12 °C without any surviving to the next stage and all neonate larvae died. In addition, at 36 °C, no eggs hatched. Developmental time for each stage was significantly influenced by temperature: incubation period (\(F = 2961.97; \text{df} = 5, 742; \ P < 0.0001\)), larval (\(F = 1941.75; \text{df} = 5, 348; \ P < 0.0001\)), prepupal (\(F = 173.14; \text{df} = 4, 274; \ P < 0.0001\)), pupal (\(F = 670.42; \text{df} = 4, 240; \ P < 0.0001\)), and overall immature stages (\(F = 2479.46; \text{df} = 4, 240; \ P < 0.0001\)) (Table 1). The larval developmental time ranged 24.37 ± 0.31 to 10.16 ± 0.18 d at 20 and 30 °C, respectively. Moreover, comparing the number of stadia in larval stage indicated that an extra (sixth) stadium was observed at extreme temperatures (16, 30, and 32 °C). In fact, no larvae required more than five stadia at 20, 24, and 28 °C.

The survival rate of overall immature stages indicated that the lowest survival rate occurred at 16 °C (4%). Although egg hatching occurred at 12 °C, all neonate larvae died due to the exposure to low temperature. Furthermore, survival of total larval stage of G. pyloalis at six constant temperatures revealed that the survival was highest (65%) at 28 °C, followed by 24 °C (Table 1).

### Model Evaluations

The developmental rate of G. pyloalis increased linearly within the examined temperature range (20–30 °C). Developmental time at >30 °C (32 °C) was outside the linear segment of the growth curve and therefore excluded from the linear regression. Results of parameter estimation of linear models (traditional and Ikemoto–Takai), coefficients of determination (\(R^2\) and \(R^2_{\text{adj}}\)), lower temperature thresholds and thermal constants are presented in Table 2. The estimated lower temperature thresholds for total developmental time were 10.30 and 11.22 °C, while the thermal constants were 429.18 and 401.88 DD, using the traditional and Ikemoto–Takai linear models, respectively. The thermal requirements were lowest at the prepupal stage and the highest at the larval stage. The curves of influence of temperature on developmental rate of overall immature stages fitted by two linear models are shown in Fig. 1.

Four nonlinear models (Analytis, Briere-2, Lactin-2, and SSI) were fitted to the data on developmental rate of egg, larval, prepupal, pupal, and overall immature stages of G. pyloalis at the temperature range from 20 to 32 °C (Table 3). The values of \(R^2_{\text{adj}}\) were

![Fig. 1. Fitting the linear models (line) to observed developmental rates (×) of Glyphodes pyloalis.](image-url)

| Stage                  | Regression equation | \(R^2\)% | \(R^2_{\text{adj}}\)% | \(K\) | \(T_{\text{min}}\) |
|------------------------|---------------------|----------|-------------------------|-------|---------------------|
| Traditional linear     |                     |          |                         |       |                     |
| Egg                    | \(1/D = -0.197 + 0.0172 T\) | 97.10    | 95.70                   | 11.45 ± 1.77 | 58.14 ± 7.07 |
| Larvae                 | \(1/D = -0.0658 + 0.00548 T\) | 97.60    | 96.40                   | 12.01 ± 1.54 | 182.48 ± 20.16 |
| Prepupa                | \(1/D = -0.508 + 0.0374 T\) | 92.65    | 85.30                   | 13.58 ± 5.87 | 26.74 ± 13.87 |
| Pupa                   | \(1/D = -0.0786 + 0.00801 T\) | 99.14    | 98.70                   | 9.81 ± 2.02 | 124.84 ± 16.27 |
| Immature               | \(1/D = -0.0240 + 0.00233 T\) | 98.06    | 97.09                   | 10.30 ± 1.58 | 429.18 ± 43.09 |

Ikemoto–Takai linear

| Stage       | Regression equation | \(R^2\)% | \(R^2_{\text{adj}}\)% | \(K\) | \(T_{\text{min}}\) |
|-------------|---------------------|----------|-------------------------|-------|---------------------|
| Egg         | \(DT = 60.278 + 10.977 D\) | 97.23    | 95.85                   | 10.98 ± 1.3 | 60.28 ± 6.14 |
| Larvae      | \(DT = 170.22 + 12.89 D\) | 98.68    | 98.02                   | 12.89 ± 1.05 | 170.22 ± 16.92 |
| Prepupa     | \(DT = 23.19 + 14.9 D\) | 98.86    | 97.71                   | 14.93 ± 1.60 | 23.19 ± 5.12 |
| Pupa        | \(DT = 124.14 + 9.89 D\) | 98.81    | 98.21                   | 9.89 ± 0.76 | 124.14 ± 6.79 |
| Immature    | \(DT = 401.88 + 11.22 D\) | 97.93    | 96.89                   | 11.22 ± 1.15 | 401.88 ± 37.04 |

Developmental times at 16 and 34 °C were excluded from linear regressions.
Analytis

Model Parameters Egg Larva Prepupa Pupa Immature

Table 3. Estimated parameters and goodness of fit of the nonlinear models fitting to developmental rates of *Glycophylos pyloalis*

| Model | Parameters | Egg | Larva | Prepupa | Pupa | Immature |
|-------|------------|-----|-------|---------|------|----------|
| Analytis | $a$ | 0.0180805941 | 0.0093445459 | 0.0026737994 | 0.0099970236 | 0.00006334287 |
| | $T_{\text{min}}$ | 12.087979091 | 14.55 | 15.977576718 | 10.953642573 | 12.4 |
| | $T_{\text{max}}$ | 32 | 32.002136251 | 37.028156352 | 32 | 36.659062923 |
| | $n$ | 0.9971826195 | 0.8459044687 | 1.295953193 | 0.944708698 | 1.2456828095 |
| | $m$ | 0.0020776935 | 0.0360820395 | 0.9232286618 | 0.0026302548 | 0.3586178111 |
| | $T_{\text{est}}$ | 31.9 | 31.9 | 28.3 | 31.9 | 31.1 |
| | $R^2_{\text{adj}}$ | 0.9711 | 0.9782 | 0.9465 | 0.9907 | 0.9898 |
| Briere-2 | $a$ | 0.0006457008 | 0.0000707783 | 0.0002463715 | 0.0002935356 | 0.000035978 |
| | $d$ | -443.286614 | 1.7128474553 | 1.1378065837 | -1.039928966 | 1.1992415702 |
| | $T_{\text{min}}$ | 12.85 | 14.159022666 | 16.037151313 | 9.75530105 | 12.92356455 |
| | $T_{\text{max}}$ | 32.1111 | 35.649026102 | 36.01026167 | 30.77 | 35.968777593 |
| | $T_{\text{est}}$ | 32.9 | 30.4 | 27.7 | 31.9 | 31.1 |
| | $R^2_{\text{adj}}$ | 0.9529 | 0.9548 | 0.9655 | 0.9829 | 0.9817 |
| Lactin-2 | $p$ | 0.0125922236 | 0.0049437231 | 0.1096400671 | 0.0067671533 | 0.1238102145 |
| | $\Delta T$ | 0.0813549794 | 0.7008941528 | 8.687942051 | 0.0778880862 | 8.0661976772 |
| | $\lambda$ | -1.1387397799 | -1.060232293 | -0.509717205 | -1.0630055655 | -0.01478378 |
| | $T_{\text{max}}$ | 32.336013185 | 34.649397346 | 37.653516342 | 32.339177483 | 38.88 |
| | $T_{\text{est}}$ | 31.8 | 14.8 | 11.9 | 31.3 | 30.8 |
| | $R^2_{\text{adj}}$ | 0.9764 | 0.9685 | 0.9326 | 0.9912 | 0.9853 |
| SSI | $\rho$ | 0.28662211 | 0.06756835 | 0.3332183 | 0.1108385 | 0.03337244 |
| | $T_{\text{opt}}$ | 28.20088 | 24.38995 | 22.663 | 23.654 | 24.6338 |
| | $T_{\text{est}}$ | 11.13197 | 12.97607 | 16.9636 | 13.0422 | 13.0422 |
| | $T_{\text{est}}$ | 32.451 | 32.8627 | 31.4021 | 34.0533 | 34.0533 |
| | $\Delta H_{\text{f}}$ | 13.29241 | 15.23667 | 20.31741 | 12.14471 | 13.20504 |
| | $\Delta H_{\text{f}}$ | -76.64364 | -138.1597 | -127.2336 | -143.8497 | -73.2348 |
| | $\Delta H_{\text{f}}$ | 786.2286 | 122.6415 | 76.7569 | 92.3954 | 103.394 |
| | $T_{\text{est}}$ | 31.5 | 30 | 29.1 | 31.3 | 30.7 |
| | $X^2$ | 0.0008039253 | 0.0008813896 | 0.0139181 | 0.00037991 | 0.000274224 |
| | $R^2_{\text{adj}}$ | 0.9827 | 0.9324 | 0.8079 | 0.9797 | 0.9557 |
study confirmed that at 16°C matured larvae developed to prepupae and prepupal developmental time lasted 101.68 d, suggesting that the overwintering matured larvae in Mathur (1980) research might be the same as prepupae. Since Mathur (1980) did not concentrate on the prepupal period of G. pyloalis as a distinct stage, this assumption seems to be presumable. No more information is currently available on overwintering of G. pyloalis, hence probability of hibernation or diapause occurrence in prepupal stage could be proposed cautiously.

The results of the current study indicated that the egg-to-adult developmental time was completed in 29.34 d at 24°C. Based on Khosravi and Jalali Sendi (2010), total developmental time of G. pyloalis were 28.77 and 29.21 d for female and male, respectively. It seems that our findings for total developmental time were consistent with those of Khosravi and Jalali Sendi (2010) at 24°C. Whereas Oftadeh et al. (2015) reported a higher value of total developmental time at 24°C in their study wherein G. pyloalis completed the development from 35.04 to 37.64 d on different mulberry varieties.

As temperature exerts noticeable influence among the climate factors, by directly affecting insect phenology and distribution, most of the models that describe insect development are temperature driven (Wagner et al. 1984). Several models have been proposed to describe developmental rate response curves over the wide range of temperatures, in which the linear model has the advantage of being easy to calculate and is the only model enabling the estimation of the thermal constant (Kontodimas et al. 2004) but it can be measured only at moderate temperatures (Wagner et al. 1984). The current study showed that developmental time of different stages (egg, larva, prepupa, and pupa) of G. pyloalis decreased with increasing temperature from 16 to 30°C, and came out from linear mode at 32°C. Assuming that developmental rate of all immature stages is a linear function of temperature within the 20–30°C range, whereas a nonlinear response occurred at extreme temperature 32°C. Therefore, the data deviated from linearity at 32°C was excluded from linear regressions. Moreover, developmental rate of G. pyloalis at 16°C was omitted because very low survivorship (4%) was observed at this temperature.

According to the results of the present study, the lower developmental threshold for overall immature stages of G. pyloalis was estimated at 10.30 and 11.22°C based on traditional and Ikemoto–Takai linear models, respectively. Both linear models had high values of $R^2$ and $R^2_{adj}$, indicating a high degree of confidence. It should be noted that the higher $T_{min}$ values were estimated by traditional (13.58°C), Ikemoto–Takai (14.93°C), Analytis (15.98°C), Briere-2 (16.04°C), Lactin-2 (14.8°C), and SSI (16.96°C) models for prepupal stage compared with other stages, suggesting that the prepupal stage showed sensitivity to lower temperatures. With regard to higher $T_{min}$ values for prepupal stage of G. pyloalis compared with other (egg, larval, and pupal) stages, the prepupal stage might be assigned as critical stage for diapause or hibernation. Generally, low temperature might enable to stop development and induce hibernation at prepupal stage of G. pyloalis as Mathur (1980) observed.

![Fig. 2. Fitting the nonlinear models to observed developmental rates of Glyphodes pyloalis. (□) observed data. In SSI model (○) indicates data points outside the range of the linear model. (□) denotes the predicted developmental rates at $T_L$, $T_{opt}$, and $T_H$.](image-url)
under field conditions. However, a continued study is necessary to determine different factors affecting diapause and overwintering of *G. pyloalis*, as well as physiological experiments for understanding the hormonal mechanisms responsible for it.

The obtained results of the present study revealed that the thermal constants for overall immature stages were 429.18 and 401.88 DD estimated by traditional and Ikemoto–Takai linear models. Considering that *G. pyloalis* required high thermal constant for completion of entire immature stages, the late incidence of *G. pyloalis* during the post commercial season of mulberry could be justifiable. Ramegowda et al. (2012) and Borgohain et al. (2015) stated that the peak of incidence and severity of *G. pyloalis* were distinct during the late season and the pest damage was limited in spring crop of silkworm. In fact, those results could support our findings on high thermal constant of *G. pyloalis*, explaining some reasons for the pest prolonger in the late spring and summer. So far no information exists on temperature-dependent development of *G. pyloalis* and in the current study its critical temperatures and thermal requirements were estimated for the first time. Hence, further physiological and ecological studies would warrant to quantify the phenology of *G. pyloalis* based on thermal requirements.

Since the linear models is insecure in predicting development in extreme temperatures, several nonlinear models provide critical temperatures such as lower and upper temperature thresholds, fastest development temperature and intrinsic optimum temperature (Analytis 1981, Schoolfield et al. 1981, Lactic et al. 1995, Briere et al. 1999, Ikemoto 2005, Shi et al. 2011b). To describe the developmental rate more realistically and over a wider temperature range, four nonlinear models (Analytis, Briere-2, Lactic-2, and SSI) have been applied in the current investigation. Based on our results, the adjusted coefficients of determination ($R^2_{adj}$) in all mentioned nonlinear models fitting to overall developmental rate were higher than 0.95, suggesting the high degree of confidence in estimated parameters. Nonetheless, to select the models which provide satisfactory fit to observed data, the $R^2_{adj}$ is not sufficient. It should be noticed that although the Lactic-2 gave a good fit to the observed data for total developmental times as indicated by the high values $R^2_{adj}$, the model underestimated the $T_{\text{min}}$ values. Comparing the $T_{\text{min}}$ estimated by Lactic-2 using observed total developmental rate under laboratory conditions indicated that the Lactic-2 did not provide a realistic estimate of this critical temperature. In fact, the Lactic-2 underestimated $T_{\text{min}}$ at 9°C, whereas failure of *G. pyloalis* development was observed at 12°C. Furthermore, $T_{\text{min}}$ of 12.09, 12.85, and 11.13°C for egg stage estimated by the Analytis, Briere-2, and SSI models were strongly provided by experimental observations, in which, eggs of *G. pyloalis* could hatch at 12°C but no neonate larvae survived and developed to next stages. The survivorship of larvae at higher temperatures compared with egg stage resulted in estimating the higher $T_{\text{min}}$ values for larval stage.

Our findings revealed that the Analytis, Briere-2, and SSI models approximately provided satisfactory estimates of $T_{\text{max}}$ (36.66, 35.97, and 34.05°C, respectively) for total immature stages which are consistent with those of experimental observations. Whereas the Lactic-2 overestimated $T_{\text{max}}$ values for overall immature stages of *G. pyloalis* at 38.88°C.

Based on current study, $T_{\text{opt}}$ for overall immature stages at which the highest developmental rates were estimated, ranged 30.7–31.1°C using the Analytis, Briere-2, Lactic-2, and SSI models. These four models seem to provide realistic values of $T_{\text{opt}}$ because the shortest developmental time of *G. pyloalis* was recorded at 30°C under laboratory conditions. Many earlier researchers documented that the temperature, at which the developmental time is shortest, should be considered as the optimal temperature (Ranjbar-Aghdam et al. 2009, Zahiri et al. 2010), ignoring the intrinsic optimum temperature ($T_{\text{opt}}$) has different concepts from $T_{\text{opt}}$. In fact, the temperature at which the population size reaches its maximum is not the temperature ($T_{\text{opt}}$) that can make insects develop fastest with low survival and net reproductive rate. The current study showed that the values of $T_{\text{opt}}$ estimated by SSI model for overall immature stages of *G. pyloalis* was at 24.63°C, although the highest developmental rate was estimated at 30.7°C. Based on thermodynamic concepts of SSI model, at $T_{\text{opt}}$ of 24.63°C determined for overall immature stages, the maximal active state enzymes involved in the developmental process (Shi et al. 2011b, 2012; Padmavathi et al. 2013). The intrinsic optimum temp at which no enzyme inactivation is hypothesized could represent the most important thermal parameter that determine the fitness of an optimum life history strategy for insects. Therefore, it could be proposed to evaluate the life table parameters of *G. pyloalis* at different temperatures because of lack of such information. In that case, the seasonal prediction of the occurrence as well as severity of the pest would be accurately clarified.

Accordingly, the importance of the seasonal occurrence prediction of the pest for developing management strategies has led to different linear and nonlinear models that describe the developmental rate of *G. pyloalis* in relation to temperature. The results of the present study could provide essential information on temperature-dependent development of *G. pyloalis* and its critical temperatures. Using those valuable information with other ecological data such as intrinsic rate of increase, survival rate and climate factors would enable researchers to predict the population dynamics of *G. pyloalis* for applied IPM implementation.

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**References Cited**

Analytis, S. 1981. Relationship between temperature and development times in phytopathogenic fungus and in plant pests: a mathematical model. Agric. Res. (Athens): 5:133–159.

Borgohain, A., J. Battacharjee, L. C. Dutta, B. Bhattacharya, and T. A. Singh. 2015. Influence of climatic factors on infestation and damage of mulberry plant by *Glyphodes pyloalis* Walker in Jorhat (Assam). J. Exp. Zool. India. 18: 821–824.

Braman, S. K., P. E. Sloderbeck, and K. V. Yeargan. 1984. Effects of temperature on the development and survival of *Nabis americoforus* and *N. roseipennis* (Hemiptera: Nalidae). Ann. Entomol. Soc. Am. 77: 592–596.

Briere, J. F., P. Pracros, A. Y. Le Roux, and S. Pierre. 1999. A novel rate model of temperature dependent development for arthropods. Environ. Entomol. 28: 22–29.

Campbell, A., B. D. Frazer, N. Gilbert, A. P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Davidson, J. 1944. On the relationship between temperature and the rate of development of insects at constant temperatures. J. Animal. Ecol. 13: 26–38.
Hon (1996). Geographical variation in thermal requirements for insect development. Eur. J. Entomol. 93: 303–312.

Ikemoto, T. 2005. Intrinsic optimum temperature for development of insects and mites. Environ. Entomol. 34: 1377–1387.

Ikemoto, T. 2008. Tropical malaria does not mean hot environments. J. Med. Entomol. 45: 963–969.

Ikemoto, T., and K. Takai. 2000. A new linearized formula for the law of total effective temperature and the evaluation of fine-fitting methods with both variables subject to error. Environ. Entomol. 29: 671–682.

Jafari, S. H., Y. Fathipour, and F. Faraji. 2012. Temperature-dependent development of Neoseiulus barkeri (Acari: Phytoseiidae) on Tetranychus urticae (Acari: Tetranychidae) at seven constant temperatures. Insect Sci. 19: 220–228.

Karimi-Malati, A., Y. Fathipour, and A. A. Talebi. 2014. Development response of Spodoptera exigua to eight constant temperatures: Linear and nonlinear modeling. J. Asia Pac. Entomol. 17: 349–354.

Khosravi, R., and J. Jalali Sendi. 2010. Biology and demography of Glyphodes pyloalis Walker (Lepidoptera: Pyralidae) on mulberry. J. Asia Pac. Entomol. 13: 273–276.

Kontodimas, D. C., P. A. Eliopoulos, G. J. Stathas, and L. P. Economou. 2004. Comparative temperature-dependent development of Nephus includens (Kirsch) and Nephus ignatutus (Boheman) (Coleoptera: Coccinellidae), preying on Plamococcus citri (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various non-linear models using specific criteria. Environ. Entomol. 33: 1–11.

Kumar, V., V. Kumar, S. Rajadurai, A. M. Babu, R. L. Katiyar, B. K. Kariappa, V. Thiagarajan, and K. P. Jayaswal. 2002. The chronic architecture and shell structure of Diaphania pulverulentalis (Hampson) (Lepidoptera: Pyralidae). Russ. Entomol. J. 11: 307–310.

Lacin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigie. 1995. Improved rate of temperature dependent development by arthropods. Environ. Entomol. 24: 68–75.

Madyarov, S. R., A. S. Khamraev, D. O. Otarbaev, S. G. Kamita, and B. D. Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigie. 1995. Improved rate of temperature dependent development by arthropods. Environ. Entomol. 24: 68–75.

Mathur, R. N. 1980. Biology of the mulberry defoliator Glyphodes pyloalis (Lepidoptera: Pyralidae). Ind. Forest. Bull. 273: 1–6.

Ofteadch, M., J. Jalali Sendi, A. Zibae, and B. Valizadeh. 2014. Effect of four varieties of mulberry on biochemistry and nutritional physiology of mulberry pyralid, Glyphodes pyloalis Walker (Lepidoptera: Pyralidae). J. Entomol. Acarol. Res. 46: 42–49.

Ofteadch, M., J. Jalali Sendi, and R. Khosravi. 2015. Life table parameters of Glyphodes pyloalis Walker (Lep.: Pyralidae) on four varieties of mulberry Morus alba L. (Moraceae). J. Asia Pac. Entomol. 18: 315–320.

Padmavathi, C., G. Katti, V. Sailaja, A. P. Padmakumari, V. Jhansilakshmi, M. Prabhakar, and Y. G. Prasad. 2013. Temperature thresholds and thermal requirements for the development of the rice leaf folder, Capnodis crassipes. J. Insect Sci. 13: 1–14.

Ramegowda, G. K., L. Illahi, V. Mittal, I. Akhter, A. Dhar, and M. A. Khan. 2012. Influence of weather on the incidence and severity of lesser mulberry pyralid and mulberry looper in Kashmir. Indian J. Entomol. 9: 422–428.

Ranjbar-Aghdam, H., Y. Fathipour, G. Radjabi, and M. Rezapanah. 2009. Temperature dependent development and temperature thresholds of codling moth (Lepidoptera: Tortricidae) in Iran. Environ. Entomol. 38: 885–895.

Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and developmental rate of Stethorus punctillum (Coleoptera: Coccinellidae) and its prey Tetranychus medanieli (Acari: Tetranychidae). Environ. Entomol. 31: 177–187.

SAS Institute. 2007. JMP Statistics and Graphics Guide, Release 7. SAS Institute, Cary, NC.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J. Theor. Biol. 88: 719–731.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction kinetics of poikilo-therm development. J. Theor. Biol. 64: 649–670.

Shi, P., F. Ge, Y. Sun, and C. Chen. 2011a. A simple model for describing the effect of temperature on insect developmental rate. J. Asia Pac. Entomol. 14: 13–20.

Shi, P., T. Ikemoto, C. Egami, Y. Sun, and F. Ge. 2011b. A modified program for estimating the parameters of the SSI model. Environ. Entomol. 40: 462–469.

Shi, P., B. L. Li, and F. Ge. 2012. Intrinsic optimum temperature of the diamondback moth and its ecological meaning. Environ. Entomol. 41: 714–722.

Shi, P., H. S. Sandhu, and F. Ge. 2013. Could the intrinsic rate of increase represent the fitness in terrestrial ectotherms? J. Therm. Biol. 38: 148–151.

Tobin, C. P., S. Nagarkatti, and M. C. Saunders. 2003. Phenology of grape berry moth (Lepidoptera: Tortricidae) in cultivated grape at selected geographic locations. Environ. Entomol. 32: 340–346.

Watanabe, H., Y. Kurihara, Y. X. Wang, and T. Shimizu. 1988. Mulberry pyralid, Glyphodes pyloalis: Habitual host of nonoccluded viruses pathogenic to the silkworm, Bombyx mori. J. Invertebr. Pathol. 52: 401–408.

Wagner, T. L., H. Wu, P. J. H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect development rate: a literature review and application of a biophysical model. Ann. Entomol. Soc. Am. 77: 208–225.

Yazdani, E., J. Jalali Sendi, and J. Hajizadeh. 2014. Effect of Thymbra vulgaris L. and Origanum vulgare L. essential oils on toxicity, food consumption, and biochemical properties of lesser mulberry pyralid Glyphodes pyloalis Walker (Lepidoptera: Pyralidae). J. Plant Prot. Res. 54: 53–61.

Zahiri, B., Y. Fathipour, M. Khanjani, S. Moharramipour, and M. Zaluki. 2010. Preimaginal development response to constant temperatures in Hypopa postica (Coleoptera: Curculionidae): picking the best model. Environ. Entomol. 39: 177–189.