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A THESIS FOR THE DEGREE OF

MASTER OF SCIENCE

Phenology model of *Leptocorisa chinensis* (Dallas)

(Hemiptera: Alydidae)

호리허리노런계 계절 발생 모형

BY

HWANG KIM

ENTOMOLOGY PROGRAM

DEPARTMENT OF AGRICULTURAL BIOTECHNOLOGY

SEOUL NATIONAL UNIVERSITY

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A THESIS FOR THE DEGREE OF

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Phenology model of *Leptocorisa chinensis* (Dallas)  
(Hemiptera: Alydidae) in Korea

UNDER THE DIRECTION OF ADVISER JOON-HO LEE
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF SEOUL NATIONAL UNIVERSITY

By
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Entomology Program
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ABSTRACT

Phenology model of *Leptocorisa chinensis* (Dallas) (Hemiptera: Alydidae)

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*Leptocorisa chinensis* (Hemiptera: Alydidae) is known to cause pecky rice by sucking rice panicles at the milking stage of rice in Japan. In Korea, *L. chinensis* occurs only on Jeju Island, and in southern coastal area, and its damage to rice has not been reported yet. However, if *L. chinensis* expands northward and increases its abundance under global warming, it may become an important rice pest. To understand changes of its status in the future, a phenology model of *L. chinensis* was developed in this study. For this model, immigration model of overwintered adult *L. chinensis* was constructed based on literature information. In addition, development and oviposition models of *L. chinensis* were developed by conducting experiments. The phenology model was validated using field occurrence
data of *L. chinensis* in 2015. Phenology of *L. chinensis* in the present and future were compared to understand effects of global warming to *L. chinensis* under the representative concentrated pathways (RCP) 8.5 climate change scenario using the phenology model of *L. chinensis*. The 50 % immigration time of overwintered adults moved forward from Julian day 179 in 2015 to 172 in 2050s, and 159 in 2090s. The generation number increased from three in 2015, and 2050s to four in 2070s, and 2090s. The peak abundance time of adults moved forward from Julian day 269 in 2015 to 260 in 2090s.

Key words: *Leptocorisa chinensis*, immigration model, development and oviposition models, phenology model, RCP 8.5

*Student number: 2014-22928*
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I. Introduction

*Leotocorisa chinensis* Dallas (Heteroptera: Alydidae), called as the slander rice bug or rice seed bug, distributes in Southeast and East Asia (Siwi and Doesburg, 1984). Genus *Leotocorisa* belongs to order Hemiptera, suborder Heteroptera, subfamily Coreoidea, family Alydidae, subfamily Leptocorisinae, tribe Leptocorisini. *L. chinensis* was firstly named at 1852 (Dallas, 1852), and *L. nitidula* (Breddin, 1913), *L. corbetti* (China, 1924) were synonymized. In Japan, *L. chinensis* is an important rice insect pest causing pecky rice (Suzuki, 2001; Takeuchi and Watanabe, 2006) and has been regarded as a pest in the southern warm area, but its damage was unexpectedly reported in northern Tohoku district (Yokosuka, 2001). In Korea, *L. chinensis* occurs on Jeju Island and in the southern coastal area, and its occurrence is mainly found on *Setaria viridis*. Its damage on rice has not been reported in Korea. However, if *L. chinensis* expands northward and increases its abundance under global warming, it may cause damage to rice in Korea.

Adult *L. chinensis* overwinters on *Cryptomeria*, cedar trees (Hiroshi and Nagai, 1976). Overwintered adults immigrate into Poaceous weeds from late June to early July. First generation adults begin to appear in late...
July and second generation adults come out in mid-September (Takeuchi, 2005). *L. chinensis* has 2-3 generations per year depending on latitude (Takeuchi, 1939). Adult *L. chinensis* is highly mobile (Tsunoda and Morya, 2008), and when the rice is at the heading stage, they disperse to rice fields (Takeuchi, 2005b; Tsunoda and Morya, 2008). Rice spikelets remain for 40-50 days in Japan, and this period is long enough for *L. chinensis* to develop from eggs to adults (Takeuchi and Watanabe, 2005a). Adults generally oviposit eggs in masses, which are placed in a few rows, on the nearest two leaves of panicles. Egg masses contain generally 11-15 eggs (Yokosuka et al., 1991). *L. chinensis* has 5 nymphal stages. Previous studies investigated effects of constant temperatures on the period of egg, nymph, and pre-oviposition of *L. chinensis* (Ishizaki, 2002; Yamashita, 2005). Its host species are *Setaria viridis*, *Digitaria ciliaris*, *Echinochloa Crus-galli*, and *Oryza sativa* (Ishizaki et al, 2008).

*L. chinensis* enters facultative reproductive diapause which is affected by the short day length (13.75 h in critical day length), low temperature (< 20 °C), and food (Only female) (Tachibana, 2007; Yamashita, 2010). The adults which were reared at the short-day length condition needed longer time to start oviposition than the adults reared at the long-day length condition.

Population dynamics of *L. chinensis* was studied in Japan
(Watanabe, 2003; Takeuchi, 2005a, b; Wantanbe, 2009), and Yamashita (2005) estimated the annual generation number using the effective heat unit by the linear development model. This degree day approach has been used often because it is easy to calculate and explains quite well field observations (Obrycki and Tauber, 1981). However, degree-day approach is effective mainly in intermediate temperatures. Linearity of the development rate relationship with temperatures falls off significantly at lower and higher temperatures beyond the optimal temperature region. (Wagner et al, 1984a). The penology model can more appropriately estimate the generation number and describe phenology of insects because it comprises more realistic components, and if models were constructed properly and validated, the long-term predictions can be possible (Kim and Lee, 2010; Lee et al., 2016).

In this study, a phenology model of *L. chinensis* was developed to understand its seasonal population dynamics in the present, and future under global warming. For doing this, an immigration model of overwintered adults, temperature dependent development and oviposition models were developed.
2. Materials and Methods

2-1. Immigration model of overwintered adult *L. chinensis*

2-1-1. Monitoring *L. chinensis* in fields

*L. chinensis* was monitored in the fallow fields covered with Poaceae plants on the hill near the sea in Namhae-gun (34.934222, 127.908666), Gyungsangnam-do from May 27 to November 30 in 2015. Three pheromone sticky traps (Fuji Flavor Co., Ltd., Japan) were placed at a distance of 30 m, and 1 m above the ground. The pheromone lure was replaced every 2 weeks and sticky paper was replaced every week. In addition, sweeping sampling was conducted every week in the same field. For each sweeping sampling occasion, 30 sweeps were carried out with the sweep net (36cm diameter).
2-1-2. Immigration model of overwintered adults

Pheromone trap and sweeping catch data were not appropriate to construct an immigration model of overwintered adults because of low abundance of overwintered adults. Instead, published investigation data in Tsukuba, Japan (Takeuchi et al., 2005) and daily temperature data in Korea Meteorological Administration (KMA), 2003, and 2004, Japan were used. Degree day was calculated by using the single sine method (Allen, 1976). The base temperature for the overwintered adult flight of L. chinensis was determined as follows. First, 11 sets of degree days from 1 January to late July were calculated using 11 potential base temperatures from 7 to 17°C with 1°C increments for 10, 30, 50, 70, 90% cumulative capture. Second, the potential temperature was selected that has least average deviation between degree days for observed and estimated 10, 30, 50, 70, 90% cumulative capture. The degree days at each % of cumulative capture was calculated by linear interpolation from nearest two observed data. In this step, 12 °C was selected. Then, to obtain the further refined base temperature from 12 °C, 9 sets of degree days from 1 January to late July were calculated using 9 potential base temperatures from 11.6 to 12.4 °C.
with 0.1°C increments for 10, 30, 50, 70, 90% cumulative capture. The relationship between the cumulative proportion of adult flight and the cumulated degree days calculated using the determined base temperature was fitted with a 2-parameter Weibull function.

\[
F(DD) = 1 - \exp(-(DD/\alpha)^\beta)
\]  

(Equation 1)

\(F(DD)\) is the cumulative proportion of immigration of overwintered adults at \(DD\), \(\alpha, \beta\) are the parameters. Degree-days were calculated from January 1.

2-2. Temperature-dependent development and oviposition models of \(L. \ chinensis\)

2-2-1. Test insect

\(L. \ chinensis\) were collected in the \(S. \ viridis\) fields in Hanla mountain on Jeju Island in July 4, 2014. They were reared in acrylic cages (45cm × 30cm × 35cm) in an incubator at 25 °C, a photoperiod of 16:8 (L:D) h, and 75-80% RH. Rice panicles at the milky stages and wet floral foam (23cm ×
11cm × 8cm, Smithers-Oasis Co. Korea) were provided for supplying food and water, respectively. Colonies have been maintained for experiments.

2-2-2. Development experiment

To collect eggs of the similar early age for development experiments for L. chinensis, gauze was hanged in the breeding cages for adults to lay eggs on the gauze. Gauze was replaced every day. Newly laid eggs were collected. Development experiment was conducted at eleven constant temperatures (16, 18, 20, 22.5, 27.5, 30, 32, 33, 34, and 35 °C), a photoperiod of 16:8 (L:D) h, and 75-80% RH. The lid of dishes had ventilation hole (4cm diameter, 0.053 µm mesh pore) To determine higher critical temperatures for development of immatures experimentally, increment was made with 1°C at higher temperatures. The temperatures inside the incubators were measured using a temperature logger (Hobo, OnSet Computer, Pocasset, MA, USA). The actual mean temperatures were 16.2, 18.4, 20.3, 22.7, 25.3, 27.8, 30.4, 32.0, 33.3, 34.4, 35.3 °C, respectively. Newly laid eggs (egg masses) were placed on the small petri dish (5cm in diameter × 1.3cm height, SPL) and this dish was placed on the wet cotton pad in the larger petri dish (10cm in diameter × 2cm height, SPL).
In each dish, several egg masses were placed to be 20 eggs per dish. For each temperature, 177 - 203 eggs were tested. Eggs were checked daily for survival and hatch. Newly hatched nymphs were transferred to the plastic tube (2.6 cm in diameter × 15 cm in length) in which wet cotton pad was inserted on the bottom for providing moisture, and rice panicles at milk and dough stage were provided for food. The basal part of panicles was wrapped with this cotton pad. Then, tubes were covered with sponge. Rice panicles were replaced every day. Nymphs were checked daily. For each temperature, 50 nymphs were tested. To verify temperature effects on development, ANOVA and Turkey test were conducted using SPSS Statistics v23 (SPSS Inc.)

2-2-3. Oviposition experiment

Newly emerged adults were placed in a square plastic dish (7.2cm × 7.2cm × 10cm, SPL) at 22, 25, 28, 31, 35 °C, a photoperiod of 16:8 (L:D) h, and 75-80% RH. The actual mean temperatures were 22.3, 25.2, 28.0, 31.4, 35.3 °C, respectively. The lid of dishes had ventilation hole (4cm diameter, 0.053 µm mesh pore). Rice panicles were wrapped with the cotton pad and laid on the dish, and were replaced every day. For each
temperature, 20 female adults were tested. While checking eggs laid, escape of adults was prohibited using the fluorescent light (36 W) because they were strongly attracted to this light. Laid eggs were counted and removed every day, and survival of adults were also checked every day. When male adults were dead, they were replaced with sexually matured ones. To verify temperature effects on longevity, fecundity, and pre-oviposition period, ANOVA and Turkey test were conducted using SPSS Statistics v23 (SPSS Inc.)

2-2-4. Construction of temperature-dependent development and oviposition models

Linear development rate model

Development rates were expressed as reciprocals of development times (in days) of each immature stage. Development rates of linear portion for each stage were regressed against temperature using SPSS Statistics v23 (SPSS Inc.). The lower threshold temperature for development was calculated as the x-intercept of the fitted equation for each stage (Arnold, 1959). Heat unit requirements for the development of each stage was estimated by solving the 1/slope of the fitted equation.
\[ r(T) = ax + b \]  \hspace{1cm} \text{(Equation 2)}

\( r(T) \) is the temperature-dependent development rate at temperature \( T (^\circ C) \).
\( a, b \) are the parameters.

**Non-linear development rate model**

Development rates at each temperature were fitted against temperatures using the Logan-6 model (Logan et al., 1976.). Model fitting was conducted using TableCurve (Jandel Scientific, 1996)

\[ r(T) = \psi \left( e^{\rho T} - e^{\left( \frac{T_{\text{max}} - T_{\text{max}} - T}{\Delta T} \right)} \right) \]  \hspace{1cm} \text{(Equation 3)}

\( r(T) \) is the temperature-dependent developmental rate at temperature \( T (^\circ C) \).
\( \psi \) is the maximum development rate. \( \rho \) is the constant defining the rate of optimal temperature. \( T_{\text{max}} \) is the high temperature threshold. \( \Delta T \) is the temperature range over which physiological breakdown becomes the overriding influence.

**Cumulative distribution model of development completion**

The cumulative proportional distribution of development completion
for each immature stages were calculated by cumulating proportion of daily transferred individuals from one stage to the next stage at a particular physiological time.

To calculate physiological time ($P_x$) of each stage, $P_x$ of $i$th stage on $j$th day was calculated as

$$P_x = \sum_{j=0}^{n} r(T_{ij})$$

(Equation 4)

Where $r(T_{ij})$ is the development rate in $i$th stage at temperature $T$ ($^\circ$C) of $j$th day.

The two-parameter Weibull function was used for model fitting.

$$F(px) = 1 - e^{-\left(\frac{px}{\alpha}\right)^\beta}$$

(Equation 5)

$F(px)$ is the cumulative proportion (%) of stage emergence at physiological time $px$, $\alpha$, $\beta$ are the parameters.

**Survival rate model**

Survival rate (%) was calculated as the number of insects alive divided by the initial number of insects tested. The relationship between the survival rate and temperature was described by a nonlinear function.
Equation was selected from the library of Table-Curve (Jandal Scientific, 1996).

\[ S(T) = e^{a + bT + ce^{-T}} \]  \quad (Equation 6)

\( S(T) \) is the temperature-dependent survival rate (\%) at temperature \( T \) (°C). \( a, b, c \) are fitted constants.

However, since survival rates for 3rd, 4th, 5th instar nymphs similar over temperature rages tested, the model fitting was not applied.

**Adult physiological age**

Adult development rate, the reciprocal of mean longevity (in days) of adults was modeled as a function of temperature using an equation which was selected from the library of Table-Curve (Jandal Scientific, 1996).

\[ r(T) = a + bT^2 + ce^T \]  \quad (Equation 7)

\( r(T) \) is the temperature-dependent development rate at temperature \( T \) (°C). \( a, b, c \) are fitted constants.

The physiological age of female adult was calculated using the above fitted model according to the equation 5.
Temperature-dependent total fecundity model

The mean total number of eggs laid per female adult at each temperature was fitted to the extreme-value function (Kim and Lee, 2003)

\[ f(T) = a \cdot e^{\left[1 + \left(\frac{b-T}{k}\right) - e^{\left(\frac{b-T}{k}\right)}\right]} \]  \hspace{1cm} (Equation 8)

\( f(T) \) is the number of total eggs produced by a female at temperature \( T \) (°C), \( a \) is the maximum reproductive capacity, \( b \) is the temperature (°C) at which maximum reproduction occurs, \( k \) is a fitted constant.

Age-specific cumulative oviposition rate model

The cumulative oviposition rate of adults at a specific physiological age was fitted to the two-parameter Weibull function.

\[ F(px) = 1 - e^{-\left(\frac{px}{a}\right)^\beta} \]  \hspace{1cm} (Equation 9)

\( P(px) \) is the cumulative oviposition rate at a physiological age of adults, \( px \). \( a, \beta \) are the parameters.
Age-specific survival rate model

The survival rate at the physiological age of adults was calculated by dividing the number of insects alive at a given physiological age with the initial number of adults tested. Equation was selected from the library of Table-Curve (Jandal Scientific, 1996).

\[ S(px) = a + b(px)^2 + c(px)^4 \] (Equation 10)

\(S(px)\) is the adult survival rate at a physiological age, \(px\). \(a, b, c\) are fitted constants.

Daily egg production

The number of eggs laid by an female adult at \(i\)th day (physiological age \(Px_i\)) was calculated in relation to the temperature-dependent total fecundity \([f(T)]\), the age-specific cumulative oviposition rate \([p(Px_i)]\), and the age-specific survival rate \([s(Px_i)]\) (Kim and Lee, 2003). The equation is expressed:

\[ f(T) \cdot [p(Px_{i+1}) - p(Px_i)] \cdot [(s(Px_i) + s(Px_{i+1}))/2] \] (Equation 11)
2-3. Simulation of the phenology model of *L. chinensis* under the present and future climate conditions

In general, the insect phenology model can be consisted of the immigration model of overwintered adults, temperature-dependent development model for life stages, and adult oviposition model, . (Kim and Lee, 2010). For phenology simulation for *L. chinensis*, single cohort of 100 overwintered adults were assumed to immigrate into the field. Immigrated adult *L. chinensis* was assumed to lay eggs according to temperature conditions. Oviposition of adults was assumed to stop on 30th August in the simulation because adult *L. chinensis* is under reproductive diapause at 13 h day length (Tachibana, 2007). Sex ratio was assumed as 1:1. The driving variable was daily mean air temperature. Daily air temperature data in Korea Meteorological Administration (KMA), Namhae-gun, 2015 were used as a present climate data. For describing the future climate conditions, the representative concentration pathway (RCP) 8.5 scenarios in 2030s, 2050s, 2070s, and 2090s were used. Phenology model was simulated by PopModel 1.0 BASE program (Choi and Kim, 2013). The phenology model in present was validated with field sweeping data in Namhae-gun, 2015.
Fig. 1. The structure of the phenology model of *L. chinensis*. 
3. Results

3-1. Immigration model of overwintered adult *L. chinensis*

Deviations of observed degree days from predicted ones at each potential base temperature from 7 to 17 °C with 1 °C increments are shown in Table 1. The least mean degree-day deviations at each cumulative % of captured adults in both years were different, but overall values were considered for determining the base temperature. 12 °C yielded the least mean deviation at 1 °C interval. Table 2 shows degree-day deviations at each cumulative % of captured adults in both years with each potential base temperature from 11.6 to 12.4 °C with 0.1 °C increments. 12.3 °C was found to yield the least deviation, and thus was selected as the base temperature for the flight of overwintered adult *L. chinensis*.

Fig. 2 shows comparison of observed and estimated immigration flight of overwintered adults of *L. chinensis*. The immigration model of overwintered adult *L. chinensis* well described observed cumulative immigration of overwintered adult *L. chinensis* in 2003 and 2004, Tsukuba \( (r^2=0.98) \). Estimated values of parameters \( \alpha \) and \( \beta \) of the 2-parameter Weibull function were 575.1180 and 11.9889, respectively.
Table 1. Degree day deviation between observed and predicted cumulative capture dates of overwintered adult *L. chinensis* for 10, 30, 50, 70, and 90% for different potential base temperatures

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<th>Base temperature (°C)</th>
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<th>50%</th>
<th>70%</th>
<th>90%</th>
<th>Mean±S.E.</th>
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<td>2.9</td>
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<td>±1.99</td>
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<td>23.9</td>
</tr>
<tr>
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<td>16.2</td>
<td>17.5</td>
<td>18.7</td>
<td>18.8</td>
<td>14.6</td>
<td>±1.99</td>
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</table>
Table 2. Degree day deviation between observed and predicted cumulative capture dates of overwintered adult *L. chinensis* for 10, 30, 50, 70, and 90% for refined potential base temperatures from 11.6 to 12.4 °C with 0.1 °C increments

<table>
<thead>
<tr>
<th>Base temperature (°C)</th>
<th>10%</th>
<th>30%</th>
<th>50%</th>
<th>70%</th>
<th>90%</th>
<th>Mean±S.E.</th>
</tr>
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<tr>
<td>11.69+</td>
<td>11.5</td>
<td>8.1</td>
<td>4.8</td>
<td>3.9</td>
<td>10.2</td>
<td>18.5</td>
</tr>
<tr>
<td>11.7</td>
<td>11.4</td>
<td>7.9</td>
<td>4.7</td>
<td>4.1</td>
<td>10.4</td>
<td>18.3</td>
</tr>
<tr>
<td>11.8</td>
<td>11.4</td>
<td>7.7</td>
<td>4.6</td>
<td>4.3</td>
<td>10.0</td>
<td>18.7</td>
</tr>
<tr>
<td>11.9</td>
<td>11.4</td>
<td>7.4</td>
<td>4.9</td>
<td>4.2</td>
<td>10.1</td>
<td>18.7</td>
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<td>11.5</td>
<td>7.0</td>
<td>4.2</td>
<td>5.1</td>
<td>10.1</td>
<td>18.8</td>
</tr>
<tr>
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<td>11.6</td>
<td>6.5</td>
<td>4.4</td>
<td>5.1</td>
<td>10.0</td>
<td>18.9</td>
</tr>
<tr>
<td>12.2</td>
<td>11.4</td>
<td>6.5</td>
<td>4.5</td>
<td>5.1</td>
<td>9.9</td>
<td>19.1</td>
</tr>
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<td>12.3</td>
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<td>4.6</td>
<td>5.2</td>
<td>10.2</td>
<td>18.8</td>
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<tr>
<td>12.4</td>
<td>11.5</td>
<td>5.7</td>
<td>4.6</td>
<td>5.4</td>
<td>9.9</td>
<td>19.2</td>
</tr>
</tbody>
</table>
Fig. 2. Observed and estimated cumulative captures of overwintered adult *L. chinensis* in Italian ryegrass fields in Tsukuba in 2003 and 2004. (Data from Takeuchi et al. (2005))
3-2. Temperature-dependent development model.

*L. chinensis* survived to adults at 18.4 °C -32 °C (Table 3). Eggs did not hatch at 16.2 and 35.3 °C. At 33.3 and 34.4 °C, significant number of eggs hatched but all hatched 1st instar nymphs were dead within 2 days. The egg development period ranged from 19.5 days at 18.4 °C to 5.5 days at 33.3 °C. The total nympha1 period ranged from a maximum of 56.5 days at 18.4 °C to a minimum of 16.8 days at 32.0 °C. Linear development relationship against temperatures for each stage are shown in Fig. 3. Estimates of parameters of the linear model and low threshold temperatures for each stage are given in Table 4. Nonlinear development relationship against temperature and estimates of parameters of the nonlinear model for each stage are presented in Fig. 4, and Table 5, respectively. The cumulative proportional distribution of development completion for each stage and estimates of parameters of the model are given in Fig. 5, and Table 6, respectively. Temperature-dependent survival rates for each stage are displayed in Fig. 6, and their estimates of parameters are given in Table 7. Overall, survival rates for all stages were similar and relatively high at 20-32 °C, and it was sharply decreased at temperatures beyond this range.
<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Egg</th>
<th>1&lt;sup&gt;st&lt;/sup&gt; instar</th>
<th>2&lt;sup&gt;nd&lt;/sup&gt; instar</th>
<th>3&lt;sup&gt;rd&lt;/sup&gt; instar</th>
<th>4&lt;sup&gt;th&lt;/sup&gt; instar</th>
<th>5&lt;sup&gt;th&lt;/sup&gt; instar</th>
<th>Total Nymph</th>
</tr>
</thead>
<tbody>
<tr>
<td>16.2</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>18.4</td>
<td>19.5±1.29a** (133/182)***</td>
<td>12.9 ± 3.20a (24/50)</td>
<td>9.3 ± 1.50a (19/24)</td>
<td>8.2 ± 1.17a (19/19)</td>
<td>10.5 ± 1.38a (18/19)</td>
<td>16.5 ± 1.88a (15/18)</td>
<td>56.5 ± 5.07a (15/50)</td>
</tr>
<tr>
<td>20.3</td>
<td>15.1 ± 0.49b (136/186)</td>
<td>8.9 ± 1.62b (45/50)</td>
<td>5.9 ± 0.88b (44/45)</td>
<td>6.5 ± 0.67b (43/44)</td>
<td>8.0 ± 1.26b (42/43)</td>
<td>13.0 ± 1.41b (40/42)</td>
<td>42.0 ± 3.57b (40/50)</td>
</tr>
<tr>
<td>22.7</td>
<td>11.0 ± 0.64c (158/190)</td>
<td>6.5 ± 1.60c (47/50)</td>
<td>4.8 ± 0.79c (46/47)</td>
<td>4.7 ± 0.82c (46/46)</td>
<td>5.9 ± 0.62c (46/46)</td>
<td>9.2 ± 0.69c (41/46)</td>
<td>30.7 ± 2.20c (41/50)</td>
</tr>
<tr>
<td>25.3</td>
<td>8.7 ± 0.55d (133/177)</td>
<td>5.4 ± 0.92d (47/50)</td>
<td>3.8 ± 0.96d (46/47)</td>
<td>3.6 ± 0.72d (45/46)</td>
<td>4.0 ± 0.54d (42/45)</td>
<td>6.4 ± 0.50d (41/42)</td>
<td>23.3 ± 1.63d (41/50)</td>
</tr>
<tr>
<td>27.8</td>
<td>7.1 ± 0.47e (168/203)</td>
<td>3.8 ± 1.12e (45/50)</td>
<td>3.4 ± 0.79de (42/45)</td>
<td>3.1 ± 0.75de (41/42)</td>
<td>4.3 ± 1.10de (41/41)</td>
<td>5.5 ± 0.75e (40/41)</td>
<td>20.1 ± 1.58e (40/50)</td>
</tr>
<tr>
<td>30.4</td>
<td>6.0 ± 0.15f (138/186)</td>
<td>3.4 ± 0.61e (44/50)</td>
<td>2.8 ± 0.75e (40/44)</td>
<td>3.0 ± 0.77de (39/40)</td>
<td>3.5 ± 0.64ef (38/39)</td>
<td>5.02 ± 0.72e (36/38)</td>
<td>17.8 ± 1.15ef (36/50)</td>
</tr>
<tr>
<td>32.0</td>
<td>5.7 ± 0.47gh (111/190)</td>
<td>2.9 ± 0.57e (34/50)</td>
<td>3.1 ± 0.90e (23/34)</td>
<td>2.7 ± 0.65e (22/23)</td>
<td>3.2 ± 1.05g (22/22)</td>
<td>4.95 ± 0.39e (20/22)</td>
<td>16.8 ± 1.60f (20/50)</td>
</tr>
<tr>
<td>33.3</td>
<td>5.5 ± 0.50h (115/182)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>34.4</td>
<td>5.9 ± 0.29fg (23/182)</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>35.</td>
<td>-</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
</tbody>
</table>

* No individual successfully developed or tested
** Means within a column for each stage followed by the same letter are not significantly different (P>0.05; Tukey’s HSD test at 95% confidence intervals)
*** Numbers in parentheses indicate the numbers of individuals that completed their development / total
Fig. 3. Linear model of developmental rates (1/day) in each stage of *L. chinensis* at constant temperatures. (●: Observed, ○: Excluded in the linear model, —: Estimated)
Table 4. Linear development model, lower temperature threshold and thermal requirement for each stage of *L. chinensis*

<table>
<thead>
<tr>
<th>Stage</th>
<th>Model</th>
<th>$r^2$</th>
<th>Lower Temperature threshold (°C)</th>
<th>Thermal constant, DD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>$0.0095x - 0.1259$</td>
<td>0.99</td>
<td>13.4</td>
<td>105.3</td>
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<tr>
<td>1&lt;sup&gt;st&lt;/sup&gt; instar</td>
<td>$0.0192x - 0.2805$</td>
<td>0.99</td>
<td>14.6</td>
<td>52.1</td>
</tr>
<tr>
<td>2&lt;sup&gt;nd&lt;/sup&gt; instar</td>
<td>$0.0191x - 0.2291$</td>
<td>0.99</td>
<td>12.0</td>
<td>52.4</td>
</tr>
<tr>
<td>3&lt;sup&gt;rd&lt;/sup&gt; instar</td>
<td>$0.0217x - 0.2792$</td>
<td>0.99</td>
<td>12.9</td>
<td>46.1</td>
</tr>
<tr>
<td>4&lt;sup&gt;th&lt;/sup&gt; instar</td>
<td>$0.0157x - 0.1859$</td>
<td>0.95</td>
<td>11.8</td>
<td>63.7</td>
</tr>
<tr>
<td>5&lt;sup&gt;th&lt;/sup&gt; instar</td>
<td>$0.0123x - 0.1671$</td>
<td>0.99</td>
<td>13.6</td>
<td>81.3</td>
</tr>
<tr>
<td>Total Nymph</td>
<td>$0.0031x - 0.0389$</td>
<td>0.99</td>
<td>12.5</td>
<td>322.6</td>
</tr>
<tr>
<td>Egg to Adult</td>
<td>$0.0023x - 0.0291$</td>
<td>0.99</td>
<td>12.7</td>
<td>434.8</td>
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</tbody>
</table>
Fig. 4. Nonlinear model of developmental rates (1/day) in each stage of *L. chinensis* under constant temperatures. (●, Observed; —, Estimated; ----, Excluded)
Table 5. Estimates (±SE) of parameters in nonlinear development model of each stage of *L. chinensis*

<table>
<thead>
<tr>
<th>Stage</th>
<th>( \Psi )</th>
<th>( P )</th>
<th>( T_{\text{max}} )</th>
<th>( \Delta T )</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0.0056±0.0024</td>
<td>0.1283±0.0332</td>
<td>38.7180±1.0040</td>
<td>3.8755±1.7964</td>
<td>0.99</td>
</tr>
<tr>
<td>1(^{st}) instar</td>
<td>0.0107±2.7152</td>
<td>0.1816±3.0025</td>
<td>38.5670±13.5355</td>
<td>5.0106±93.0986</td>
<td>0.97</td>
</tr>
<tr>
<td>2(^{nd}) instar</td>
<td>0.0145±0.8756</td>
<td>0.1807±1.0085</td>
<td>35.8898±2.3266</td>
<td>4.9069±29.9279</td>
<td>0.99</td>
</tr>
<tr>
<td>3(^{rd}) instar</td>
<td>0.0413±36.0956</td>
<td>0.1621±5.0283</td>
<td>38.2082±11.3595</td>
<td>5.8112±190.6521</td>
<td>0.96</td>
</tr>
<tr>
<td>4(^{th}) instar</td>
<td>0.0297±24.3503</td>
<td>0.1520±6.0045</td>
<td>40.5102±31.9733</td>
<td>6.0871±264.1370</td>
<td>0.95</td>
</tr>
<tr>
<td>5(^{th}) instar</td>
<td>0.0070±0.6122</td>
<td>0.1905±1.0953</td>
<td>35.8335±1.9202</td>
<td>4.7790±29.5704</td>
<td>0.99</td>
</tr>
<tr>
<td>Total Nymph</td>
<td>0.0026±0.1345</td>
<td>0.1641±0.8961</td>
<td>37.3918±3.9270</td>
<td>5.3239±32.7457</td>
<td>0.99</td>
</tr>
<tr>
<td>Egg to Adult</td>
<td>0.0017±0.0277</td>
<td>0.1602±0.4092</td>
<td>37.5686±2.5106</td>
<td>5.2532±15.6799</td>
<td>0.99</td>
</tr>
</tbody>
</table>

Logan-6 model (Logan, 1976) was applied
Fig. 5. Cumulative distributions of development in each stage of *L. chinensis* against physiological times. (●, Observed; —, Estimated)
Table 6. Estimates (±SE) of parameters of the distribution model of developmental time for each stage of *L. chinensis*

<table>
<thead>
<tr>
<th>Stage</th>
<th>Parameters</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\alpha$</td>
<td>$\beta$</td>
</tr>
<tr>
<td>Egg</td>
<td>1.0182±0.0028</td>
<td>26.1453±2.3904</td>
</tr>
<tr>
<td>1st instar</td>
<td>1.0651±0.0096</td>
<td>5.4455±0.3500</td>
</tr>
<tr>
<td>2nd instar</td>
<td>1.0503±0.0090</td>
<td>6.7039±0.4548</td>
</tr>
<tr>
<td>3rd instar</td>
<td>1.0647±0.0096</td>
<td>6.1583±0.4384</td>
</tr>
<tr>
<td>4th instar</td>
<td>1.0425±0.0058</td>
<td>8.6477±0.5195</td>
</tr>
<tr>
<td>5th instar</td>
<td>1.0238±0.0021</td>
<td>13.9807±0.5007</td>
</tr>
<tr>
<td>Total Nymph</td>
<td>1.0219±0.0021</td>
<td>16.0296±0.6423</td>
</tr>
<tr>
<td>Egg to Adult</td>
<td>1.0178±0.0015</td>
<td>20.3974±0.7581</td>
</tr>
</tbody>
</table>

A two-parameter Weibull function was applied.
Fig. 6. Survival rate model in each stage of *L. chinensis* at constant temperatures. (●, Observed; —, Estimated; ----, Average)
Table 7. Estimates (±SE) of parameters of the survival rate model of *L. chinensis* at constant temperatures

<table>
<thead>
<tr>
<th>Stage</th>
<th>Parameters</th>
<th>Average</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$a$</td>
<td>$b$</td>
<td>$c$</td>
</tr>
<tr>
<td>Egg</td>
<td>4.38±4.73E-02</td>
<td>-1.63e-15±4.00e-16</td>
<td>-2.44e+07±9.15e+06</td>
</tr>
<tr>
<td>1st instar</td>
<td>4.55±1.60E-02</td>
<td>-4.16e-15±6.03e-16</td>
<td>-6.37e+07±6.21e+06</td>
</tr>
<tr>
<td>2nd instar</td>
<td>4.58±1.29E-02</td>
<td>-4.68E-15±5.09E-16</td>
<td>-2.01E+07±3.44E+06</td>
</tr>
<tr>
<td>3rd instar</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4th instar</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5th instar</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Egg to Adult</td>
<td>4.20±1.69E-02</td>
<td>-1.32E-14±1.10E-15</td>
<td>-1.06E+08±9.22E+06</td>
</tr>
</tbody>
</table>

* is average of observed survival rate. 3rd, 4th, 5th instar was not applied model function because of independentity under different temperature ($Y= a^x+be^{x}+ce^{-x}$)
3-3. Temperature-dependent oviposition model

The mean longevity and fecundity of female adult *L. chinensis* at different temperatures are shown in Table 8. As the temperature increased, longevity decreased significantly (*F* = 8.99; *d.f* = 3, 60; *P* < 0.0001). Adult longevity was longest as 193.1 days at 22.3 °C, ranging from 49 days to 326 days. Adult development rate model shows that longevity decreased sharply above 33 °C (Fig. 7). Adults did not lay eggs at 35.3 °C. The temperature also affected the fecundity (*F* = 2.998; *d.f* = 3, 60; *P* = 0.038). The highest fecundity were 1360 eggs at 28.0 °C. Pre-oviposition period decreased as the temperature increased (*F* = 8.99; *d.f* = 3, 60; *P* < 0.0001). Fig. 8 described temperature dependent fecundity model. Age-specific cumulative oviposition rate model (Fig. 9) and age-specific adult survival rate model were developed (Fig. 10). Fig. 11 shows simulated daily egg production per female adult in relation to age (days) and temperature (°C) from 10 to 40 °C with 0.5°C increments. The highest daily egg production and total fecundity was at 29 °C according to the output of the oviposition model simulation.
Table 8. Mean longevity, fecundity, and pre-oviposition period (mean ± S.D.) of female adult *L. chinensis* at constant temperatures

<table>
<thead>
<tr>
<th>Temp (°C)</th>
<th>n</th>
<th>Longevity (day) (min - max)</th>
<th>Fecundity (min - max)</th>
<th>Daily eggs per female (total fecundity / n)</th>
<th>Pre-oviposition period (day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.3</td>
<td>17</td>
<td>193.1 ± 86.88a* (49 - 326)</td>
<td>324.8 ± 249.48a (43 - 826)</td>
<td>2.08 ± 0.74</td>
<td>32.8 ± 11.49a</td>
</tr>
<tr>
<td>25.2</td>
<td>15</td>
<td>152.7 ± 60.93ab (38 - 249)</td>
<td>526.6 ± 268.35a (34 - 1166)</td>
<td>4.29 ± 1.33</td>
<td>22.5 ± 4.96b</td>
</tr>
<tr>
<td>28.0</td>
<td>15</td>
<td>124.7 ± 49.34bc (26 - 185)</td>
<td>585.8 ± 414.57a (10 - 1360)</td>
<td>5.70 ± 2.20</td>
<td>16.6 ± 4.10bc</td>
</tr>
<tr>
<td>31.4</td>
<td>17</td>
<td>89.4 ± 25.17c (42 - 121)</td>
<td>372.1 ± 173.45a (83 - 674)</td>
<td>4.95 ± 1.60</td>
<td>11.4 ± 2.89c</td>
</tr>
<tr>
<td>35.3</td>
<td>20</td>
<td>25.4 ± 11.94d (6 - 40)</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Means within a column for each stage followed by the same letter are not significantly different (P>0.05; Tukey's HSD test at 5% error rate)
Fig. 7. Adult development rate curve (1/mean longevity) of *L. chinensis*. A nonlinear function selected from the library of TableCurve (Jandel Scientific, 1996) was applied. (*Y* = *a* + *bx*² + *ce*¹)
Fig. 8. Temperature-dependent total fecundity curve of *L. chinensis*. An extreme value function was selected from the library of TableCurve. (Jandel Scientific, 1996)
Fig. 9. Age-specific cumulative oviposition rate curve of *L. chinensis*. A two-parameter Weibull function was applied.
Fig. 10. Age-specific adult survival rate curve of *L. chinensis*. A nonlinear model function selected from the library of TableCurve (Jandel Scientific, 1996) was applied. \( Y = a + bx^2 + cx^4 \)
Fig. 11. Predicted oviposition density curves of *L. chinensis* in relation to age and temperature (°C)
Table 9. Estimates of parameters (±SE) of the oviposition models of *L. chinensis*

<table>
<thead>
<tr>
<th>Models</th>
<th>Parameters</th>
<th>Estimated values</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developmental rate model</td>
<td>$a$</td>
<td>-0.00051541 ± 0.000514854</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$b$</td>
<td>1.11774e-05 ± 1.19E-08</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>$c$</td>
<td>1.21261e-17 ± 2.14293e-19</td>
<td></td>
</tr>
<tr>
<td>Survival rate model</td>
<td>$a$</td>
<td>0.9966 ± 0.0183</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$b$</td>
<td>-0.6174 ± 0.0353</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>$c$</td>
<td>0.0940 ± 0.0136</td>
<td></td>
</tr>
<tr>
<td>Temperature-dependent total fecundity model</td>
<td>$a$</td>
<td>600.8429 ± 19.6278</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$b$</td>
<td>27.8157 ± 0.1706</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>$T_e$</td>
<td>-4.1427 ± 0.2244</td>
<td></td>
</tr>
<tr>
<td>Cumulative oviposition rate model</td>
<td>$\alpha$</td>
<td>0.7069 ± 0.0025</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>$\beta$</td>
<td>1.8627 ± 0.0177</td>
<td></td>
</tr>
</tbody>
</table>
3-4. Simulation of the phenology model of *L. chinensis* under the present and future climate conditions

The phenology model simulated that three generations of *L. chinensis* occurred in 2015. Population increased explosively in the second generation and abundance of the third generation was very low (Fig. 12a). The output of simulation was validated by comparing ratio of total adult occurrence with field observation data in 2015 (Fig. 12b). The simulation output well described field adult occurrence. The peak time in the second generation almost coincided between observation and simulation output. Fig. 13 describes population dynamics of adult *L. chinensis* under the future climate. The 50% immigration time of overwintered adults were predicted to delay in 2030s, and then advance after 2050s. The number of generation was predicted to increase after 2070s. The peak abundance of adult *L. chinensis* is predicted to increase significantly.
Fig. 12. Proportional adult occurrence patterns of *L. chinensis* for each generation by the simulation of its phenology model (a) and comparison of total adult occurrence between simulation and observation in 2015, Namhae-gun (b)
Fig. 13. Predicted proportional adults occurrence patterns of *L. chinensis* for each generation in 2030s, 2050s, 2070s, and 2090s in Namhae-gun, Korea.
Table 10. Simulation results of phenology of *L. chinensis* under present and future climate conditions

<table>
<thead>
<tr>
<th></th>
<th>2015</th>
<th>2030s</th>
<th>2050s</th>
<th>2070s</th>
<th>2090s</th>
</tr>
</thead>
<tbody>
<tr>
<td>50% immigration day</td>
<td>175</td>
<td>182</td>
<td>172</td>
<td>163</td>
<td>159</td>
</tr>
<tr>
<td>Generation number</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Peak time</td>
<td>269</td>
<td>267</td>
<td>265</td>
<td>262</td>
<td>260</td>
</tr>
<tr>
<td>Peak abundance (Initial: 1)</td>
<td>3.38</td>
<td>6.61</td>
<td>33.13</td>
<td>138.28</td>
<td>268.12</td>
</tr>
</tbody>
</table>
4. Discussion

4-1. Immigration model of overwintered adult *L. chinensis*

Determining base temperature for the immigration model of overwintered adults, various values can be considered; standard deviation in days, standard deviation in degree-days, coefficient of variation, and regression coefficient (Arnold 1959). In this study, mean of degree-day deviation between observed and estimated data was, in fact, best for identifying the base temperature.

4-2. Development and oviposition models of *L. chinensis*

Earlier studies on development time and pre-oviposition period of *L. chinensis* (Ishizaki, 2002; Yamashita, 2005) reported development times of eggs and nymphs, and pre-oviposition period at different temperatures. However, nymphal development period was given only for total nymphal period in both studies. Our study is the most comprehensive one and also
the first to present essential components of the phenology model for *L. chinensis*, development and oviposition models. Egg development times were similar at intermediate temperatures (22-31 °C) between these studies and the current study. However, egg periods at similar low temperatures were rather varied as 18.3 days at 19 °C (Ishizaki, 2002), 14.9 days at 18 °C (Yamashita, 2005), and 19.5 days at 18.4 °C (present study). Pre-oviposition periods at each temperature in the present study were similar to results of Yamashita (2005).

At 16.2° and 35.3 °C, nymphs were observed to develop inside of eggs, but failed to hatch. At 33.3 °C and 34.4 °C, eggs were hatched but they appear to be significantly less viable, being legs usually attached to the egg shell and not detached. They walked unsteadily and all died in two days. Linear development models described development rates well at intermediate temperatures. Lower threshold temperatures for each stage varied from 12.0 °C (2nd instar nymph) to 14.6 °C (1st instar nymph). Logan-6 model described development rates very well over the temperature range tested, but it appeared to overestimate development rate of *L. chinensis* at lower temperature region below 15 °C compared to the linear models and estimated lower threshold temperatures from the linear model. Thus, it is recommended that for *L. chinensis*, Logan-6 model would be better for using
at temperatures above 15 °C.

Results of survivorship of *L. chinensis* indicates that the optimal temperature range of immature *L. chinensis* is 20 - 30 °C. Early immature stages (eggs, 1st and 2nd instar nymphs) were observed that at low temperatures they are more vulnerable than late immature stages (3rd, 4th, and 5th instar nymphs).

Adult longevity and fecundity were rather highly variable among individuals. Observed mean total fecundity was fitted well to the extreme value function ($r^2 = 0.99$), but it rather overestimated the fecundity at the lower temperature region below 20 °C. Thus, the fecundity model is recommended for use above 20 °C because *L. chinensis* is known to enter reproductive diapause below 20 °C and a critical photoperiod of 13.75 h day length (Tachibana, 2007; Yamashita 2010). Mean longevity was estimated to decrease sharply above 33 °C, and this temperature region was also detrimental to survival and development of immatures. Overall, based on daily reproductive potential shown in Fig. 11, temperature range of 21 °C - 32 °C is thought to be optimal for adult *L. chinensis*.

4-3. Simulation of the phenology model of *L. chinensis* under the present and future climate conditions
Phenology simulation results showed that the peak population will appear in the second generation in the present, 2030s and 2050s, but it will be changed to the third generation in the 2070s and 2090s. Accordingly, peak abundance is predicted to increase ten times in 2050s, forty times in 2070s, eighty times in 2090s than 2015. Peak times of adult *L. chinensis* abundance in the future would advance a little.

The heading stage of rice appears mostly in early August in Namhae-gun, 2015. There is about 50-day gap between the peak time of adult *L. chinensis* and heading stage of rice. Lee et al. (2016) predicted optimal rice transplanting time would be delayed about 50 days in 2090s. Then, it is likely that proper rice phenology for *L. chinensis* and time of adult *L. chinensis* peak abundance might be matched. Also, current distribution of *L. chinensis* is likely to expand northward under global warming, then *L. chinensis* may become a pest.
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호리허리노린재의 계절 발생 모형

김 황

초 록

호리허리노린재는 벼 이삭을 가해하여 반점미를 유발하며, 주로 일본에서 피해를 주고 있는 해충이다. 한국에서는 제주도와 남해안 일부 지역의 강아지풀 군락에서 발견할 수 있고, 아직까지 호리허리노린재에 의한 피해가 보고되지 않아. 그러나 지구온난화에 의해 분포가 확장될 경우, 한국에서도 벼에 피해를 입히는 중요한 해충이 될 가능성이 있다. 이 연구는 미래에서 호리허리노린재 발생양상 변화를 비교분석하기 위해 계절 발생 모형을 개발하였다. 월동에서 깨어난 호리허리노린재 성충의 유입모델은 문헌자료를 이용했으며, 항온조건에서 온도발육 및 산란실험을 수행하였다. 시뮬레이션 결과는 2015년 남해군에서 실시한 야외발생조사와 비교분석하였다. 또한 미래 지구온난화 기후예측모델인 RCP 8.5 시나리오를 이용하여 지구온난화에 따른 발생양상을 비교 분석하였다. 50%의 월동성충이 유입되는 시기는 2015년 175일에서 2050년대 172일, 2090년대 159일로 점차 앞당겨질 것으로 예측되었고, 연간 세대수는 2030s, 2050s는 3세대, 2070s, 2090s는 4세대가 발생할 것으로 나타났다. 또한 최성기는 2015년 269일에서 2090년대 260일로 점차 앞당겨질 것으로 예측되었다.

주요어: 호리허리노린재, 유입모델, 발육 산란모델, 계절 발생 모델, RCP 8.5
학번: 2014-22928