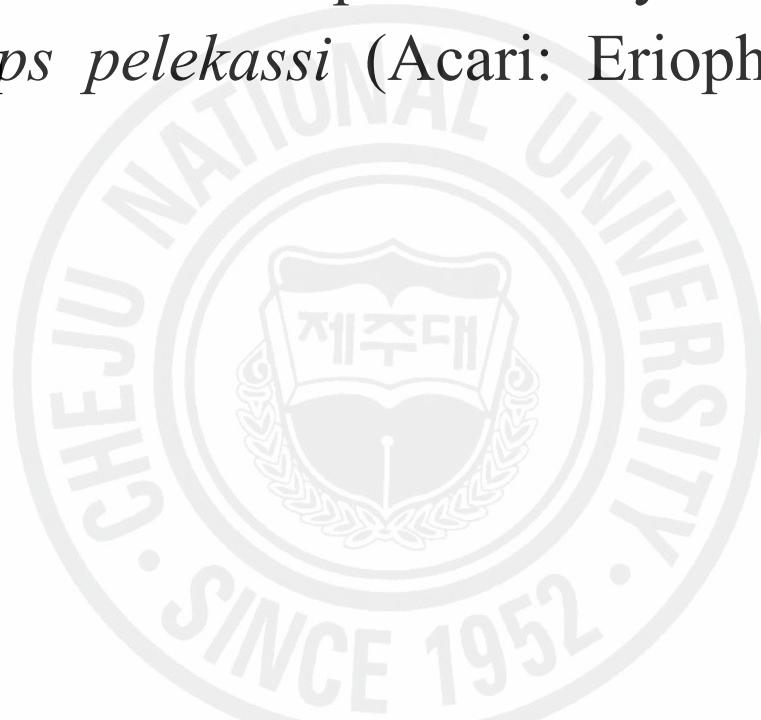Thesis for the Degree of Master of Agriculture

A Temperature-dependent Matrix Model for the Population Dynamics of *Aculops pelekassi* (Acari: Eriophyidae)

CHEJU NATIONAL UNIVERSITY

DEPARTMENT OF AGRICULTURE

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碩士學位論文

귤녹응애 개체군 동태 분석을 위한 온도의존 행렬모형

濟州大學校 大學院

農 學 科

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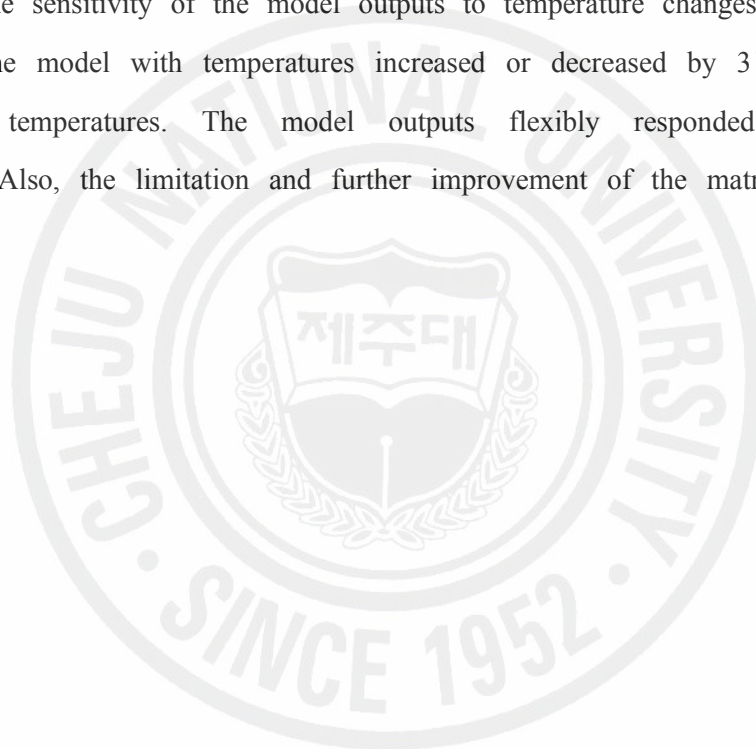
ABSTRACT

Pink Citrus Rust Mite, *Aculops pelekassi* (Keifer), is an important Eriophyoid pest (Acari: Eriophyoidae) in the citrus orchards of Jeju, Korea. The most damages occur on fruits resulting in serious economic losses. This study was carried out to develop a temperature-dependent matrix model that can be used for the projection of the population dynamics of *A. pelekassi* in citrus orchards. The temperature-dependent development and fecundity of *A. pelekassi* were investigated, and biological parameters were estimated to construct the matrix model. Egg development times decreased with increasing temperature and ranged from 6.59 d at 16℃ to 1.93 d at 35℃. Total development times of nymphs decreased from 8.18 d at 16℃ to 3.30 d at 35℃. The egg to adult durations were 14.76, 11.59, 9.71, 8.03, 7.32, 6.13, and 5.23 d at 16, 20, 24, 26, 28, 32, and 35℃, respectively. By fitting linear models to the data the lower developmental threshold temperatures for eggs, nymphs, and total (egg + nymph) were calculated as 9.30, 4.33, and 6.68℃, respectively. The thermal constants were 54.00, 101.76, and 153.84 degree-days for each of the above stages. The non-linear model was based on a biophysical model, which well fits the relationship between development rate and temperature for all stages. The Weibull function provided a good fit for the distribution of development times of each stage. Adult longevity decreased with increasing temperature and ranged from 24.17 d at 16℃ to 14.60 d at 35.0℃. *A. pelekassi* had a maximum fecundity of 33.07 eggs per female at 28℃, which declined to 18.75 eggs per female at 16℃. Also, three temperature-dependent components for an oviposition model of *A. pelekassi* were developed including models for total fecundity, age-specific cumulative oviposition rate, and age-specific survival rate. A temperature-dependent matrix model was developed to analyze the population dynamic of *A. pelekassi*, based on the above experiment data. The age class of *A. pelekassi* was categorized into three stages: egg, nymph and adult. Transition probabilities from an age class to the next

age class or the probabilities of remaining in an age class were obtained from development rate function of each stage (age classes). The fecundity coefficients of adult population were estimated by the product of adult longevity completion rate (1/longevity) and temperature-dependent total fecundity. Model outputs showed the typical form of exponential population growth. The matrix model outputs were compared with the actual field data in 2007, to test its validation ability. On leaves in early season, the model outputs pursued the actual population of *A. pelekassi* during a considerable days ≈20 d. On fruits in mid-season, however, the model outputs showed a larger discrepancy with the actual. The sensitivity of the model outputs to temperature changes was examined by running the model with temperatures increased or decreased by 3℃ from 30 yr average air temperatures. The model outputs flexibly responded to changing temperatures. Also, the limitation and further improvement of the matrix model were discussed.

I. INTRODUCTION

Pink Citrus Rust Mite (PCRM), *Aculops pelekassi* (Keifer), is an important Eriophyoid pest (Acari: Eriophyoidae) in the citrus groves of Jeju, Korea. *Aculops pelekassi* gives damages on leaves, stems, and developing fruits of citrus, especially in organic citrus orchards (Lindquist and Amrine, 1996). The most damages occur on fruits resulting in serious economic losses.

Aculops pelekassi has four developmental stages during its life cycle: egg, first instar (larva), second instar (nymph), and adult (Childers et al., 2007). The egg of *A. pelekassi* is a half-sphericity in shape, 0.04mm in diameter, translucent and yellow to pink in color. The newly hatched larva (0.12 - 0.15 mm in length) resembles the adult, changing in color from clear to pink after molting to the nymphal stage. The first nymphal stage resembles the larval and requires a few days to molt to an adult.

Aculops pelekassi has two types of female: protogynes and deutogynes (Lindquist and Amrine, 1996). The protogyne female is the reproductive form in the growing season, while the deutogyne female is the overwintering stage. The deutogyne females overwinter between bud scales of citrus trees and become active in the spring. Before blooming, they are usually found on the stalks of leaves and fruit, and then disperse to new foliage. In cases of damages on leaves, the color of the damaged leaves turns "rust-like" (hence, the name "rust mite") and sometimes the shape of the leaf is deformed. When fruits are initially damaged, parts of the fruits turn grey in color and if further damage occurs, the surface of the fruit become rust-like as well as blackening.

Because the size of *A. pelekassi* is very small, it is difficult to detect their first occurrences on the fruits. Also, the initial damage is so obscure that their damage is frequently overlooked. This is one of the major reasons why farmers sometimes miss the control time. *A. pelekassi* populations rapidly increase once they have met an optimal environmental condition in humidity and temperature for oviposition and

breeding, and then rapidly lead to losses on citrus. However, a few studies have been conducted for the biology and life history, which can be used for the forecasting and controling of *A. pelekassi* populations (Seki, 1979; Seki, 1981; Childers and Achor, 1999). The all data were obtained in orchards from Japan or Unite States, where the weather conditions are different than Jeju. Thus, their direct application is limited in the Jeju area. No designed study on the biology and ecology of *A. pelekassi* has been conducted in Jeju, and there is no information that can be used in field applications.

Thus, this study was carried out to develop a temperature-dependent matrix model that can be used for the projection of the population dynamics of *A. pelekassi* in citrus orchards. Temperature-dependent development and fecundity of *A. pelekassi* were investigated, and biological parameters were estimated to construct the matrix model.
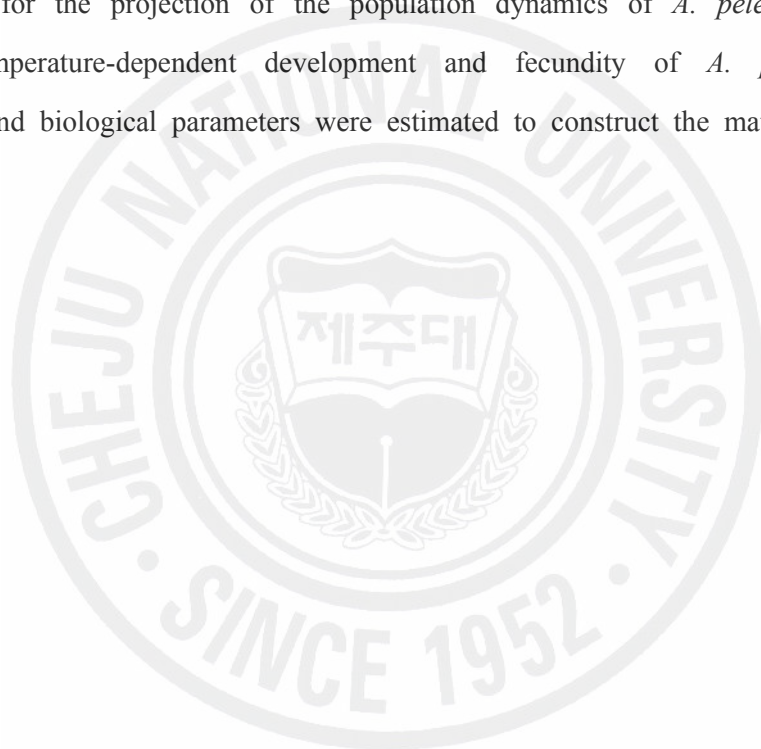
II. HISTORICAL REVIEW

The family Eriophyidae, usually called as gall mite, bud mite or blister mite (Keifer et al., 1982). The eriophid mite are small in size with average 200 μm adult body length ranging from 80 to 500 μm, and golden yellow to pink in color (Keifer, 1975; Mohanasundaram, 1984; Smith et al., 1997, 1984; Lindquist, 1996a). The idiosoma (body) is wormlike, with an elongated and transversely annulated opisthosoma, and with only 2 pairs of legs having a empodial feather claw instead of paired true claws (Lindquist, 1996). The mite commences the life as an egg, passes through two immature stages and finally emerges as an adult (Lindquist, 1996). The eggs are laid on leaves or among buds. It is are small, about 20~60 μm in diameter. The eggs is hemispheric shape and translucent. The extremely small size and secret habits of eriophyid mite cause them to be ignored or overlooked, and make them little understood and appreciated by most people (Manson, 1984). The eriophyid mites are highly specific parasites of plant and may attack all plant parts except for the roots (Westpal and Manson, 1996).

All the members of superfamily Eriophyoidae feed on living green tissue of their hosts. Some of them live on the surface of leaves or fruits, or inhabit inside buds and they are known to live and multiply only on susceptible host plant species that are usually closely related (Jeppson et al., 1975; Wespal, 1980). The Eriophyoidae is a superfamily of mites consisting of three families: Phytoptidae with 18 genera, Eriophyidae with 168 genera and Diptilomiopidae with 40 genera (Lindquist and Amrine, 1996). Especially, Nalepa (1886~1929) as by far dominant and leading worker of the early days in the eriophyoid field, described 12 genera and 479 species. At the modern age, Keifer (1930-1982) played an important role in advancing the systematics and biology of eriophyoid mites through describing a total of 113 genera and 711 species as author or coauthor (Lindquist and Amrine, 1996). The family Eriophyidae has

3,192 described species in 227 valid genera, accounting for about 87% of all known species in the superfamily Eriophyoidae that consist of 3,667 species in 301 valid genera (Amrine et al., 2003). The family Eriophyidae is at present considered as a group of 6 subfamilies such as Aberoptinae, Ashieldophyinae, Cecidophyinae, Eriophyinae, Phyllocoptinae and Nothopodinae (Amrine et al., 2003).

The Eriophyoidae occur on a wide range of flowering plants, conifers and ferns throughout the world (Oldfield, 1996; Knihinicki and Boczek, 2003). The wide range feeding of eriophyid mite have relation to fruits quality and production loss as changed browning by result damaged to fruits surface (Yothers, 1930; McCoy el al., 1976). The eriophyoid mite forms a significant component of the pest complex on citrus throughout the world and occur in both arid and humid citrus growing regions. The species complex of eriophyoid mite on citrus worldwide is described in Table 1 (Childers and Achor, 1999). In Jeju, Korea, pink citrus rust mite, *Aculops pelekassi*, was only recorded on citrus (Lee, 2006).

The major eriophid mites that occur in Florida, Unite States, have been reported as pink citrus rust mite (PCRM), *Aculops pelekassi* and citrus rust mite (CRM), *Phyllocoptruta oleivora*. The CRM is found throughout the world (Jeppson et al., 1975) and was first reported on Florida citrus by Ashmead (1879) (Childers and Achor, 1999). And CRM has been recognized generally as the most important arthropod pest on Florida citrus (Yothers and Mason, 1930; Childers, 1994). CRM are generally yellow to straw colored and somewhat wedged-shaped. The prodorsal shield is well defined and distinctly different by having very short dorsal setae that do not extend beyond the distal margin of the shield (Childers and Achor, 1999). The pre-oviposition period of CRM was 1.8 d and total egg production ranged from 26 to 29 per female or 1 or 2 eggs per day (Yothers and Mason, 1930; Swirski and Amitai, 1959). The generation time (the period of egg to adult) of CRM is 6 d at 30℃. A female lays total 30 eggs during the life time of 4-6 weak (Smith et al., 1997). The population growth of CRM decreases with decreasing humidity (Hobza and Jeppson, 1974; Childers and Achor, 1999). The PCRM differs from the citrus rust mite by having a concave back

(opisthosomal area) and dorsal tubercles that arise at the rear shield margin (Keifer, 1959). The dorsal setae extend beyond the distal margin of the prodorsal shield. The female are 140-150 ㎛ in length and golden yellow to pink in color (Childers and Achor, 1999). PCRM begins to feed on very small fruit during April or May. Numerous young 'Hamlin' and 'Valencia' fruit 3 cm or less in diameter were completely russetted by PCRM (Childers and Achor, 1999).

In Croatia, PCRM had 18 - 22 generation per year between May and October (Mijuskovic, 1973). The time required from egg to adult varied with temperatures and ranged from 6.3 d at 30℃ to 14.9 d at 20℃. The pre-oviposition period was 1.8 d and the number of days from egg to egg was 7.5 d at 30℃. Oviposition was maximum at 25℃ with 21.8 eggs per female and oviposition ceased when temperature dropped to 1 5℃ (Seki, 1979).

Table 1. Eriophyoid mites found on citrus and their geographical distribution (Childers and Achor, 1999)

Species	Distribution
Eriophyidae	
Aceria sheldoni (Ewing)	Worldwide
Aculops pelekassi (Keifer)	Japan, Thailand, Paraguay, Italy, Croatia, Florida, Greece
Aculops suzhouensis (Xin & Dong)	China
Aculus advens (Keifer)	California
Calacarus citrifolii (Keifer)	South Africa
Circaces citri (Boczek)	Thailand
Cosella fleschneri (Keifer)	India
Phyllocoptruta citri (Soliman &Abou-Awad)	Egypt
Phyllocoptruta oleivora (Ashmead)	Worldwide
Phyllocoptruta paracitri (Hong & Kuang)	China
Tegolophus australis (Keifer)	Australia
Diptilomiopidae	
Diptilomiopus assamica (Keifer)	India

PCRM overwinters only in terminal and lateral buds on citrus in Japan with migration occurring in early October (Seki, 1979). Mijuskovic (1973) found that PCRM

overwintered in bud in Croatia. In Japan, Seki (1981) found that overwintering female began laying eggs on the sprouting bud and newly emerging leaves in the spring, then moved to developing leaves in early May, and onto fruit in late June (Childers and Achor, 1999). The adult start crawl out in late April from the overwintering sites of satsuma mandarin in Japan. The eggs are deposited on the buds and newly developed leaves. The population density rapidly increases in early summer, which reaches maximum in late July (Razaq et al., 2000). The population density of the mite on leaves reaches a peak between late June and late July (Ashihara et al., 2004). Burditt et al. (1963) reported that *A. pelekassi* caused distortion of young leaves when large populations occurred on new citrus growth, a form of damage not caused by CRM (Reed et al., 1964; Seki, 1979; Childers and Achor, 1999). High population of PCRM in Japan were related to higher humidity than average spring temperature and low precipitation in early Summer (Childers and Achor, 1999).

The sex ratio of the adult is biased toward females and changes seasonally: the proportion of females were 84% in October and 100% in December (Ashihara et al., 2004; Huang 1971).

So far various computer simulation models that predict the population dynamics of mite species have developed (Dover et al., 1979; Berry et al., 1991). Such simulation models need complicate biological parameters for the construction, then require a lot of experimental data. The simplest population model that has fewer parameters is one first described by Lotka in the 1920's (Lotka, 1925) and formalized in the 1940's by Leslie (Leslie, 1945). The Leslie Matrix is a discrete and age-structured model of population growth very popular in population ecology. The Leslie Matrix (also called the Leslie Model) is one of the best known ways to describe the growth of populations (and their projected age distribution), in which a population is closed to migration and where only one sex, usually the female, is considered. Although Leslie matrix models have the longer history, an alternative approach introduced in the mid-1960's by Lefkovitch (Lefkovitch, 1965) is often more useful. Instead of using an age-structured approach, the Lefkovitch model use a stage or size-structured approach. Since arthropods go through

stages that are discrete, this approach is more appropriate than applying age scale. Also, physiological age as degree-days was incorporated into the matrix model, which allow that the model can be operated under variable temperature conditions in the field (Bommarco, 2001; Caswell, 2001). An age-structured model of a fruit-mite-fungal pathogen system using Lefkovitch's technology was developed to study interactions between the 'Hamlin' orange fruit the citrus rust mite (CRM), *Phyllocoptruta oleivora*, and its fungal pathogen *Hirsutella thompsonii* (Yang et al., 1997). The model should be useful for CRM management.

III. MATERIALS AND METHODS

1. Rearing of *A. pelekassi* in laboratory

Aculops pelekassi were originally collected on citrus trees in a green house at National Institute of Subtropical Agriculture, Odeung-dong, Jeju, in November, 2006. Two kinds of rearing method were used to keep *A. pelekassi* colonies in a laboratory. Trifoliate orange trees in pot were used for the rearing of *A. pelekassi* on a massive scale. Also, additional colonies were kept on leaves of Trifoliate or Mandarine orange. The leaves in the form of rectangular pieces (7 mm × 7 mm) were placed upside down on a water-saturated sponge block (75 mm×60 mm×20 mm) in a petri-dish (dia. 95 mm, depth 45 mm). A cotton pad (70 mm×55 mm) covered with a mesh cloth (70 mm× 55 mm) on the top was placed between the leaves and sponge block to help better water absorption or to prevent escaping of *A. pelekassi*. For the growth of Trifoliate orange, 3 fluorescent tubes were installed at 50 cm hight from the bottom of tree pots. The colony was maintained at 24 ± 2℃ and a photoperiod of 16:8 (L:D)h.

2. Temperature effect on development and fecundity

2.1 Laboratory experiments

2.1.1 Immature development

A. pelekassi that obtained from the rearing culture were used for immature development experiments. An experimental device was prepared as the same method for the additional rearing colonies. Total 10 pieces (5 mm x 5mm) of a leaf were placed in a petri-dish (dia. 95 mm, depth 45 mm), and one adult female were introduced on each piece. When *A. pelekassi* laid three egss, the adult were removed and the development process was examined everyday. Seven constant temperatures (16, 20, 24, 26, 28, 32 and 35℃) were examined at a photoperiod of 16L : 8D and 50~60% RH. Females that died

during the early stages of their life spans were excluded from the data analysis.

2.1.2 Adult reproduction

A. pelekassi that obtained from the rearing culture were used for oviposition experiments. An experimental device was prepared as the same method for the additional rearing colonies. Total 10 pieces (5 mm x 5 mm) of leaf were placed in a petri-dish, and one immature *A. pelekassi* were introduced on each piece. When *A. pelekassi* reached adult, the number of eggs were recorded daily under a binocular microscope (20 - 50x). The eggs were removed at every observation, and also adult survival was checked. A new nymph was introduced on the leaf piece where *A. pelekassi* drowned or got dead early. Seven constant temperatures (16, 20, 24, 26, 28, 32 and 35℃) were examined at a photoperiod of 16L : 8D and 50 ~ 60% RH. At each temperature, 10 *A. pelekassi* were replicated. The same experiment was conducted twice, and females that died during the early stages of their life spans were excluded from the data analysis.

2.1.3 Data analysis

Analysis of variance (ANOVA) was conducted to determine statistical differences in the development, longevity and fecundity among temperature tested. PROC GLM (SAS Institute 1999) was used and means were separated by the Tukey studentized range test (P = 0.05, SAS Institute 1999).

2.2 Temperature-dependent development model of immature stages

Development rate (1/days) were expressed as the reciprocal of development time (mean values in days) of eggs and nymphs. Temperature-dependent development model of eggs and nymphs analysed using a linear and nonlinear model.

2.2.1 Linear development model

The relationships between development rates and temperatures were described. Temperature-dependent development rates of each stage was expressed as the reciprocal of development times. The lower threshold temperatures for egg, nymph, and total (egg + nymph) development were obtained by extrapolating the linear regression lines through the x-axis. The intersection points with the *x*-axis were defined the lower thresholds. The thermal constants for egg, nymph and total (egg + nymph) development were obtained by the reciprocal of the slopes of the estimated regression lines. The heat requirement for egg and nymph development were expressed in degree-days (DD). The parameter were estimated using TableCurve 2D (Jandel Scientific, 1996).

$$r(T) = aT + b \tag{1}$$

where *r*(T) is development rate (1/days) at T℃, *a* is slope, and *b* is intercept.

2.2.2 Nonlinear development model

The mean development rates of egg, nymphs and total (egg + nymph) were calculated as the reciprocals of mean development time (in days). The various nonlinear model describing relationship between temperatures and development rates are available (Stinner et al., 1974; Logan et al., 1976; Sharpe and DeMichele, 1977; Hilbert and Longan, 1983; Moon, 1983; Ryoo and Cho, 1988). We selected the modified Sharpe and DeMichele model (Schoolfield et al., 1981) because it is based on accepted biophysical laws and has parameter that can be interpreted biologically (Wagner et al., 1984). Also, the model can describe the entire response curve over a full range of temperature.

$$r(T) = \frac{\text{RHO25} \dfrac{T}{298.15} \exp\left[\dfrac{HA}{R} \left(\dfrac{1}{298.15} - \dfrac{1}{T} \right) \right]}{1 + \exp\left[\dfrac{HL}{R} \left(\dfrac{1}{TL} - \dfrac{1}{T} \right) \right] 1 + \exp\left[\dfrac{HH}{R} \left(\dfrac{1}{TH} - \dfrac{1}{T} \right) \right]} \tag{2}$$

where *r(T)* is the mean development rate at temperature *T* (K), R is the universal gas constant (1.987 cal · degree[-1] · mole[-1]), *RH025* is the development rate at 25℃ (298.15K)

assuming no enzyme inactivation, *HA* is enthalpy of activation of the reaction catalyzed by a rate-controlling enzyme, *TL* is Kelvin temperature at which the rate-controlling enzyme is half active and half low-temperature inactive, *HL* is change in enthalpy associated with low temperature inactivation of the enzyme, *TH* is Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive, and *HH* is the change in enthalpy associated with high-temperature inactivation of the enzyme. The parameters of biophysical model were estimated using the TableCurve 2D program.

2.2.3 Distribution model of development time

The variation in the development times of eggs, nymphs and total (egg + nymph) was fitted by a three-parameter Weibull-function.

$$f(px) = 1 - \exp(-[(px - \gamma)/\beta]^{\delta})$$ (3)

where *f(px)* is the cumulative probability of complete development at normalized age (physiological age) *px*, and γ, η and β are parameter to be estimated. Before fitting data with the Weibull function, the cumulative frequency distributions for the development times of each stage were constructed by adding up the frequencies in successive ages of each stage in days. Dividing each age by the median development time normalized the age scales in days of each stage. Normalizing age scales in each stage placed the cumulative probability distribution at different temperature approximately in the same position. The parameters of Weibull model were estimated using the TableCurve 2D program.

2.3 Adult oviposition model

The model was constructed using the method by Kim and Lee (2003). The oviposition of insect can be described by three temperature-dependent components : temperature-depe

ndent total fecundity, age-specific cumulative oviposition rate, age-specific survival rate (Curry and Feldman, 1987).

2.3.1 Adult development model

The reciprocal of mean longevity (in days) was regarded as adult development rate for the purpose of modeling, and was modeled as a function of temperature using the biophysical model (equation 2). The estimated development model was used for calculating the physiological age of *A. pelekassi* adult. The physiological age (*Px*) of adults from the starting time to the *n*th time step was defined as (Curry and Feldman, 1987).

$$Px = \int_0^n r(T_i) \approx \sum_{i=0}^n r(T_i) \tag{4}$$

where $r(T_i)$ is the development rate at temperature T (K) of ith day after the adult emergence.

2.3.2 Temperature-dependent total fecundity model

Total number of eggs per female was obtained by summing up the eggs laid during the whole adult female life span. The mean total fecundity was calculated by dividing sum of total eggs laid by all female by the number of females examined. The relationship between the mean total fecundity and temperature (℃) was fitted by a Gaussian model (equation 6). The equation produces the number of total eggs laid by a female adult during her whole life span at temperature (℃).

$$f(T_c) = R_{max} \exp[-0.5((T - T_{max})/k)^2] \tag{5}$$

where $f(T_c)$ is the number of total eggs produced by a female adult during her whole life span at temperature T_c(℃). The parameters are defined as follows : R_{max} is the maximum reproductive capacity, and T_{max} is the temperature (℃) at which the maximum

reproduction occurs. The values of the parameters were estimated using TableCurve 2D (Jandel Scientific, 1996).

2.3.3 Age-specific cumulative oviposition rate model

The age-specific cumulative oviposition rate is the proportion of the total lifetime reproductive potential that elapses during each time period. It was fitted by two-parameter Weibull model.

$$p(Px) = 1 - \exp - (Px/\alpha)^{\beta} \tag{6}$$

where *p(Px)* is the cumulative proportion of eggs laid by physiological age *Px* by a female adult, and α and β are fitted constant.

The equation calculates the cumulative proportion of eggs laid by a female adult of physiological age *Px*. The cumulative oviposition rates at each temperature were calculated as the total cumulative number of eggs laid up to a specific physiological age divided by the total number of females alive at the age. The physiological age was calculated using equation 4. The mean cumulative oviposition rates were regressed against the physiological age to estimate the parameters of age-specific oviposition curve using TableCurve 2D (Jandel Scientific, 1996).

2.3.4 Age-specific survival rate model

The sigmoid function was used to describe the age-specific survival distribution of *A. pelekassi* for its simplicity and shape fitting ability. The survival proportions at physiological age *(Px)* were fitted to this function :

$$s(Px) = \frac{1}{1 + \exp^{(\gamma - Px)/\delta}} \tag{7}$$

where *s(Px)* is the proportion of live females at the physiological age *Px*, γ the

physiological age at 50% survival, and δ a fitted constant. The parameter were estimated using TableCurve 2D (Jandel Scientific, 1996).

2.3.4 Daily egg production

The cumulative number of eggs laid by a female adult at ith time (i.e., physiological age Px_i) is the product of the temperature-dependent total fecundity [$f(T_c)$], the age-specific cumulative oviposition rate [$p(Px_i)$], and the age-specific survival rate [$s(Px_i)$]. Therefore, the number of eggs laid by a female during the physiological age interval between Px_i and Px_{i+1} can be calculated as :

$$f(Tc)[p(Px_{i+1}) - p(Px_i)]\frac{s(Px_i) + s(Px_{i+1})}{2} \tag{8}$$

3. Matrix model construction and field validation
3.1 General form of matrix model

To analysis population dynamics of *A. pelekassi*, Lefkovitch matrix model (Lefkovitch, 1965) was used. The age class of *A. pelekassi* was categorized into three development stages; eggs, nymphs, adult. The matrix-model takes the form,

$$n_i(t+1) = A(t)n_i(t) \tag{9}$$

where n is a columm vector whose elements $n_i(t)$ are the numbers of individuals that belong to the *i-th* development stage at time t, and $n_i(t+1)$ is the number of individuals at time $t+1$. In this study, a time interval of 1 day (24 hours) was applied. The projection matrix A is the non-negative square matrix whose elements a_{ij} represent the transition probabilities or the fertility coefficients that provide the contributions from individuals in the *i*-th stage to the *j*-th stage over the time projection interval.

The age structure vector $n(t)$ representing the populationm (population dynamic) at time t

is,

$$n(t) = \begin{bmatrix} n_e(t) \\ n_l(t) \\ n_a(t) \end{bmatrix} \tag{10}$$

where $n_e(t)$, $n_l(t)$ and $n_a(t)$ denote the numbers of eggs, nymphs adults at time t, respectively.

The projection matrix $A(t)$ at time t takes the form,

$$A(t) = \begin{bmatrix} P_e(t) & 0 & f(T_t) \\ M_e(t) & P_l(t) & 0 \\ 0 & M_l(t) & P_a(t) \end{bmatrix} \tag{11}$$

where $f(T_t)$ is the fecundity coefficients of adult population at $T℃$ at time t, and $M_i(t)$ is the transition probabilities that estimate shifted individuals from ith stage to $i+1$th. The $P_i(t)$ is the probabilities of remaining in ith stage within a unit interval (e: egg; l: nymph; and a: adult).

In this study, we describe a matrix model for *A. pelekassi* which incorporates temperature-dependent transition rates into the model, based on development rate function as a physiological scale. The parameters needed for immature development and adult fecundity of *A. pelekassi* were taken from the previous studies.

The transition probabilities and remaining probabilities for each stage were estimated as:

$$M_i(t) = r_i(T_t) \tag{12}$$

$$P_i(t) = 1 - M_i(t) \tag{13}$$

where $r_i(T_t)$ is development rate by ith stage at $T℃$. The fecundity coefficients takes the form,

$$f(T_t) = Fc(T_t) \cdot r_a(T_t) \qquad (14)$$

where $Fc(T_t)$ is adult development rate (1/longevity) by total number of eggs per female at T℃ and $r_a(T_t)$ is adult development rate (1/longevity) at T℃. When the survivals of each stage were concerned, the forms of $M_i(t)$ have $r_i(T_t) \cdot S_i$ (S_i is an overall survival rate of ith stage) with assuming that the mortality occur just before transition.

3.2 Field validation

3.2.1 Field phenology data collection

To evaluate the fitting ability of the developed matrix-model, model outputs were compared with field data of *A. pelekassi* which were obtained from 3 citrus orchards in Jeju city and one orchard in Seogwiopo city in 2007. Total 20 leaves were collected at 7 d intervals from randomly selected trees in each orchard. The collected leaves were put in a paper bag and then sealed in a vinyl bag (20 cm x 30 cm), and placed in a refrigerator at 4℃ until examined. The numbers of *A. pelekassi* on the collected leaves were examined under a binocular-microscope with 20 to 50 x magnification.

For the field validation in the early season on leaves, model running was started from 28 April with an initial densities comprised of eggs 1.2 and adult 2.5 per leaf, which were obtained from the orchard in Seogwipo city. For the projection of *A. pelekassi* population on fruits in the mid-season, initial 578 adults on 9 July were used for the input value of the model, which were obtained from orchards in Jeju city. Survival rate of eggs and nymphs was arbitrarily selected as 0.8, and sex ratio was 1.0. The outputs of matrix model were represented as the total number of nymphs to adults.

Daily average air temperatures for the orchards of Jeju city were obtained from Jeju weather station located 4km away from the orchards where the phenological data were collected. The Seogwipo temperatures were provided by a site-specific weather information system, Seoul National University, College of Agriculture & Life Sciences.

3.2.2 Sensitivity analysis

The sensitivity analysis of the matrix-model was conducted with changing driving temperatures by ± 3℃ from average temperatures in normal years.

V. RESULTS

1. Temperature-dependent development and fecundity

1.1 Immature development period

The mean development periods of *A. pelekassi* at constant temperatures are shown in Table 2. Temperature significantly affected *A. pelekassi* egg and nymph development (F = 50.96; df = 6, 113; p < 0.0001), nymph development (F = 39.38; df = 6, 113; p < 0.0001) and total (egg + nymph) (F = 65.52; df = 6, 113; p < 0.0001). The development times of *A. pelekassi* was decreased with increasing temperature. The shortest egg development time was 1.93 d at 35℃, and the longest 6.59 d at 16℃ in the range of temperature examined. Also, the nymphal development period was shortest at 35℃. Nymph development time was 2.5 times longer at 16℃ than at 35℃. The egg to adult durations were 5.23, 6.13, 7.32, 8.03, 9.71, 11.59, and 14.76 d at 16, 20, 24, 26, 28, 32, and 35℃, respectively.

1.2 Adult longevity and fecundity

The longevity of *A. pelekassi* female adult were affected by temperature (Table 3) (F = 4.77; df = 6, 80 ; p = 0.0003). The longevity decreased significantly with increasing temperature, and ranged from 24.17 days at 16℃ to 15.50 days at 32℃. But the longevity showed similar values about 14 to 15 days from 32℃ to 35℃. The fecundity was also affected by temperature (Table 3) (F = 5.25; df = 5, 72 ; p = 0.0004). The fecundity was increased with increasing temperature up to 28℃, and then declined little thereafter. In the range of 16 - 35℃, egg production was highest at 28℃. The highest total number of eggs laid by a female was 33.07 eggs at 28℃ and the lowest number of egg laid by a female was 18.75 eggs at 16℃.

Table 2. Development period (days, mean ± SE) for eggs and nymphs of *Aculops pelekassi* at various temperatures in the laboratory

Temperature(℃)	Developmental stage					
	Egg		Nymph		Total (egg + nymph)	
16	6.59 ± 0.50a[a]	(17)[b]	8.18 ± 0.41a	(17)	14.76 ± 0.86a	(17)
20	5.22 ± 0.15b	(18)	6.35 ± 0.20b	(18)	11.59 ± 0.23b	(18)
24	4.12 ± 0.14c	(17)	5.59 ± 0.19bc	(17)	9.71 ± 0.22c	(17)
26	3.40 ± 0.14cd	(15)	4.63 ± 0.17cd	(15)	8.03 ± 0.23cd	(15)
28	2.73 ± 0.15de	(22)	4.59 ± 0.33cd	(22)	7.32 ± 0.34de	(22)
32	2.63 ± 0.13de	(16)	3.50 ± 0.20de	(16)	6.13 ± 0.25ef	(16)
35	1.93 ± 0.09e	(15)	3.30 ± 0.12e	(15)	5.23 ± 0.16f	(15)

[a]Means followed by the same letter within a column are not significantly different (P>0.05, Tukey studentized range test).

[b]The number in parentheses are sample size.

Table 3. Adult longevity (mean ± SE) and total fecundity of *A. pelekassi* on citrus leaves at constant temperature

Temperature(℃)	Longevity of adult female		Fecundity (No. of egg per female)	
16	24.17 ± 2.17 a[a]	(12)[b]	18.75 ± 0.95c	(12)
20	21.64 ± 1.22 ab	(19)	22.47 ± 2.47bc	(19)
24	20.00 ± 1.14 b	(14)	25.21 ± 2.40abc	(14)
26	18.33 ± 1.20 ab	(9)	-	
28	16.47 ± 1.13 b	(15)	33.07 ± 1.64a	(15)
32	15.50 ± 1.07 b	(8)	29.63 ± 2.83abc	(8)
35	14.60 ± 1.28 b	(10)	29.80 ± 3.12ab	(10)

[a]Means followed by the same letter within a column are not significantly different ($P > 0.05$, Tukey studentized range test).

[b]Number in parentheses are sample size.

2. Estimation of basic sub-models

2.1 Temperature-dependent development model of immature stages

2.1.1 Low threshold temperature and thermal constant

The linear regression lines of mean development rates against temperatures provided estimates of the lower threshold temperatures of 9.30℃ for eggs (r^2 = 0.94), 4.33℃ for nymphs (r^2 = 0.97), and 6.68℃ for the total of egg and nymph combined (r^2 = 0.98) (Table 4 and Fig. 1). The thermal constants for egg, nymph were 54.0, and 101.76 degree-days (DD), respectively. The thermal requirement for total (egg + nymph) development was 153.84 DD.

2.1.2 Nonlinear development model

The relationship between development rates and temperatures was well described by two-parameter biophysical model of Sharpe and DeMichele (1977) (Fig. 1). The development rates increased constantly with increasing temperature without an high or low temperature inhibition in the range of temperature examined (Fig. 1). The estimated parameter values are shown in Table 5.

2.1.3 Distribution model of development time

The cumulative distribution of development completion for each stage of *A. pelekassi* at different temperatures are seen in Fig. 2. The position of curves along the development time (age scale in days) showed a large variation. However, the variation was greatly reduced by the normalization of the age scale. The cumulative distributions of development time against the normalized age of each stage are shown in Fig. 3. Distributions of the different stages had a similar shape, and they were adequately described by the Weibull function. The estimated parameter values of the distribution functions are shown in Table 6. The value of parameter η was lower for the egg stage

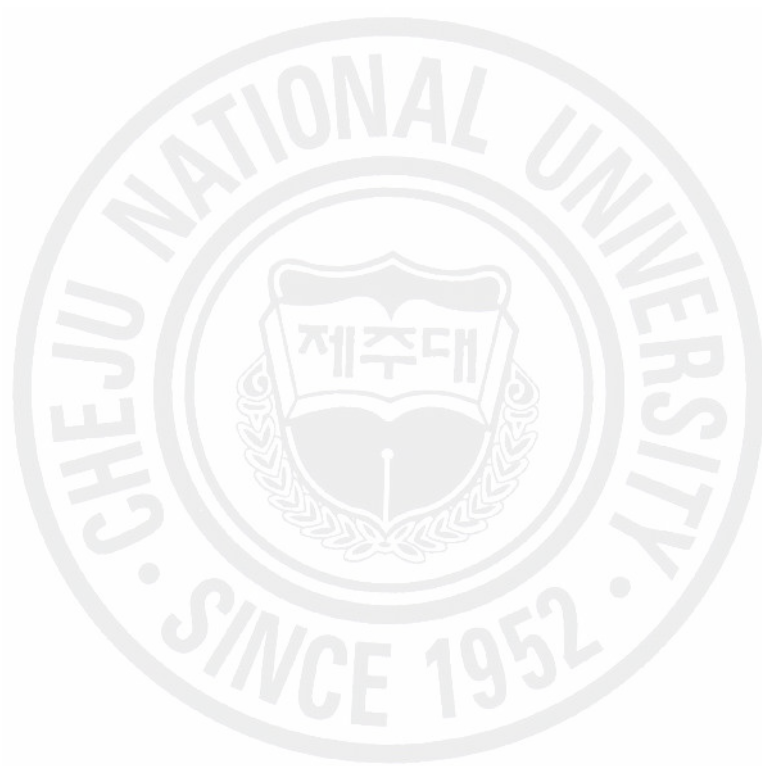than those for other stages, indicating that egg development time was more variable.

Table 4. Lower developmental thresholds (℃) and thermal requirements in degree-days (DD) for *A. pelekassi* eggs and nymphs

Stage	Regression equation[a]	Lower threshold temperature (℃)	Thermal constant (degree-days, DD)	r^2
Egg	y=0.0185x-0.1699	9.30	54.00	0.94
Nymph	y=0.0098x-0.0425	4.33	101.76	0.97
Egg + nymph	y=0.0065x-0.0434	6.68	153.84	0.98

[a]$y = ax + b$, where y is the rate of development (1/day), b is the intercept, a is the slop, and x is the temperature (℃).

Table 5. Estimated parameter values of biophysical development model of *A. pelekassi* at constant temperature

Development stage	RHO25	HA	r^2
Egg	0.2638 ± 0.01108	10648.3931 ± 1069.03792	0.96
Nymph (1st-2nd)	0.1902 ± 0.00415	7841.2635 ± 578.81838	0.98
Egg + nymph	0.1102 ± 0.00138	8962.0455 ± 327.33953	0.99

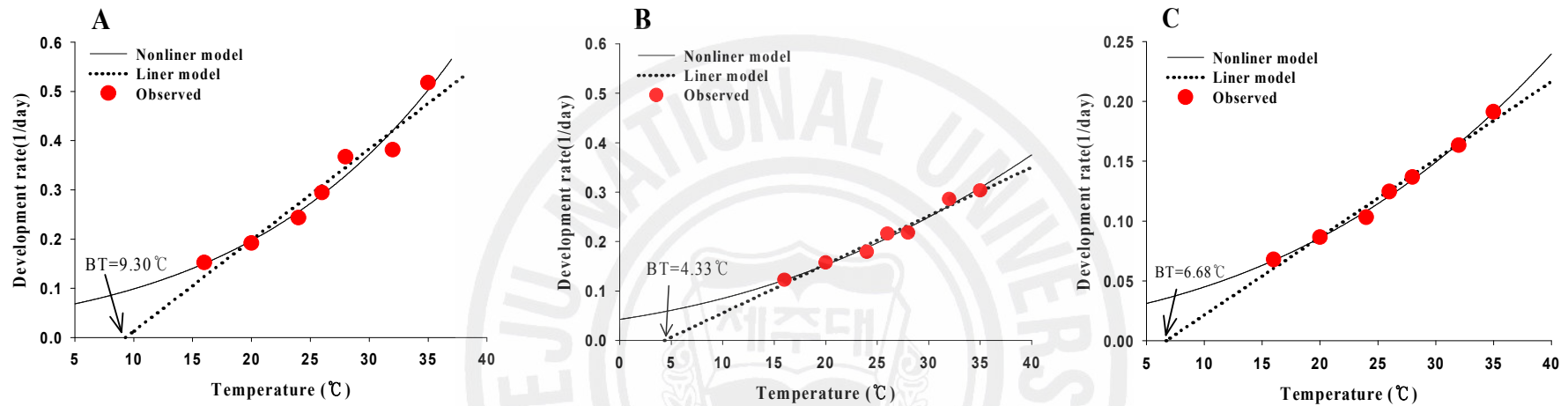Biophysical model of Sharpe and DeMichele (1977) was applied.

Fig. 1. Development rate (1/days) curve for egg, nymph of *A. pelekassi* as a function of temperature. BT indicates estimated base threshold temperature. (A) eggs, (B) nymphs, and (C) total (eggs + nymphs).
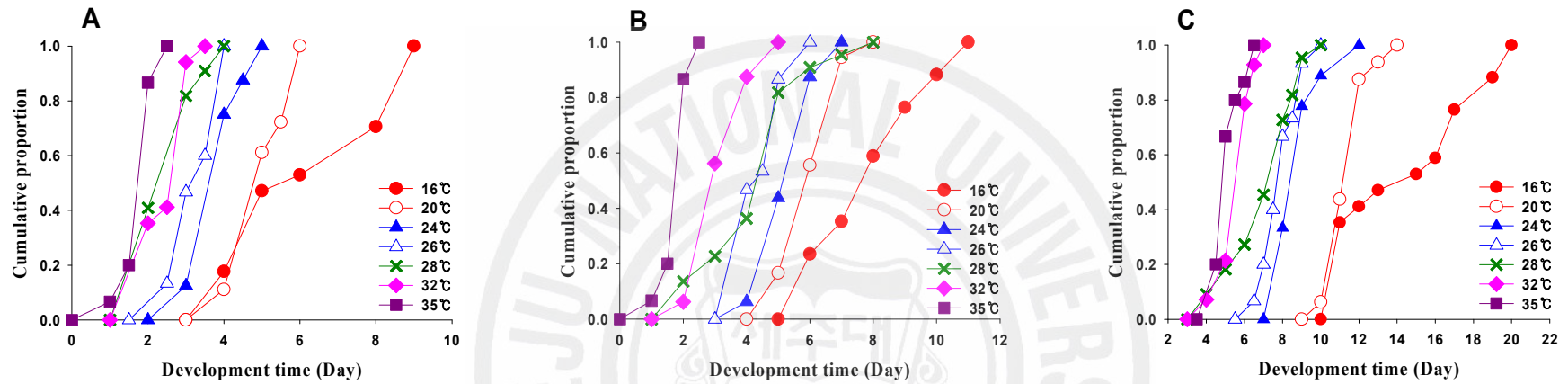
Fig. 2. Cumulative distribution of development completion for each stage of *A. pelekassi* at different temperatures. (A) eggs, (B) nymphs, and (C) total (eggs + nymphs).

Table 6. Estimated parameter values of distribution model of development time for each stage of *A. pelekassi* calculated with three-parameter Weibull function

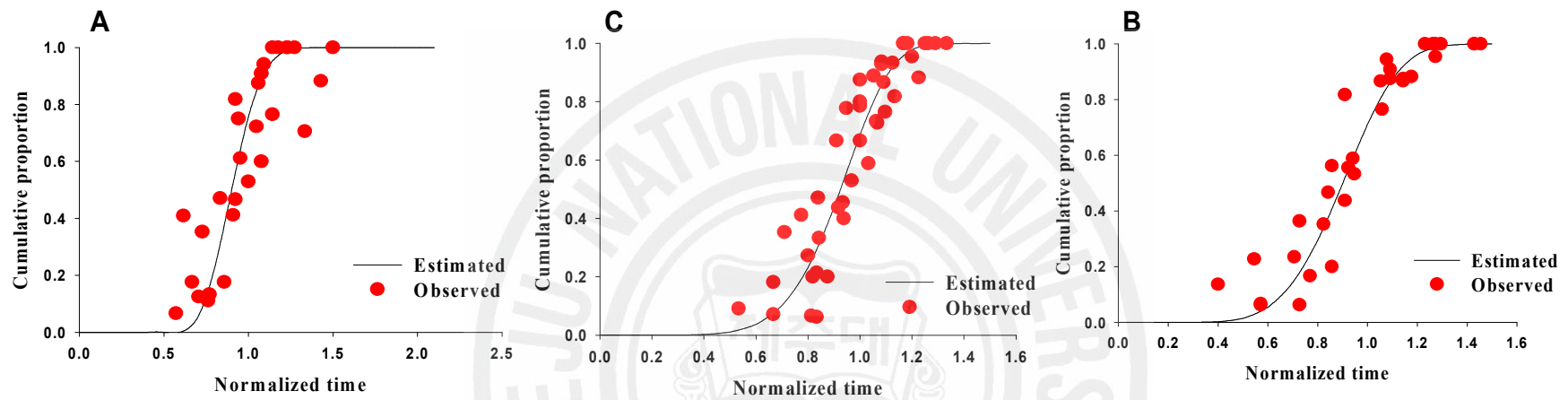| Development stage	Parameter			r^2
	ɣ	η	β	
Egg	0.571 ± 0.2597	0.377 ± 0.2691	2.715 ± 2.188	0.87
Nymph	0.235 ± 0.4587	0.726 ± 0.4646	4.183 ± 2.8356	0.95
Egg + nymph	0.047 ± 1.3747	0.930 ± 1.382	6.285 ± 9.6848	0.87

Fig. 3. Distribution curves of development completion for each stage of *Aculops pelekassi* as a function of normalized age. Three-parameter Weibull function was applied. (A) eggs, (B) nymphs, and (C) total (eggs + nymphs).

2.2 Adult oviposition model

2.2.1 Adult development model

Adult longevity was regarded as adult development. The mean development rate of adult were calculated as the reciprocals of mean longevity (in day). The adult development rates (1/mean longevity) were fitted to the nonlinear biophysical developmental model (Schoolfield et al. 1981) (Fig. 4, Table 7). High or low temperature inhibition of development was not found. The parameters were within the range as recommended by Wagner et al. (1984).

2.2.2 Oviposition model components

The estimated model components (temperature-dependent total fecundity, age-specific cumulative oviposition rate and age-specific survival rate) for the oviposition model of *A. pelekassi* are shown in Fig. 5 and their parameters are present in Table 8.

The relationship between total fecundity and temperature was well describe by equation (5) (Fig. 5a, Table 8). In the estimated total fecundity model, the highest total number of eggs laid by a female was ≈30.8 (parameter R_{max}) at ≈31.2℃ (parameter T_{max}). Age-specific cumulative oviposition rate curve was well fitted to the Equation (6). The variations of cumulative egg production at different temperatures were clearly reduced using physiological age scale, and are well described by the two-parameter Weibull function (Fig. 5b, Table 8). Fifty percent of the total eggs were laid by ≈0.84 physiological age (parameter α) in the model.

The relationship between survivorship and adult physiological age was well described by a sigmoid function (Fig. 5c, Table 8). The overall survival curve exhibited low initial mortality, linear decrease in survival during mid-age, decreasing mortality at late age. Fifty percent mortality occurred at ≈1.37 physiological age (parameter ɤ).

Table 7. Estimated values of parameter for development rate curves (1 / mean longevity) of *A. pelekassi* female adults

Model	Parameter	Estimated value	SEM	r^2
Nonlinear model[a]	*RH025*	0.0517	0.00062	0.98
	HA	4254.6039	333.85991	

[a]Biophysical model of Sharpe and DeMichele (1977) modified by Schoolfield et al. (1981) was applied.
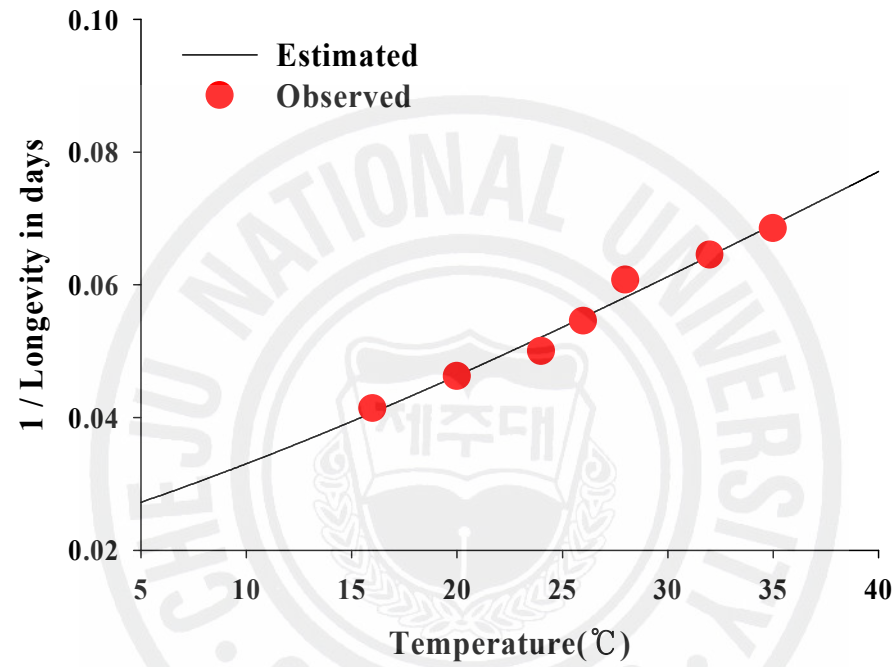
Fig. 4. Developmental rate curve (1/mean longevity) of *A. pelekassi* female adults. Two-parameter biophysical model of Sharpe and DeMichele (1977) modified by Schoolfield et al. (1981) was applied.

Table 8. Estimated values of parameter for oviposition model components of *A. pelekassi* female adults

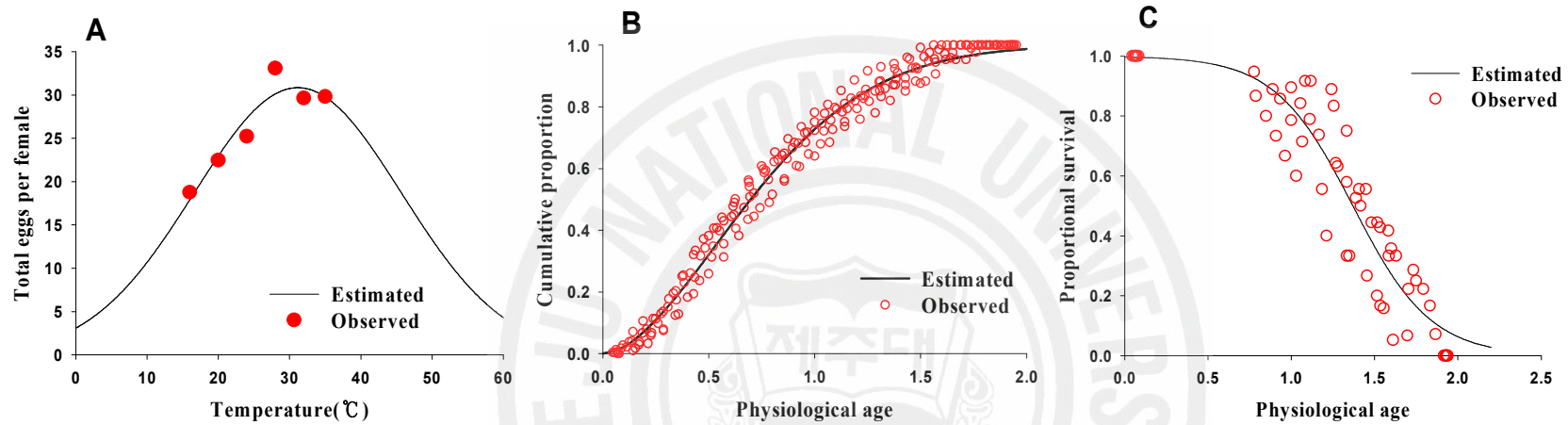| Model	Parameter	Estimated values	SEM	r^2
Temperature-dependent total fecundity model	R_{max}	30.8388	1.30812	0.89
	T_{max}	31.1554	2.42817	
	k	14.5313	3.21740	
Age-specific cumulative oviposition rate model	α	0.8434	0.00504	0.99
	β	1.7293	0.02617	
Agge-specific survival rate model	γ	1.3698	0.01992	0.88
	δ	-0.2337	0.02083	

Fig. 5. Major components of oviposition model of *A. pelekassi* female adult. (A) Temperature-dependent total fecundity curve, (B) Age-specific cumulative oviposition rate curve, (C) Age-specific survival rate curve.

2.2.3. Daily egg production

The predicted reproductive density curve in relation to the adult cohort ages and temperature is shown in Fig. 6. The fecundity of *A. pelekassi* was dependent on the temperature and age. At low temperatures, the fecundity density curve showed longer opviposition period and lower peak fecundity. As temperature increased the peak fecundity sharply increased with shorter oviposition period up to optimal temperature, and then the peak decreased.
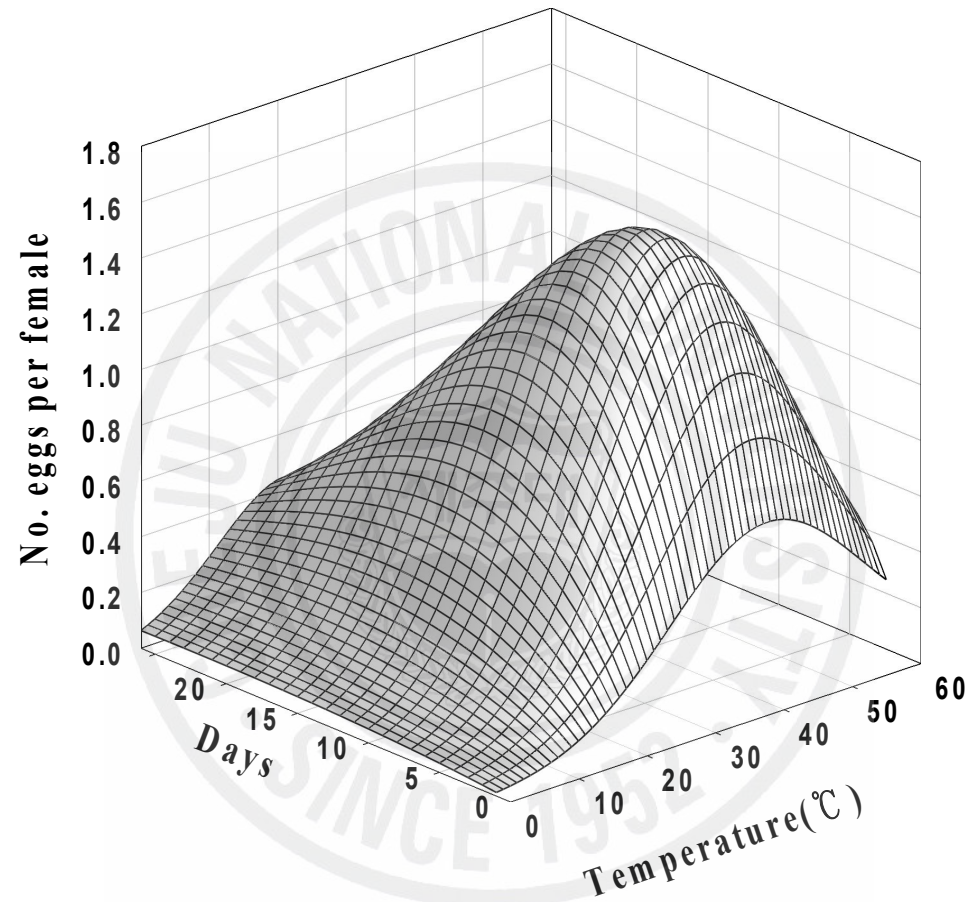
Fig. 6. Predicted oviposition density curves of *A. pelekassi* in relation to cohort age and temperature.

3. Field validation and sensitivity analysis of matrix model

3.1 Field Validation

  The observed population densities of *A. peleakssi* on leaves and fruits are shown in Fig. 7. The leaves population densities of *A. pelekassi* occurred first from late April in a low density. The density on leaves increased rapidly in late May, had a peak in late June, and then decreased (Fig. 7). The population densities of *A. pelekassi* on fruits occurred from mid-June and had a peak in July and then decreased.

  Observed and model predicted *A. peleakssi* population patterns on leaves and fruits in 2007 are shown in Fig. 8. On leaves in early season, the model outputs showed little difference with the observed actual, and generally followed the actual pattern for about 20 d after model starting. On fruits in mid-season, however, the model outputs showed a larger discrepancy with the actual.
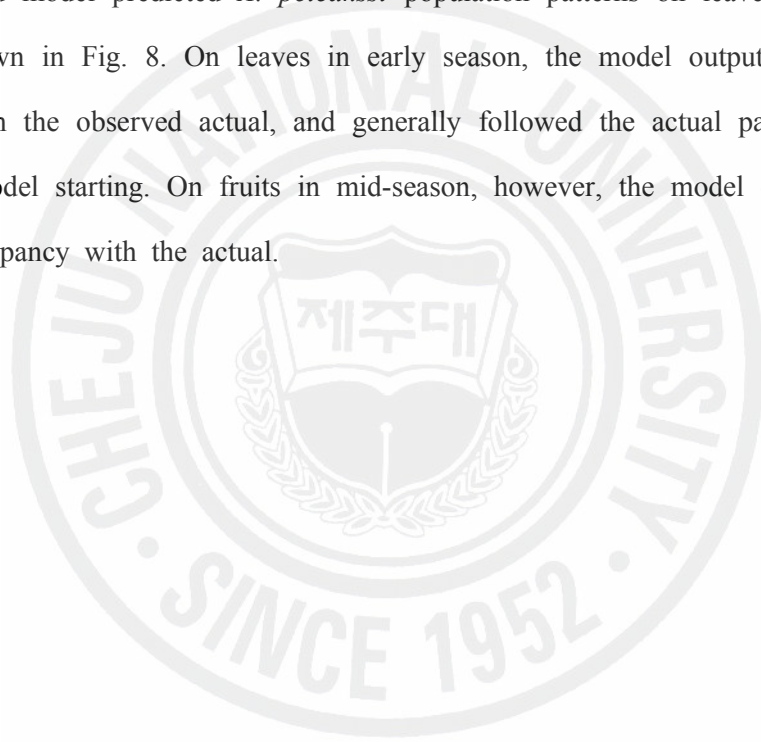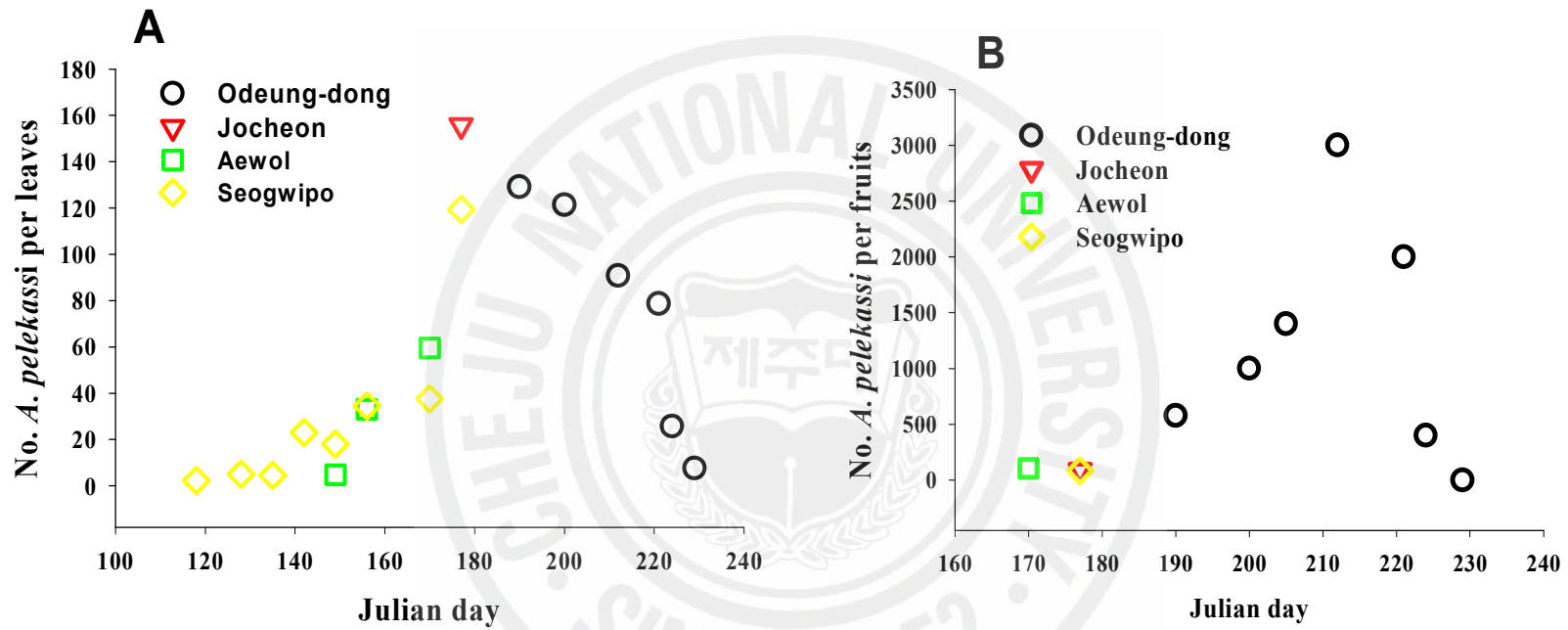
Fig. 7. Population density of *A. pelekassi* on leaves (A) and fruit (B) in Jeju, 2007.
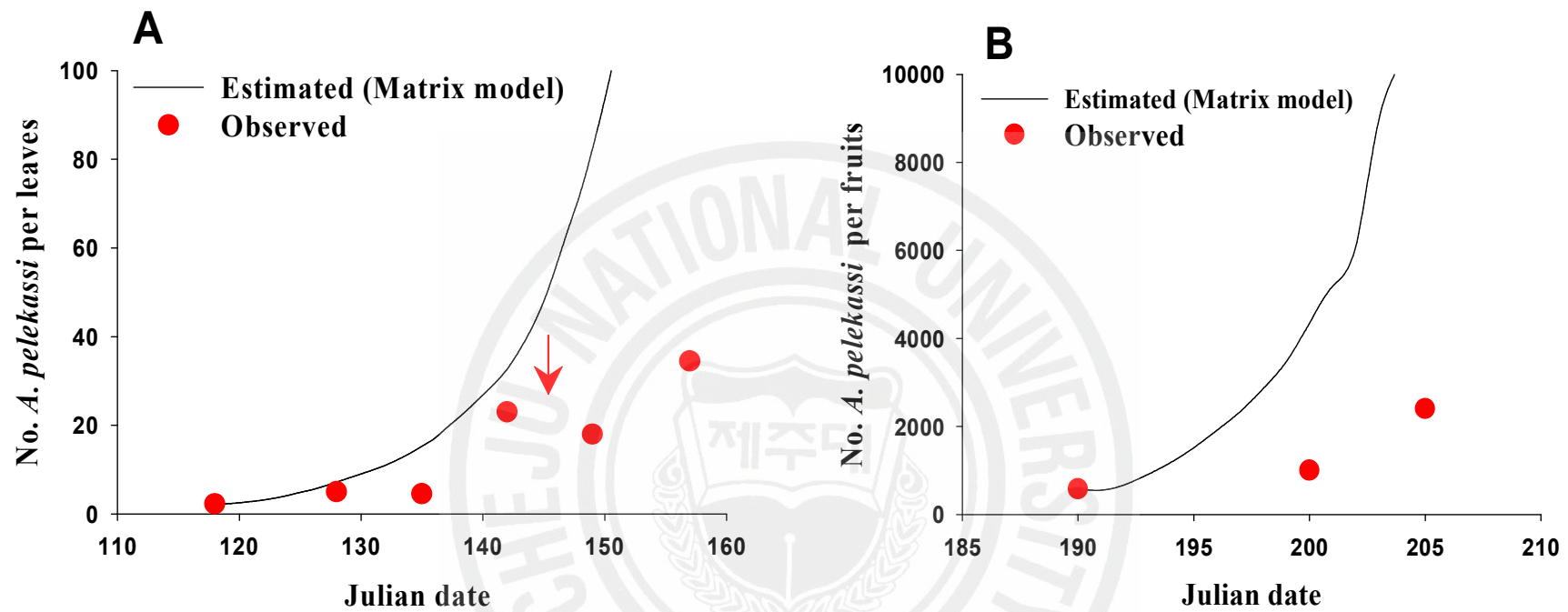
Fig. 8. Observed actual and matrix model-predicted outputs of *A. pelekassi* (nymphs and adult). A: on leaves at Seogwiop, B: on fruits at Odeung-dong. The arrow on the figure indicates an insecticide spray.

2.2 Sensitivity analysis

The results of sensitivity analysis are seen in Fig. 9, which were conducted with temperature changes by 3℃ from normal temperatures. According to temperature changes, the outputs of matrix model were flexibly changed. Time in days taken to an threshold density of *A. pelekassi* was much shorter with higher temperatures than with lower temperatures.
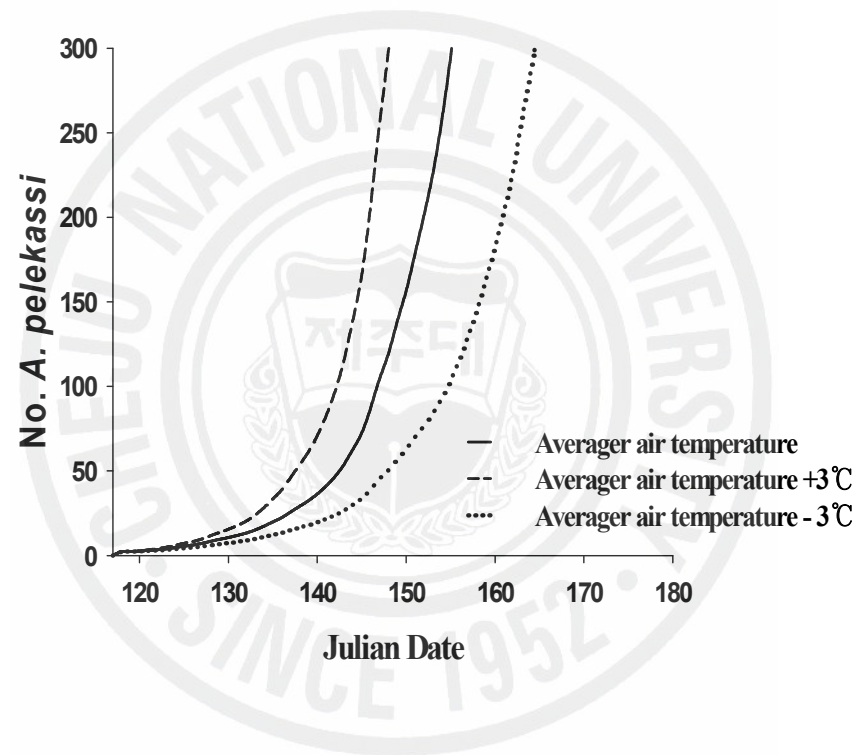
Fig 9. Comparison of model outputs according to temperature changes.

V. DISCUSSION

1. Temperature-dependent development and fecundity

Little information is available in the literature on the effect of temperature on development of *A. pelekassi*. In Croatia, *A. pelekassi* had 18‑22 generations per year between May and October (Mijuskovic, 1973). The time required from egg to adult varied with temperature and ranged from 6.3d at 30°C to 14.9 d at 20°C (Seki, 1979). These results differ from our experiments in low temperature region, where total development of egg to adult was 11.6 d at 20℃, considerably shorter than the 14.9 d in Seki's (1979) experiments. The development time at 20℃ reported by Seki was about the same at 16℃ in our experiment. In high temperature region, however, a similar development times were observed between Seki and our experiments. The egg to adult development period of *Phyllocoptruta oleivora,* another important rust mite species on citrus, was 6 d at 30℃ (Smith et al., 1997), which was comparable to above results. The tomato rust mite, *A. lycopersici,* which is belongs to the same genus but has different host plant species with *A. pelekassi*, showed much lower egg to adult development time of 4.57 d at 30℃ (Haque, 2002). Such difference is likely related to food quality, i.e. the different host plant, experiment condition such as humidity and strain of a species.

A limited information has been available on the fecundity and longevity of *A. pelekassi*. Oviposition was maximum at 25°C with 21.8 eggs per female and oviposition ceased when temperatures dropped to 15°C (Seki, 1979). The fecundity at 25℃ was not much different than our result 25.21 eggs. However, present study showed a maximum fecundity 30.07 eggs at 28℃. Also, *A. pelekassi* successfully produced eggs at 16℃, which was a comparable temperature where the oviposition did not occur in Seki

(1979). Some studies provide data on life cycle parameters for other rust mite species. For instance, the fecundity and longevity of *P. oleivora* was 26 - 29 eggs per female at unknown temperature (Yothers and Mason, 1930). *Aculops lycopersic* on tomatoes deposited 21.9 eggs at 15℃, 31.9 eggs at 20℃, 51.7 eggs at 25℃ and 42.7 eggs at 30℃ (Haque, 2002), considerably higher than the comparative value reported in other rust species. Regardless of rust mite species, all showed optimal fecundity between 25 and 28℃. The reported differences among rust mite species in terms of fecundity and longevity may be characteristics of the species but they may also be related to the different host plants and experimental conditions used by the investigators. Consequently, present studies provide an essential data for *A. pelekassi* biology in the wide range of temperature.

2. Temperature-dependent development and oviposition models

The relationships between temperatures and development rates analyzed using linear and nonlinear models. The linear lines of mean development rates against temperatures provided the estimate of low-threshold temperature 9.3℃ for egg, 4.33℃ for nymph and 6.68℃ for total stage (egg to adult) in our study. The thermal constants (effective heat units) were 54.00, 101,76, 153.84 degree-days for each of the above stages. In a previous study, Seki (1979) reported that the developmental zero and effective heat units from egg to adult of *A. pelekassi* were 10.6°C and 119 degree-days, respectively. Thus, his results were largely different from our results. Such difference can be occur as a result of the differences of the temperature range examined. He did not test temperatures <20℃ or >30℃, and estimated low-threshold temperatures without <20℃ data points, while our estimates were estimated by including observations at <20℃. Variations of threshold temperatures due to the different ranges of temperatures used may indicate the limitation of using a linear model to calculate a developmental threshold.

Low-temperature thresholds of Seki (1979) would underestimate the degree-day under the low temperatures of early season, and would result in significant errors in predicting early phenology of *A. pelekassi*. Therefore, for a reliable forecasting of *A. pelekassi* phenology, our results will be better.

The *A. pelekassi* development showed the typical characteristic of insect development which is well described by the two-parameter model of Schoolfield et al. (1981). The biophysical model assumes a single enzyme controlling development rate, which accordingly control insect development in low, optimal, and high temperature regions. Because there was no a high or low temperature inhibition, the parameters *TH* and *HH* for high temperature region were set to 1,000 and 100,000,000, and *TL* and *HL* for low temperature region were set to 100 and -100,000000, respectively, as recommended by Schoolfield et al. (1981).

The general theory for predicting cohort emergence (stage emergence) using development rate models and distribution models of development time was developed by Curry and Feldman (1987). The two component models for *A. pelekassi* development can be easily coupled to project stage emergence for eggs, and nymphs under variable temperature conditions. The development rate model provides an estimate of the mean rate of development per day at a given temperature, and the distribution model similarly estimates the cumulative proportion of cohort development at a given accumulated development rate. In other words, the cumulative proportion of the cohort, which shifted from one stage to the next, can be estimated by the probabilities calculated by the Weibull function for each stage at a given normalized age (accumulated development rate). In addition, the component models was successfully incorporated into the temperature-dependent matrix model.

Temperature is known to be the main abiotic factor influencing the fecundity in insect, although the fecundity may be modified by other abiotic factors such as light intensity (Wyatt and Brown, 1977) and biotic factors such as food (Leather and Dixon, 1982; Kaaken and Dutcher, 1993). Also, the humidity can be an

important factor of rust mite species in survival and fecundity (Haque and Kawai, 2004). We selected an optimal humidity condition for *A. pelekassi*, and temperature was concerned as the essential driving variable. Oviposition of insects can be described by three temperature-dependent components: total fecundity, age-specific oviposition, and age-specific survival rate (Curry and Feldman, 1987). The oviposition component models can be used to simulate daily egg production of *A. pelekassi* under variable temperature conditions similar to the method described by Kim and Lee (2003). The cumulative number of eggs laid by a female adult at the *i*th time (i.e., at physiological age px_i) can be calculated from the product of the temperature-dependent total fecundity, the age-specific cumulative oviposition rate, and the age-specific survival rate. The parameter values for the component models of *A. pelekassi* development and oviposition were estimated from the actual experimental data in the laboratory study. Consequently, the biological parameters were useful for the construction of matrix model.

3. The construction of matrix model and its field validation

 The Lefkovitch model (Lefkovitch, 1965) was applied in this study. The Lefkovitch model use a stage or size-structured approach instead of using an age-structured approach in the Leslie Matrix (Leslie, 1945). Also, physiological age was incorporated into the matrix model via the temperature-dependent development models of eggs, nymphs, and adults, and the oviposition rate model. So, it allowed for the model to be operated under the variable temperature conditions in the field. On leaves in early season, the model outputs pursued the actual population of *A. pelekassi* during a considerable days. We speculated that the dropped actual population around Julian date 150 (Fig. 8) was because of the spraying of insecticide for other insect pests. Thus, we expected that the model outputs would pursue the actual during more days if there was no spray. On fruits in mid-season, the model outputs showed a larger discrepancy with

the actual. The biological parameters that were used in the matrix model were obtained from the experiments on leaves. The quality of fruits for the development of *A. pelekassi* can be different from those of leaves. No information is available on the fruit quality effects for *A. pelekassi* development. Also, abiotic factors such as humidity can affect on *A. pelekassi* population (Kawai and Haque, 2004). In present matrix model, the humidity factor was not concerned.

Although our matrix model has not incorporated some factors that could operate in the population dynamics of *A. pelekassi*, the temperature-driven parameter values for the component models of *A. pelekassi* development and oviposition were estimated from the actual experimental data in the laboratory study. Therefore, we expect that the corresponding equations are realistic and adequately describe the underlying biological processes of *A. pelekassi*. And the comparison of model outputs with the actual field observation would provide a better understanding of the *A. pelekassi* population in the field and useful directions for improving the model. Other environmental factors such as humidity and leaf age of host plant can affect on population increase of *A. pelekassi*. These factors should be included into the model to improve the fitting ability of the matrix model in the future.

VI. 適 要

　귤녹응애 (Pink Citrus Rust Mite, *Aculops pelekassi*)는 제주도 감귤원에서 중요한 혹 응애류 해충으로 과실에 심각한 피해를 유발하여 경제적 손실을 야기 시킨다. 본 연구는 감귤원에서 귤녹응애 개체군 동태를 추정하기 위한 온도의존 행렬모형을 작성하고자 수행하였다. 귤녹응애의 온도발육 및 산란실험을 실시하였고, 행렬모형 작성에 필요한 매개변수를 추정하였다. 알기간은 온도가 증가함에 따라 16℃ 6.59일에서 35℃ 1.93일 감소하였다. 약충 기간은 온도에 따라 16℃ 8.18일에서 35℃ 3.30일로 감소하였다. 알 및 약충 총 기간은 16℃에서 14.76일, 20℃ 11.59일, 24℃ 9.71일, 26℃ 8.03일, 28℃ 7.32일, 32℃ 6.13일, 그리고 35℃ 5.23일 이었다. 선형 회귀를 이용하여 알, 약충, 알 및 약충의 발육영점온도를 추정한 결과 각각 9.3, 4.33 그리고 6.68℃ 이었다. 각 발육단계의 발육완료에 요구되는 적산온도는 54.00, 101.76 그리고 153.84일 이었다. 생물리적 비선형 발육모형은 모든 발육단계의 발육율과 온도 간 관계를 잘 설명하였다. Weibull 함수는 각 발육단계의 발육완료기간 분포에 잘 적용되었다. 성충수명은 온도증가에 따라 16℃ 24.17에서 35.0℃ 14.60일로 감소하였다. 귤녹응애는 28℃에서 33.07개의 최대 산란수를 보였고 16℃에서는 18.75개까지 감소하였다. 산란모형 작성을 위한 3가지 온도의존 하부모형 즉 총산란수 모형, 연령별 산란율 모형 그리고 연령별 생존율 모형을 개발하였다. 이 기본 모형을 바탕으로 귤녹응애의 개체군 동태를 분석하기 위한 온도의존 행렬모형을 작성하였다. 귤녹응애의 연령계급은 알, 약충, 성충 등 3단계로 구분하였다. 어떤 연령계급에서 다음 연령계급으로 전환확률 또는 잔존확률은 각 연령계급의 발육율 함수를 이용하여 추정하였다. 산란계수는 성충 발육율과 총산란 모형의 곱으로 추정하였다. 행렬모형의 결과는 전형적인 지수함수적 개체군 성장 양상을 보였다. 모형의 포장적합성을 검정하기 위하여 모형 값과 2007년 실제 포장 자료와 비교하였다. 계절초기 잎에 정착한 귤녹응애 개체군에서는 약 20일 동안은 모형 값과 실측값에 큰 차이가 없었다. 하지만 계절중기 과실에서는 실제와 편차가 심하였다. 평년온도 (30년 평균온도)에서 3℃ 감소시키거나 증가시켜 온도변화에 따른 모형 값의 변동을 검토하는

민감도 분석을 실시하였다. 모형은 온도변화에 따라서 민감하게 반응하였다. 또한 행렬모형의 제한 요소와 향후 개선방안에 대하여 고찰하였다.

검색어 : 귤녹응애, 행렬모형, 개체군 동태, 발육율, 산란모형, 산란력, 감귤

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