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오리엔탈과실파리 개체군 모형 및 생물기후 적합도 기반의 국내 잠재적 정착능력 평가

Evaluation for the establishment potential of *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) based on bioclimatic population modeling in Korea

濟州大學校 大學院

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Evaluation for the establishment potential of *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) based on bioclimatic population modeling in Korea

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ABSTRACT

1. Estimation of model parameters for the development and reproduction of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae)

The oriental fruit flies, *Bactrocera doralis* (Hendel) (Diptera: Tephritidae) is a destructive insect pest not only threatening tropical and subtropical areas, but also spreading gradually along with climate change. This species is a potentially highly invasive fruit fly to Jeju area of Korea. We collected previously published experimental data sets of *B. dorsalis* complex, including *B. philippinensis*, *B. papayae* and *B. invadens*, and estimated various temperature-dependent models to construct the population model; 1) temperature-dependent development rate and distribution model of development time for the stage transition model, and 2) female aging rate model, temperature-dependent total fecundity model, age-specific oviposition and survival rate model for the oviposition model. As a result, the estimated models expressed the thermal reaction of *B. dorsalis* well. In the linear model, the lower threshold of eggs, larvae and pupae were 9.6, 7.1 and 8.6 ℃, respectively, and the thermal constants were calculated as 25.4, 163.9 and 178.7 degree days (DD), respectively. The developmental thresholds and temperature constants for egg to egg period were 9.5 ℃ and 717 DD, respectively. In the temperature-dependent total fecundity model, the highest number of egg was obtained 1,947.8 at 21.7 ℃. We also developed a stage-transition model of eggs, larvae and pupae, and an oviposition model for the basic population modeling of *B. dorsalis*. These temperature-driven models are essential for the development of a population model that would useful for evaluating the establishment of *B. dorsalis* in Korea and for developing its control strategy.

2. CLIMEX Simulated prediction for the potential distribution of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) considering the northern boundary: with special emphasis on Jeju, Korea

Along with global climate change, *B. dorsalis* has recently expanded from

Southeast Asia, which is a source area, to mainland China, where its latitude is similar with Jeju. In order to evaluate the establishment of *B. dorsails* in Korea, it is necessary to determine the climate suitability. Based on the CLIMEX model, various data sets of *B. dorsalis* were used to obtain the set of parameters for the best estimation of the northern limit. The biological and climatic data in the current established region, especially China were used. That is, parameters for the calculation of cold stress (CS) value were adjusted to include Wuhan in 2009 (Scenario 1: Wuhan-based model) or Wuxi in 2006 (Scenario 2: Wuxi-based model). As a result, the applied parameters explained well the distribution and occurrence characteristics of *B. dorsalis* in the world (Wuhan-based model). Climate suitability of *B. dorsalis* in Korea was calculated using the obtained set of parameters (Wuhan-based model) and the future Korean climate according to the Representative Concentration Pathway (RCP) 8.5 scenario of Intergovernmental Panel on Climate Change (IPCC). In Korea, *B. dorsalis* could be established in the small part of Jeju Island in the 2010s, and the range gradually spread until the 2090s, and many parts of the lowland of Jeju Island were assigned in the marginal to optimal range.

3. A tentative evaluation for population establishment of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) based on the population modeling: considering the temporal distribution of host plants in a selected area in Jeju, Korea

When *B. dorsalis* invades Korea, especially in Jeju, temporal distribution of host plants as well as climatic suitability of the region plays an important role in its survival and population dynamics. We investigated the abundance of the host plants of *B. dorsalis* in a selected site in Jeju and parameterized them in terms of temporal availability to incorporate into the population model. The contribution of host plants for the population growth of *B. dorsalis* in the selected site was different according to the group of host plants. For example, *B. dorsalis* populations largely decreased by 93%, when host plants belong to Moraceae (mainly *Ficus* sp.) were removed in the simulation. Also, we found that the host plants of *Prunus persica*, *Ficus carica*,

P. mume and *Eriobotrya japonica* in this order contributed greatly to population abundance of *B. dorsalis* in the selected area, which was important in terms of mid-season host plants connecting the early adult population of *B. dorsalis* to citrus plants in the late season. Finally, we discussed a seasonal management strategy against *B. dorsalis* while considering the availability of host plants and the biology of this fruit fly in an invaded area.

I. General Introduction

The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) is a destructive fruit pest in a wide of cultivated fruit crops and wild plants (Liquido et al., 2015). *B. dorsalis* forms a large genus composed of 85 species (Drew and Romig, 2013). Among them, recently *B. philippinensis* Drew and Hancock, *B. papayae* Drew and Hancock, and *B. invadens* were merged into one species, *B. dorsalis* (Drew and Romig, 2013; Schutze et al., 2015a). This regrouping has greatly increased the geographic range of *B. dorsalis* in the native tropical areas of Asia (Vargas et al., 2015): Pakistan, India, Sri Lanka, Myanmar, Indonesia, Malaya, Thailand, Cambodia, Laos, Vietnam, southern China, Taiwan, Philippine Islands, Ryukyu Islands (including Okinawa), Bonin Islands, Micronesia, Mariana Islands (Guam, Rota, Saipan, Tinian) and the Hawaiian Islands.

Bactrocera dorsalis was known as the most frequently intercepted tephritid (80%) in prohibited fruits in passengers' baggage at Osaka airport, Japan (Matsumoto et al., 1992). In California, a total of 1,558 detections occurred between 1960 and 2012 (Vargas et al., 2015). The invasions and eradication of *B. dorsalis* are being repeated in many regions (Reviewed in De Meyer et al., 2010; Vargas et al., 2015). The economic impacts caused by the invasion of *B. dorsalis* can be enormous, and especially the control or eradication project has to be done at enormous public cost (Kim and Kim, 2016). It has been estimated that the establishment of a major fruit fly invasion would cause crop losses of US $910M annually in the Californian fruit industry, and an eradication program would cost the US $290M (Dowell and Wange, 1986). Also, annual losses linked to fruit fly infestations are estimated to be US $192M in the eastern Mediterranean region, including Israel, Palestinian Territories and Jordan (Enkerlin and Mumford, 1997). Furthermore, indirect losses can be provoked because of quarantine restrictions imposed by importing countries to prevent entry of prohibited fruit fly species.

B. dorsalis is a tropical species which would be unable to survive during the winter in most Korean regions, except possibly in the Jeju area. The results of GARP (genetic algorithm for rule-set prediction), MAXENT (maximum entropy method) or CLIMEX modeling for the prediction of potential distribution of *B. dorsalis* showed that Jeju area or the same latitude in China is assigned to a higher level of presence or marginal region (De Meyer et al., 2010; Sridhar et al., 2014). The invasion risk of *B. dorsalis* into Jeju has been increasing at a rapid rate, as many detections of *Bactrocera* larvae have been reported. In 2017, a total of 490 pests were detected in 116 goods imported from 32 countries through international airports and harbors in Korea. Among them, *B. dorsalis* was the most frequently detected pest with 31 cases (Yoon et al., 2018). Global warming might also have contributed to this phenomenon.

In spite of serious economic risk of *B. dorsalis* in Korea, especially in Jeju area, its potential distribution and climatic suitability have not been evaluated yet. Therefore, this study was conducted to develop the following subjects.

1) Estimation of model parameters for the development and reproduction of *B. dorsalis* (Diptera: Tephritidae)

2) CLIMEX simulated prediction for the potential distribution of *B. dorsalis* considering the northern boundary: with special emphasis on Jeju, Korea.

3) A tentative evaluation for population establishment of *B. dorsalis* by its population modeling: considering the temporal distribution of host plants in a selected area in Jeju, Korea.

II. Review of Literature

Basic information

Bactrocera dorsalis Hendel (Diptera: Tephritidae) is a tropical-subtropical insect pest (CABI, 2018). Dacine fruit flies, species belonging to subfamily Dacinae, have been considered the most destructive pests of fruit and vegetable in the world and occupy a high level in the quarantine list (Clarke et al., 2005). Among them, *B. dorsalis* is an economically important insect pest damage wide range of cultivated fruit trees and wild plants (Clarke et al., 2005; Ekesi et al., 2007; Liquido et al., 2015). *B. dorsalis* is one of the 43 fruit flies registered in quarantine prohibited pest in Korea, and the importation and/or transportation of its host plants into the domestic land is strictly forbidden.

Species complex and world distribution

Total of 52 fruit flies belong to the *B. dorsails* complex in Asia, and eight of them, including *B. carambolae*, *B. papayae*, and *B. philippinensis* are economically important insect pests (Drew and Hancock, 1994). However, *B. carambolae* was identified by Schutze et al. (2015b) as a discrete species later. *B. invadens* identified in Kenya (Lux et al., 2003) and West Africa (Vayssieres, 2007) were additionally included in the *B. dorsalis* complex in the 2000s. Further, *B. philippinensis* has recently synonymized with *B. papayae* (Drew and Romig, 2013). The *B. dorsalis* complex is now occupied in 41 countries in Africa, 19 in Asia, some islands in the Pacific, and Hawaii in the United States. Their distribution is shown in SD Table 1.

Temperature-dependent development and reproduction

B. dorsalis, mainly distributed in the tropical-subtropical region, shows a high survival rate of more than 50% in the range of temperature 16-32℃ (Vargas et al., 1996). The appropriate temperature range for its development is 25-33℃ (Stephens et al., 2007; Li et al, 2012), and data on the biological response of *B. dorsalis* in several temperature collected from other literature are shown in the SD Table 2.

Global invasion and/or eradication history

The invasion pathway of *B. dorsalis* can be divided into two major groups; natural spread through flight and artificial movement of infested fruits (CDFA, 1994; Ohno et al., 2009; EPPO, 2010). The high flight ability of *B. dorsalis* adults can be a threat by spreading naturally from infested adjacent region or countries. Steiner (1956) reported that *B. dorsalis* can flight through 39km by his mark-recapture experiment. Liang et al. (2001) reported for its flight ability through their laboratory experiments that *B. dorsalis* adults could fly up to 44-46 km. Iwahashi et al. (1972) found that *B. dorsalis* adults could fly at least 50 km through the island by their re-trapping experiment in the Ogasawara Islands. Christenson and Foote (1960) mentioned that small flying insects such as fruit flies could travel long distances with the help of the strong winds such as storm, typhoon and hurricane. Muraji et al. (2008) and Ohno et al. (2009) suggested that the frequent recurrence of *B. dorsalis* in the southern islands of Japan is due to the insect flight from nearby native countries such as Taiwan, China, and the Philippines.

On the other hand, California Department of Food and Agriculture (CDFA) (1994) stated that the invasion of *B. dorsalis* into California was mainly due to an artificial movement by human. Similarly, European and Mediterranean Plant Protection Organization (EPPO) (2010) predicted that *B. invadens* would not be likely to spread naturally to the Mediterranean in the near future, and artificial spreading was the main invasion pathway; imports of major/non-major host fruits or plants attached with growth media from infested area, and infested fruits owned by travelers. The invasion and/or eradication history of *B. dorsalis* in each region is as follows.

-Africa

B. dorsalis was found in Africa in June 1996 when a female was caught near the airport in Mauritius. The eradication program was implemented and it was eliminated in 1999 (Seewooruthun et al., 2000). In 2003, a larva were found in Kenya (Lux et al., 2003), which was described by Drew et al. (2005) as *B. invadens* later. *B. invadens* expanded its range throughout Africa including East Africa (Mwatawala et al,. 2004), Central-West Africa (Abanda et al., 2008; Goergen et al., 2011) and South Africa (Cassidy, 2010; Manrakhan et al., 2015).

-Asia

B. dorsalis are estimated to be native to Southeast Asia (Li et al., 2012; Wu et al., 2014) and are now expanding to mainland of China. *B. papayae* invaded Oceania is originated from the southern part of Thailand, the Malay Peninsular and eastern part of Malaysia, Singapore, the entire Indonesian islands and the Kalimantan region (Drew, 1997). It was believed to have been accidentally introduced to Irian Jaya (Papua Parat) in eastern Indonesia before 1992 (Drew, 1997; Fay et al., 1997). On the other hand, *B. invadens*, which occurred in Kenya in 2003, is presumed to be native in Sri Lnaka (Drew et al., 2005; Scutze et al., 2014).

In China, *B. dorsalis* is believed to have established in southern areas such as Yunnan and Hainan for a very long period of time since the 1930s (Li et al., 2012), and establishment of the insect was confirmed in the central part of China since the 2000s (Zhao et al., 2008; Luo et al., 2009). They appear to have invaded through domestic and foreign trade of its host fruits (Zhuo et al., 2006; Qi et al., 2008).

In Japan, *B. dorsalis* was first recorded in 1918 in Ryukyu islands (Sakae, 1968). It began to be found in the Amami Islands in 1929, expanded throughout the archipelago in 1946 (Sakae, 1968) and introduced to Tokara Islands in 1974 (Yasuda, 1978), but they were eradicated in 1986 (Nakamori et al., 1991; Fujisaki, 2016). There has been continuous capture of wind-borne population of *B. dorsalis* in recent year, but they were eradicated at that time (Ohno et al., 2009; Fujisaki, 2016).

-Australia

In 1993, *B. papayae* was found in northern islands belonging to Torres strait in

Australia, adjacent to Papua New Guinea and soon eradicated or suppressed (Drew, 1997; Fay et al., 1997). It appears to have introduced through Papua New Guinea (Sar et al., 2001) or Torres Strait to Queensland, Australia (Drew, 1997). In 1995, the fruit fly was identified in the Cairns area of northern Queensland (Fay et al., 1997; Hancock et al., 2000), and it is estimated to have been introduced 2 to 2 and a half years ago (Drew, 1997). The population inside the Queensland was eradicated in 1998 (Drew, 1997, Cantrell et al., 2002) and there was separately occurred in Mount Isa in western Queensland, but it was eradicated in 1997 (Cantrell et al., 2002).

-America

B. dorsalis has established in Hawaii since 1946 and its population was presumably introduced from Saipan (Pemberton, 1946; Culliney, 2002). *B. dorsalis* also settled on islands of Rota and Guam, but was eradicated in 1963 and 1965, respectively (Steiner et al., 1965; Steiner et al., 1970). In the US mainland, the eradication implemented in California from 1960 to 1997, but has repeatedly occurred since 2000s, and it was eradicated at that time (Weems et al., 2012; CDFA, 1994).

Host

A total of 471 species of 221 genera belonging to 78 families are known as hosts of *B. dorsalis* complex in the world. Among the plants registered in the National Plant Species Information System of Korea (http://www.nature.go.kr, Korea National Arboretum), 15, 82 and 4 species of native (wild), cultivated and exotic (naturalized) plants respectively, total of 172 species are belonging to host plant of *B. dorsalis* complex in Korea including subspecies and cultivar. Host plants that have been reported worldwide and the status in Korea are shown in SD Table 3. Among these species, the main hosts of *B. dorsalis* reported are as follows; mango (*Mangifera indica* L.), papaya (*Carica papaya* L.), guava (*Psidium guajava* L.), carambola (*Averrhoa carambola* L.), chinese date (*Ziziphus mauritiana* Lam.), loquat (*Eriobotrya* *japonica* (Thunb) Lindl.), Lemon (*Citrus limon* (L.) Burm. f.), sweet orange (*Citrus sinensis* (L.) Osbeck) (Ye, 2001; Ekesi and Billah, 2006; Chen et al., 2006; Rai et al, 2008; Rwomushana et al,. 2008; EPPO, 2010).

Economical importance

B. dorsalis damage wide range of cultivated fruit trees and wild plants, and the damage rate can vary greatly depending on the maturity of the host plants (Syed et al., 1970, Tan and Serit, 1994; Godse and Bhole, 2003). The damage rate of *B. dorsalis* in several host plant species is shown in SD Table 4. A total of $ 1,800,000 was spent in eradication costs for *B. dorsalis* in 1980s (CDFA, 1994) in California, United States. In Hawaii, damage to major crops by *B. dorsalis* is known to be greater than 13% (Culliney, 2002). In Darjeeling and Sikkim hills, India, *B. dorsalis* is highly damaging in the monsoon season and 20-30% of the total damage is caused by the insects (Gurung et al., 2017). Verghese et al. (2002) reported that the economic damage of mango and guava due to *B. dorsalis* is up to 80% in India. In China, the damage rate caused by *B. doraslis* in Taihu Lake along the Yangtze River reached 20-30% and the economic damage reached 2.2 million yuan (Luo et al., 2009). In Mauritius, a total of US $ 1 million was spent as an eradication cost for *B. invadens* (Seewooruthun et al., 2000), and in Australia, a total of AUD $ 34 million was spent for four years due to the outbreak of *B. papayae* (Cantrell et al., 2002).

Male attractant and monitoring practices

When fruit flies introduce to new areas, their ability to survive, reproduction, and establishment depends on their movement, and monitoring them is essential to conduct an effective control strategy (Weldon et al., 2014). Methyl eugenol (ME), which has long been used to monitor *B. dorsalis*, is a substance found in certain plants in nature, and male of *B. doraslis* of all ages are attracted to this material (Howlett, 1915; Steiner and Lee, 1955; Chambers, 1977). ME has been reported to be a precursor of pheromone synthesis of *B. dorsalis* males, and who ingesting ME have been reported to be more competitive when attracting females (Tan and Nishida, 1996; 2012).

According to these characteristics, traps using ME as a attractant have been widely used in various subjects; monitoring of population dynamics related to the biotic/abiotic environments (Chiu et al., 1984; Zhang et al., 1995; Chen et al., 2006; Ganie et al., 2013a; Vayssieres et al., 2014), collecting of samples for genetic or taxonomic analysis (Drew et al., 1994; Muraji et al., 2008; Schutze et al., 2012; Ganie et al., 2013b, Choudhary et al., 2016), monitoring of its movement in mark-recapture experiments (Iwahashi, 1984; Tan and Serit, 1988; Froerer et al., 2010), control method for eradication or suppression (Steiner et al., 1955; Sakae, 1968; Seewooruthun et al., 1998; 2000; Cantrell et al., 2002) and monitoring practice in the quarantine program (Sar et al., 2001, Mwatawala et al., 2004; Ohno et al., 2009).

Eradication practices for invasion of *B. dorsalis*

The male annihilation technique (MAT), designed and initiated by Steiner and Lee (1955), is a technique to distribute poisoned ME coated blocks to the surrounding environment (Shelly, 2014). MAT is an effective technique for reducing *B. dorsalis* populations, and its effectiveness has been demonstrated in the island of Rota and Guam (Steiner et al., 1965; Steiner et al., 1970) and in the Okinawa Islands (Koyama et al., 1984). In the Mariana Islands, which had difficulties in applying sterile insect technique (SIT) due to various factors, the introduction of MAT successfully eradicated *B. dorsalis* (Steiner at al., 1970). However, Steiner and Lee (1955) emphasized that this method must be carried out totally in the region isolated from other infested areas. In Japan, *B. dorsalis* was not completely eradicated in the Amami islands until the eradication program was carried out in Okinawa Islands, due to the fruit fly immigrated from neighboring infested areas (Koyama et al., 1984).

The bait application technique (BAT) is a method of spraying protein feeds mixed with pesticides on the leaves of host plants. It is used by itself or in combination with other technologies in eradication programs. In Mauritius, the *B. dorsalis* control strategy was based on a combination of the BAT and MAT, supplemented by soil drenching, cover spray and fruit clean up (Seewooruthun et al., 1998). The insect was successfully eradicated in January 1999 (Seewooruthun et al., 2000). BAT was used to control the walnut husk fly, melon fly, and Mexican fruit fly in California and Mexican fruit fly and Mediterranean fruit fly in Florida (CDFA 1994). In Australia, *B. papayae* was successfully eradicated using MAT and BAT technology (Cantrell et al., 2002).

III. Research contents

1. Estimation of model parameters for the development and reproduction of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae)

1-1. Introduction

The population models of insect pests have been used to predict their seasonal phenology and dynamics in various environments including climate (Shaffer and Gold, 1985; Kim and Lee, 2010). If there is a population model for *B. dorsalis*, it will be very effective to evaluate the population establishment in Korean regions, and further be able to use for establishing management tactics. Temperature-dependent thermal models are basically required to construct a population model, such as stage transition module using development rate model and distribution of development time model, and reproduction module consisted of temperature-dependent total fecundity, age-specific oviposition rate and survival rate models (Kim and Lee, 2010). However, temperature-driven model for constructing population model of *B. dorsalis* has not been developed yet.

Consequently, the objective of present study was to develop essential models describing the relationship between the temperatures and development or fecundity of *B. dorsalis* using previously published biological data. Also, we reported the lower threshold and thermal constant of *B. dorsalis.*

1-2. Materials and methods

1-2-1. Data source for model development

Data sets for temperature-dependent development, longevity, and fecundity of *B. dorsalis* complex were obtained from previously published studies in the world, as seen in SD Table 2. These data were combined to estimate temperature-dependent development and oviposition models of *B. dorsalis*. We used a commercial program, TableCurve 2D (Jandel Scientific, 2002), to estimate the parameters of model equations in all cases.

1-2-2. Temperature-dependent development models of immature stages

The development times of eggs, larvae, and pupae were subjected to a reciprocal (1/mean values in days) of each development time to get developmental rates. And then they were regressed to linear and nonlinear equations against temperatures to estimate parameters for each model.

Linear development model

A linear model (y = ax + b; a = the slope and b = the intercept) was applied to fit the relationships between developmental rates (y) and temperatures (x). Estimated linear models were used to provide lower threshold temperatures (−b/a) and thermal constant (Degreedays, 1/a) for eggs, larvae, pupae, egg to egg period of *B. dorsalis* (Campbell et al., 1974). The data points in linear regions were included.

Nonlinear development model

The equation of Lactin et al. (1995) modified from Logan (Logan et al., 1976) was selected to describe the nonlinear relationships between mean developmental rates of *B. dorsalis* (eggs, larvae, and pupae) and temperatures. The simple equation has three parameters and is known to show a good data-fitting ability to various dataset with statistical robustness (Kim et al., 2017; Hyun et al., 2017); thus, this model was useful for rapid parameterization of the developmental data of *B. dorsalis*.

$$r(T) = \exp(\rho T) - \exp\left(\rho T_{\max} - \frac{T_{\max} - T}{\Delta T}\right) \qquad \text{Eq. 1}$$

where $r(T)$ was the mean developmental rate at air temperature of T (°C), $T_{\max}$ was thermal maximum, ΔT was the temperature range over which "thermal breakdown" became the overriding influence, and ρ was a composite value for critical enzyme-catalyzed biochemical reactions (Logan et al., 1976; Damos and Savopoulou-Soultani, 2008).

Distribution model of development time

The cohorts of insects varied in the rates of completion of their developmental stages. Such variations have been modeled stochastically as a distribution model of development time, which determines the fraction of the cohort that completes development at each accumulated development rate (Wagner et al., 1984). Basically, the cumulative frequency distributions for the development times of each stage of insects are required to get the standard normalized distribution, which is obtained by scaling the frequencies to a unit and normalizing the development times by dividing it by the mean or median time (Wagner et al., 1984).

Unfortunately, we do not have available datasets to estimate the biological distribution model of developmental time for *B. dorsalis*. For modeling, we approximated the model parameters by assuming that the frequency distribution of developmental completion times of *B. dorsalis* shows a normal distribution. In the cumulative normal distribution function, the position of means expressed by -2.576, -1.960, -1.0, -0.675, 0.0, 0.675, 1.0, 1.960 and 2.576 standard deviations (z_i, the standard units, i = 1 for -2.576 through 9 for 2.576) correspond to the cumulative frequencies of 0.5, 2.5, 16.87, 25.0, 50.0, 75.0, 83.13, 97.5 and 99.5%, respectively (Sokal and Rohlf, 1981). The normalized ages (physiological ages, px_i) of *B. dorsalis* at each cumulative frequency were calculated by using mean ($\overline{X}$) and standard deviation (s) of each developmental stage according to the standard unit theorem above.

$$px_i = \frac{\overline{X} + z_i s}{\overline{X}} \qquad \text{Eq. 2}$$

In the same developmental stage, all cumulative frequencies along physiological ages that were obtained from mean developmental times at different temperatures were combined to estimate the two-parameter Weibull function.

1-2-3. Oviposition model components of female adults

The three temperature-dependent sub-models of temperature-dependent total fecundity, age-specific cumulative oviposition rate, and age-specific survival rate can be combined to construct an oviposition model of insect species (Curry and Feldman, 1987). The oviposition model of *B. dorsalis* females was made by using the protocol of Kim and Lee (2003).

Aging rate model of adult female

The mean longevities of *B. dorsalis* females were converted to the reciprocal for the adult aging rate model for modeling, which indicates the longevity completion rate (Kim and Lee, 2015; Choi and Kim, 2016), and this model is essential to calculate the physiological age of females. We used the Eyring equation (Eyring, 1935) modified by Curry and Feldman (1987), since it well expressed by the change of insect longevity. That is, the longevity of insect adults decreases with increasing temperature, and the insects are subjected to death at a specific critical temperature (Kang et al., 2015; Choi and Kim, 2016).

$$r(T) = \phi Texp(-\delta/T) \qquad \text{Eq. 3}$$

where *r(T)* was the aging rate at temperature *T* (°C) and δ were parameters. The estimated aging rate model was used for calculating the physiological age of *B.*

dorsalis female adults. The physiological age (*px*) of adults from the emergence day to the nth day was defined using the following equation (Curry and Feldman, 1987).

$$px = \int_0^n r(T_i) \approx \sum_{i=1}^{n} r(T_i) \qquad \text{Eq. 4}$$

where $r(T_i)$ was the aging rate at temperature T (°C) of the *i*th day after adult emergence.

Temperature-dependent total fecundity model

This component model describes the change in total fecundity of *B. dorsalis* over the temperature range (Curry and Feldman, 1987). The relationship between total fecundity and temperature was fitted to an extreme value function (Jandel Scientific, 2002) suggested by Kim and Lee (2003):

$$f(T) = \omega \exp\left[1 + \frac{\epsilon - T}{\kappa} - \exp\left(\frac{\epsilon - T}{\kappa}\right)\right] \qquad \text{Eq. 5}$$

where $f(T)$ was the total number of eggs produced by a female during its life span at temperature T °C, ω was the maximum reproductive capacity, ϵ was the temperature when the maximum reproduction occurred, and κ was a fitted constant (Kim and Lee, 2003).

Age-specific cumulative oviposition rate model

The age-specific oviposition rate indicates the proportion of the total number of eggs laid during a given age interval compared with the total lifetime (Curry and Feldman, 1987). The Weibull function with three-parameter was applied to estimate the sub-model:

$$p(px) = 1 - \exp[-((px - \gamma)/\eta)^{\beta}] \qquad \text{Eq. 6}$$

where $p(px)$ was the cumulative proportion of eggs laid until physiological age px by a female adult, and γ, η and β were fitted constants. Daily frequency of egg laying is required to estimate age-specific cumulative oviposition rate curve. Because such datasets were not available, we approximated the cumulative oviposition curves with assumption: the cumulative oviposition is completed as the rate of 0, 70 and 100% at the completion of pre-oviposition period, 25% longevity from the fist oviposition, and the mean longevity, respectively. This assumption was based on the report that a 70% completion of oviposition occurred approximately at the age of a 25% longevity of the remaining age from the first day of oviposition in the oviposition curve of Ekesi et al. (2006), which was only oviposition curve reported in *B. dorsalis* complex (*B. invadens*). Using the pre-oviposition time and longevity from the data of Vargas et al. (2000), the cumulative oviposition curves were obtained at each temperature and combined to estimate the parameters. Outlier data were excluded in the analysis: 0% at 24 and 29.5 °C. The longevity in days was transformed to the physiological age by the Eq. 4.

Age-specific survival rate model

The age-specific survival rate describes the proportion of adults alive at any given age to the initial number of adults (Curry and Feldman, 1987). A sigmoid function was fitted to describe age-specific survival distribution of *B. dorsalis* against the physiological age (px) calculated by the Eq. 4.

$$s(px) = \frac{1}{1+\exp[(\alpha - px)/\lambda]} \qquad \text{Eq. 7}$$

where $s(px)$ was the proportion of living females at physiological age px, a was the physiological age at 50% survival, and λ was a fitted constant (Kim and Lee, 2003).

The independent variable for the age-specific survival rate model was obtained by the same method applied to estimate the distribution model of development time. The completion of longevity is a transition to death, indicating mortality curve. Thus, the reverse becomes survival curve. The longevity and standard deviation of Vargas et al. (2000) were used to estimate the age-specific survival rate curve of *B. dorsalis*.

1-3. Results

1-3-1. Temperature dependent development models

Linear development model

The estimated regression lines between temperatures and development rates of eggs, larvae, pupae and egg to egg were statistically significant as seen in Table 1 (F = 111.9138; df = 1, 26; P < 0.0001, Larvae: F = 69.8526; df = 1, 26; P < 0.0001, Pupae: F = 69.2743; df = 1, 23; P < 0.0001, Egg to egg: F = 35.6748; df = 1, 6; P < 0.0001). Using the linear regression models, the lower threshold temperature was calculated to be 9.6 °C for eggs (R^2 = 0.81), 7.1 °C for larvae (R^2 = 0.73), and 8.6 °C for pupae (R^2 = 0.75) (Table 1). The thermal constants for egg, larvae, and pupae were 25.4, 163.9, and 178.7 degree-days (DD), respectively. Also, the lower threshold and thermal constant of egg to egg period (combined of eggs, larvae, pupae and pre-oviposition period) were 9.5 °C and 716.7 DD, respectively. Parameters of linear regression are summarized in Table 1.

Nonlinear development model

The nonlinear relationship between the development rate and temperature for eggs, larvae, and pupae of *B. dorsalis* fitted well with the equation of Lactin et al. (1995). The regression model was statistically significant for each stage (Eggs: F = 59.1432; df = 2, 25; P < 0.0001, Larvae: F = 31.1697; df = 2, 25; P < 0.0001, Pupae: F = 32.1469; df = 2, 25; P < 0.0001). The estimated curves were increased gradually with increasing temperatures to a maximum development rate at an optimal temperature and thereafter declined in the high-temperature region, showing typical temperature-dependent curve in insects (Fig. 1). The estimated parameter values are seen in Table 2. The estimated values of thermal maximum threshold temperatures (parameter T_m) for eggs, larvae, and pupae were 39.9, 43.6, and 34.9 °C, respectively.

Distribution model of development time

The variation of the developmental time was well fitted to the Weibull function, as described in Fig. 2. The cumulative proportion for the development completion of each stage was transitionally changed along normalized time (physiological age). The estimated parameter values of the distribution function are shown in Table 3. All curves were statistically significant (Eggs: F = 1821.97; df = 1, 43; P < 0.0001, Larvae: F = 877.234; df = 1, 80; P < 0.0001, Pupae: F = 3777.57; df = 1, 52; P < 0.0001).

1-3-2. Component models of oviposition

Adult aging rate model

Adult aging rates expressed by the reciprocal of mean longevity fitted well to the Eyring equation (Eyring, 1935) modified by Curry and Feldman (1987) (Fig. 3A). The regression analysis was statistically significant (F = 56.1398; df = 1, 2; P = 0.0174; R^2 = 0.97). The values of parameters are provided in Table 4. This model was successfully incorporated to calculate the physiological age of *B. dorsalis* adult females (Eq. 4).

Temperature-dependent total fecundity

The total fecundity of *B. dorsalis* according to temperature change was well described by the extreme value function (Jandel Scientific, 2002) (Fig. 3B) with statistical significance (F = 5.5633; df = 2, 7; P = 0.0358, R^2 = 0.61). The values of estimated parameters are seen in Table 4. The estimated total fecundity increased sharply with increasing temperature to a maximum fecundity (1948 eggs per female, parameter ω) at an optimal temperature (21.8 °C, parameter ε), and then declined in the high-temperature region.

Age-specific cumulative oviposition rate

The assumed cumulative egg production curves at different temperatures were well overlapped at the top of each other, along physiological age (Eq. 4). Thus, age-specific cumulative oviposition rates successfully fitted to the three-parameter Weibull function (Eq. 6, Fig. 3C) with statistical significance (F = 91.3030; df = 2, 9; P < 0.001; P < 0.001, R^2 = 0.95). In the estimated model, *B. dorsalis* started to lay eggs from physiological age 0.2256 (parameter γ), and 50% of the total eggs were laid at the approximate physiological age of 0.4468 (parameter $\gamma + \eta$) (Table 4).

Age-specific survival rate

The variations of survival curves at different temperatures had nearly arranged each other along the physiological age scale (Fig. 3D). And the survival curves were well regressed along the independent variable of adult physiological age by the sigmoid function (Eq. 7), with statistical significance (F = 3874.48; df = 1, 34; P < 0.001, R^2 = 0.99). The overall pattern of estimated survival curve showed a successive transition with exhibiting few initial mortality, rapid decline during mid-age, and decreasing mortality at a late age. Fifty percent mortality was fixed at 1.0 physiological age (parameter a) (Table 4) because we applied normal distribution model to generate data pairs.

1-4. Discussion

The temperature-dependent development, longevity and fecundity data of *B. dorsalis* complex were combined to estimate thermal constant and temperature-driven models in the present study. Despite the datasets obtained from different regions and strains, each dataset was generally synchronized on estimated lines except for some outliers (see Fig. 1). Larval developmental times were more spread than those of eggs and pupae, which showed the most data points of Danjuma et al. (2014) and Vargas et al. (2000) are located above, and datasets of Luo et al. (2009) are located below the estimated line. But more than 70% of variation was explained by the estimated lines. Anyway, our results may indicate a common thermal constant for this species, since four species of *B. dorsalis* complex were combined.

The lower threshold temperature and thermal constant (total degree-days) of the egg-to-egg period are importantly used to calculate the generation time (life cycle) in an eradication program of *B. dorsalis*. In other words, an eradication program ends when *B. dorsalis* is not found for three generations after the start of the program (Jeffrey, 1989; APQA, 2016). In the USDA eradication program, 660 DD based on 12.2 °C (in air temperature) has been recommended until now (Jeffrey, 1989). But this model does not include recent research achievements and has no definite grounds for estimating the thermal constant. Thus, our lower threshold temperature and thermal constant can be preferred to estimate the generation time of *B. dorsalis*.

Table 1. Lower developmental thresholds (℃) and thermal requirements in degree-days (DD) for eggs, larvae, and pupae stage of *B. dorsalis*

Stage	Regression			Lower threshold temp. (℃)	Thermal constant (DD)
	Equation[1]	*df*	R^2		
Eggs	$y = 0.03943x - 0.37733$	27	0.81	9.6	25.4
Larvae	$y = 0.00610x - 0.04339$	27	0.73	7.1	163.9
Pupae	$y = 0.00560x - 0.04816$	24	0.75	8.6	178.7
Egg to Egg[2]	$y = 0.00140x - 0.01332$	6	0.86	9.5	716.7

[1] $y = ax + b$, where y is the rate of development (1/day), b is the intercept, a is the slope, and x is the temperature (℃), Eggs: F=111.9138; *df* = 1,26; $P < 0.0001$, Larvae: $F = 69.8526$; *df* = 1,26; $P < 0.0001$, Pupae: $F = 69.2743$; *df* = 1, 23; $P < 0.0001$.

[2] Egg to egg means total combined of eggs, larvae, pupae and pre-oviposition period (Vargas et al., 2000).

Table 2. Parameter values of the non-linear developmental rate model for egg, larvae and pupae stage of *B. dorsalis* at constant temperature

Parameters	Eggs	Larvae	Pupae
ρ	0.1464 ± 0.01642	0.1149 ± 0.02340	0.1734 ± 0.01433
$T_{\max}$	39.9181 ± 1.5575	43.6474 ± 4.83569	34.9290 ± 0.25869
ΔT	6.7825 ± 0.7395	8.6797 ± 1.75448	5.7618 ± 0.47428
R^2	0.83	0.71	0.72

Lactin model (Lactin et al., 1995) modified from Logan model (Logan et al., 1976) was applied with statistical significance (Eggs: F = 59.1432; df = 2, 25; P < 0.0001, Larvae: F = 31.1697; df = 2,25; P < 0.0001, Pupae: F = 32.1469; df = 2, 25; P < 0.0001).

Table 3. Estimated values of parameters in distribution curve of development time for egg, larvae and pupae stage of *B. dorsalis* at constant temperature in the laboratory

Parameters	Eggs	Larvae	Pupae
a	1.0331 ± 0.00344	1.0259 ± 0.00410	1.0338 ±0.00241
b	13.2744 ± 0.73949	15.7932 ± 1.34645	13.10605 ± 0.50715
R^2	0.98	0.92	0.99

Two-parameter Weibull function was applied with statistical significance (Eggs: F = 1821.97; df = 1, 43; $P < 0.0001$, Larvae: F = 877.234; df = 1, 80; $P < 0.0001$, Pupae: F = 3777.57; df = 1, 52; $P < 0.0001$).

Table 4. Estimated parameter values for adult female aging rate (1/longevity), temperature-dependent total fecundity, age-specific cumulative oviposition rate, and age-specific survival rate of *B. dorsalis*

Models	Parameters	Estimated value	SEM	R^2
Female aging rate (1/longevity)[1]	ϕ	0.0034	0.00133	0.97
	δ	23.0081	10.24362	
Temperature-dependent total fecundity[2]	ω	1947.8209	415.43625	0.61
	ϵ	21.7772	0.81279	
	κ	4.0298	0.99424	
Age-specific cumulative oviposition rate[3]	γ	0.2256	0.01506	0.95
	η	0.2212	0.04258	
	β	0.9592	0.26234	
Age-specific survival rate[4]	α	1.0000	0.00538	0.99
	λ	-0.1226	0.00476	

[1] Eyring equation (Eyring, 1935) modified by Curry and Feldman (1987) was applied with statistical significance ($F = 56.1398$; $df = 1, 2$; $P = 0.0174$).

[2] Extreme value function (Jandel Scientific, 2002) was applied with statistical significance ($F = 5.5633$; $df = 2, 7$; $P = 0.0358$).

[3] The Weibull function (suggested by Kim and Lee, 2003) was applied with statistical significance ($F = 91.3030$; $df = 2, 9$; $P < 0.001$).

[4] A sigmoid function (suggested by Kim and Lee, 2003) was applied with statistical significance ($F = 3874.48$; $df = 1, 34$; $P < 0.001$).

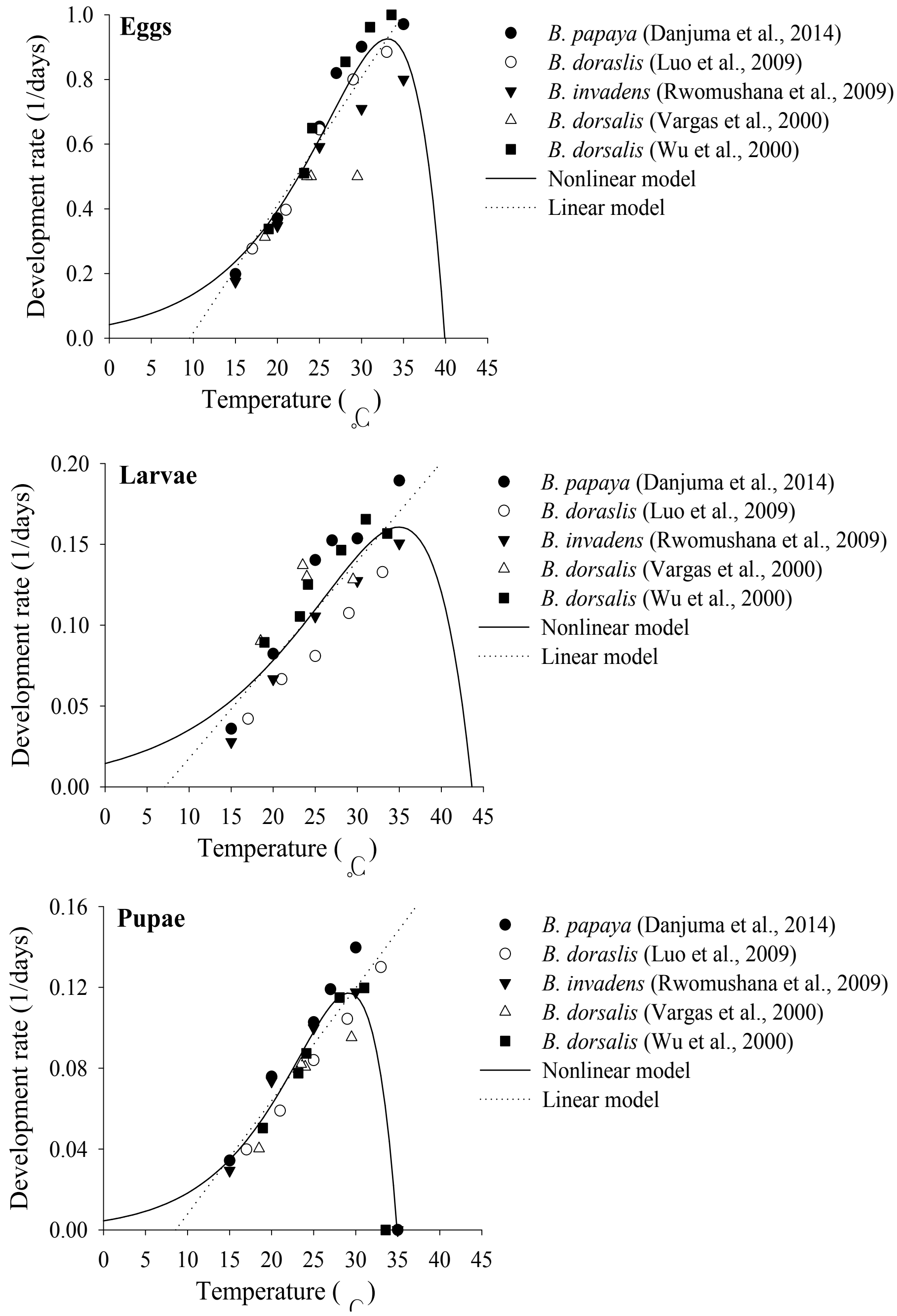


Fig. 1. Development rate (1/day) curve for eggs (A), larvae (B), and pupae (C) of *B. dorsalis* as a function of temperature.

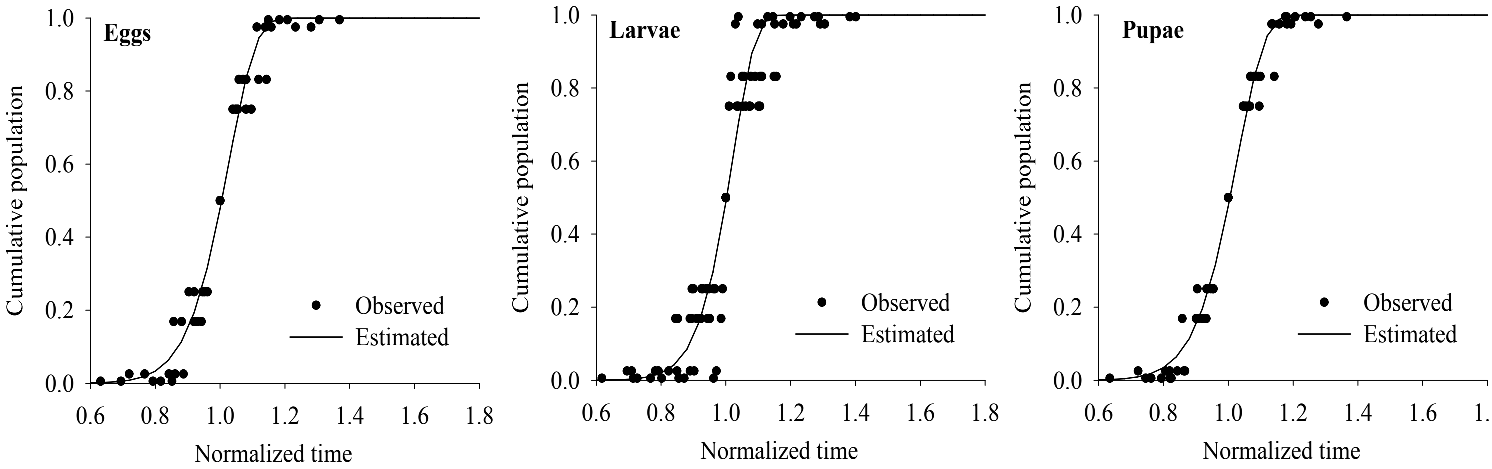


Fig. 2. Distribution model of development time for egg, larvae and pupae stage of *B. dorsalis.*

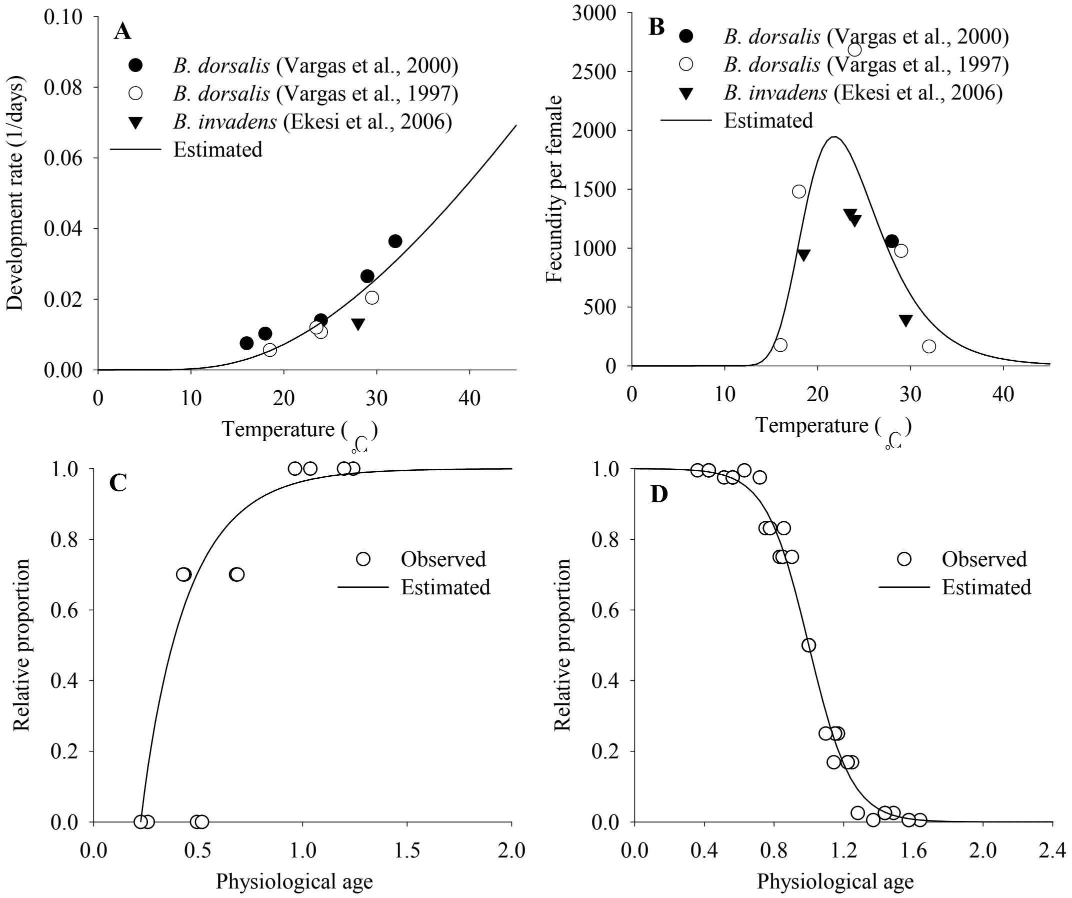


Fig. 3. Major components of oviposition model of *B. dorsalis* female adults. (A) Female aging rate curve, (B) Temperature-dependent total fecundity curve, (C) Age-specific cumulative oviposition rate curve, and (D) Age-specific survival rate curve.

2. CLIMEX Simulated prediction for the potential distribution of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) considering the northern boundary: with special emphasis on Jeju, Korea

2-1. Introduction

The studies on the potential distribution for an insect pests and natural enemy species has been widely conducted to evaluate their ability of establishment and spread in new areas (Jeschke and Strayer, 2008; Ulrichs and Hopper, 2008; De Meyer et al., 2010). A number of modeling techniques have been developed and applied for those purpose. The group of them are referred as bioclimatic models because those models predict geographic ranges of organisms as a function of climate mostly, which are also known as envelope models, or more broadly ecological niche models or species distribution models (Jeschke and Strayer, 2008).

The bioclimatic models can be categorized into two groups: the deductive mechanistic and inductive empirical model. The empirical models use data sets of direct observation, measurement and extensive records, where the predicted distribution of insects is mainly based on a climate or habitat match (Baker, 2000). This approach applies basically correlation between abiotic variables and occurrence data of insect species, and is evolving into statistical and machine learning models. The statistical models include various methods of generalized linear model (GLM), generalized additive model (GAM), multivariate adaptive regression splines (MARS), etc. And machine learning technology that has been frequently used in the prediction of insect distribution is classification and regression tree (CART), artificial neural network (ANN), genetic algorithm for rule-set production (GARP), maximum entropy (Maxent), self organizing map (SOM), etc. The mechanical model or referred to as ecophysiological models (Stephenson, 1998) is based on the intrinsic principle of the organism or system. Thus, the physiological tolerances of insect species obtained by experimental data are applied to predict the distribution potential as in spatial estimator of climate impacts on the envelope of species (SPECIES) and CLIMEX (the product name for a commercial software by CSIRO) model. Also, phenology or population models can be used as the tool of one deductive mechanical approach useful for predicting establishment of insect pests.

The potential geographical distribution of *B. dorsalis* has previously been modeled using GARP, Maxent or CLIMEX model in the world. De Meyer et al. (2010) applied GARP and Maxent model to estimate the potential distribution range of *B. dorsalis* using the presence records in Africa and Asia. The results of GARP model appeared well suited to an equatorial climate. But De Villiers et al. (2016) criticized that the estimated potential range failed to include the northern Sahelian areas in Africa where *B. dorsalis* actually distribute. Also, their Maxent model (De Meyer et al., 2010) showed a bad suitability, excluding many of the known occurrence records in Africa (De Villiers et al., 2016). Hill and Terblanche (2014) used ecological niche factor analysis (ENFA) on bioclimatic zones, and Maxent model to project the distribution range of *B. dorsalis* complex. They combined the presence data for the previously separated species in the *B. dorsalis* complex: *B. dorsalis*, *B. invadens*, *B. papayae* and *B. philippinensis*. The Maxent model predicted well general distribution range of *B. dorsalis*, but still underestimated the northern and southern limits of *B. dorsalis* within Africa as reviewed by De Villiers et al. (2016).

The inductive empirical models above are not easy to adjust the fitness by adjusting parameters when inconsistencies occur. In contrast, the deductive models such as CLIMEX can be fitted to the known species distribution by adjusting the parameters of climatic stress functions until the model results met a criterion. The stress functions are basically constructed by experimentally determined data sets.

Until now various CLIMEX models were proposed by Hou and Zhang (2005) and Wang et al. (2010) in Chinese regions, Stephens et al. (2007) and EPPO (2010) in global scale, Kriticos et al. (2007) in New Zealand, Sridhar et al. (2014) focused in India and De Villiers et al. (2016) focused in Africa. Most models were based on the CLIMEX parameters of Stephens et al. (2007), and the parameters were adjusted to include each author' interesting distribution areas of *B. dorsalis*. As a result, there was a strong overlap between the modeled distribution ranges among the previous models. But most models fell out of the climatically suitable range of *B. dorsalis* in central and Northern China, probably because these models were made with high suitability in the tropical regions.

The selection of a CLIMEX model with parameters that are well fit to the geographical distribution characteristic of *B. dorsalis* in central and northern China is essential to apply it in Korea including Jeju areas. In other words, Jeju is located in similar or slightly higher latitude from the northern boundary of *B. dorsalis* in China. Consequently, this study was conducted to establish a CLIMEX model that can be applied to predict the potential distribution of *B. dorsalis* in Jeju areas. We tried to validate previous CLIMEX parameters for the records of *B. dorsalis* in central and northern China and to find the best set of parameters that could be applied in Jeju.

2-2. Material and Methods

2-2-1. Overview of the CLIMEX model

The CLIMEX model is a modeling tool to estimate the spatial distribution of organisms in terms of the potential distribution and relative abundance, which works on the assumption that the distribution is limited by climate and predicts the physiological (fundamental niche) limits of a species (Kriticos et al., 2015). Thus, this model calculates basically the population growth of an organism using various environmental thresholds, which increases during suitable climate seasons and decreases during unsuitable seasons.

The ecoclimatic index (EI), which integrates the annual growth index (GI_A) and stress indices (SI) (include SX in some cases; stress interaction index), gives an overall assessment of the potential risks of pest establishment in the tested locations.

$$EI = GI_A \times SI \times SX \qquad \text{Eq. 8}$$

The GI describes the potential for growth of a population during the favorable season. And the SI (four types of cold, hot, wet and dry) and SX describe the extent to which the population is reduced during the unfavorable seasons.

$$GI_A = 100\sum_{i=1}^{52} GI_{Wi}/52 \qquad \text{Eq. 9}$$

The values of weekly growth index (GI_w) are averaged to produce GI_A for 52 weeks of year, and it is expressed as following;

$$GI_w = TI_w \times MI_w \times RI_w \times SVI_w \times LI_w \times DI_w \qquad \text{Eq. 10}$$

Where TI_W, MI_W, RI_W, SVI_W, LI_W and DI_W are the weekly temperature, moisture, radiation, substrate, light and diapause indices, respectively. Each index is calculated using corresponding environmental threshold: for example, the lower temperature threshold in case of TI_W.

The SI and SX have the form below;

$$SI = \left(\frac{1-CS}{100}\right)\left(\frac{1-DS}{100}\right)\left(\frac{1-HS}{100}\right)\left(\frac{1-WS}{100}\right) \qquad \text{Eq. 11}$$

$$SX = \left(\frac{1-CDX}{100}\right)\left(\frac{1-CWX}{100}\right)\left(\frac{1-HDX}{100}\right)\left(\frac{1-HWX}{100}\right) \qquad \text{Eq. 12}$$

The CS, DS, HS, and WS are the annual cold, dry, heat and wet stress indices respectively, and CDX, CWX, HDX and HWX are the annual cold-dry, cold-wet, hot-dry and hot-wet stress interaction indices. These stress indices are set to limit the species' ability to survive during adverse seasonal conditions, and so determine its geographical distribution. These indices also are calculated weekly with accumulating stress when climatic conditions exceed the stress threshold.

Finally, the EI is calculated from 'no persistence (EI = 0)' to 'maximal population size (EI = 100)': 0-0.49 (unsuitable), 0.5-9.99 (marginal), 10-19,99 (suitable), >20 (optimal) and 100 (perfect) (Sutherst et al., 2004) or EI > 25 (very favorable), EI = 10 to 25 (favorable) and EI < 10 (low to marginal suitability) (Sutherst et al., 2007).

2-2-2. Initial values of CLIMEX parameters

CLIMEX models with various parameters are available at the present as seen in Table 5. In the present study, the majority of initial parameter values except for cold stress-related parameters was obtained from the previous reports or biological data sets. The parameters for cold stress were manually iteratively adjusted until the simulated geographical distribution indicated by the Ecoclimatic Index (EI) and Cold Stress (CS) values agreed with the species known characteristic of distribution.

Temperature index

The minimum temperature for development (DV0) was set to 9.5 °C, which was for egg to egg period of four common strains of *B. dorsalis*, including *B. philippinensis*, *B. papayae*, and *B. invadens* (Table 1). The lower optimum temperature (DV1) and the optimum temperature (DV2) were set to 25 and 33 °C, respectively, as suggested by Stephens et al. (2007) who almost originally provided the CLIMEX parameters of *B. dorsalis*. The maximum temperature for development (DV3) was set to 42 °C, which value was adopted by De Villiers et al. (2016) to include the Wad Madani and Singa in Sudan as suitable area during the hot summer months of April and May. The weekly temperature index (TI_W) was calculated by using the parameters of DV0-DV3 as described by Kriticos et al. (2015).

Basically, weekly temperature index TI_W = 1 when the range of weekly temperatures is between the parameters DV1 and DV2, and TI_W = 0 when the temperature is below DV0 or above DV3. In computational process, however, the values of TI_W are intricately determined when daily temperatures change across the DV1 and DV0 or DV2 and DV3 ($TI_W = l_q \times l_h$). First, that is, degree-days (DD) are calculated by the sine curve method of Baskerville and Emin (1969) using daily maximum and minimum temperatures in week scale. And then the proportion of DD (Q) under sine curve between DV0 and DV3 compared to DD (A) between DV0 and DV1 is assigned to the weekly temperature index. That is, if $Q \leq A$, $l_q = Q/A$. And if $Q > A$, $l_q = 1$. Further, $l_h = 1 - (T_{max} - DV2)/(DV3 - DV2)$ if maximum temperature $T_{max} < DV3$ and $> DV2$. If $T_{max} \geq DV3$, $l_h = 0$. And $l_h = 1$ when $T_{max} < DV2$. Finally, the annual temperature index is the average of all year-round TI_W multiplied by 100.

The number of degree-days per generation (PDD) was set to 717, which was newly estimated in Ch. 1 as described above. Annual degree-day totals above DV0 calculated by the sine curve method were used to calculate the number of generations per year. The number of generation variable is calculated by dividing annual degree-day total by PDD. When accumulated degree-days were smaller than PDD (namely 717 DD), EI was subjected to '0' indicating no suitable for persistence although other indices are highly suitable.

Moisture index

The limiting low soil moisture (SM0) and lower optimal soil moisture (SM1) thresholds were set to 0.1 and 0.25, respectively (Stephens et al., 2007). SM (soil moisture) = 0 indicates no soil moisture; SM = 0.5 indicates soil moisture content is 50% of capacity; SM = 1 indicates that the soil moisture content is 100% of capacity; SM > 1 indicates a water content greater than the soil holding capacity of (S_{max}), namely run-off (Kriticos et al., 2015). Thus, the value of SM0 = 0.1 is normally about 10% of soil moisture and indicates the permanent wilting point of plants.

We adopted the upper optimal soil moisture threshold (SM2) and limiting high soil moisture threshold (SM3) at the values suggested by EPPO (2010), which were set to 1 and 1.6, respectively.

The moisture index (MI) ranges between 0 and 1. Population growth is maximized when MI = 1, and the value occurs between SM1 and SM2. While population growth is zero at MI = 0, and this occurs when the soil moisture is below SM0 or above SM3.

Cold stress

The stress indices in CLIMEX are set to limit the species' ability to survive during adverse seasonal conditions, and so determine its geographical distribution (Kriticos et al., 2015). Cold temperature was the most influencing factor on the seasonal occurrence of *B. dorsalis* in the northern limit of China (Ye, 2001; Chen and Ye, 2007; Liu et al., 2011b). Therefore, parameters controlling cold stress (CS) were change to evaluate the potential distribution ability of *B. dorsalis* in the selected validation sites.

In CLIMEX modeling, cold stress can be calculated in three different ways (Kriticos et al., 2015). The first, CS degree-day accumulation method (CS-DD) accumulates weekly stress at degree-day cold stress rate (DHCS), when degree-days are below a minimum degree-day cold stress threshold (DTCS), which indicates minimum DDs to maintain metabolism (namely survival). The second, CS minimum temperature accumulation method (CS-MT) uses the parameter of cold stress threshold temperature (TTCS), and CS is accumulated at the cold stress temperature rate (THCS) when weekly average minimum temperatures (T_{min}) drop below TTCS. The third is CS average temperate accumulation method (CS-AT) that uses weekly average temperature (T_{av}) instead of T_{min}, with two parameters of cold stress average temperature threshold (TTCSA) and cold stress average temperature rate (THCSA).

In this study, we selected first the CS degree-day accumulation method (CS-DD) for the CS estimation of *B. dorsalis* for the purpose of comparison with previous CLIMEX simulations, especially because the parameters of DHCS and DTCS were fitted to include the northern limit in India (Sridhar et al., 2014). The cold stress (CS_{wi}) at i-th week can be defined as following.

$$CS_{wi} = (DTCS - DD_{wi}) \times DHCS \qquad \text{Eq. 13}$$

where $CS_{wi} = 0$ if DD $\geq$ DTCS, and DD was calculated daily based on DVCS (developmental temperature threshold for cold stress) by using the calculation method of sine wave curve.

When weekly DDs were successively below DTCS for *n* weeks, then cold stress were accumulated over time in exponential manner.

$$CS_{wi} = (DTCS - DD_{wi}) \times DHCS \times i\ (week\ number) \qquad \text{Eq. 14}$$

Accordingly, CS of the *n*-th week is calculated as below.

$$CS_{wi} = [(DTCS - DD_{wi}) \times DHCS \times n] + CS_{wn-1} \qquad \text{Eq. 15}$$

When the accumulated weekly stress index equals 1.0 or greater, the species is unable to persist at the location, namely EI was automatically set to 0. The final cold stress values were an average of weekly cold stress multiplied by 100. That is, the yearly cold stress index (CS_{yr})was defined as following.

$$CS_{yr} = 100 \sum_{i=1}^{52} CS_{wi}/52 \qquad \text{Eq. 16}$$

In this study, the parameters of cold stress were manually adjusted to include known distribution regions of *B. dorsalis* (see below for details).

Heat, dry and wet stress

The environmental conditions of heat, dry and wet are not limiting factors in Jeju area as well as in most regions in Korea, because the extreme events occur very rarely in the areas. So, each parameter was set according to previous reports. The calculation protocol is same with the procedure that applied to estimate the cold stress above.

The parameters of heat stress temperature threshold (TTHS) and heat stress temperature rate (THHS) were applied to use the threshold temperature mode for calculating the heat stress (HS), and set to 42 °C and 0.005 week^{-1} as recommended by De Villiers et al. (2016), respectively. The TTHS is the same line with DV3. The weekly HS (heat stress) was calculated by accumulating THHS when average weekly maximum temperatures (T_{max}) exceeded TTHS.

Also, wet stress threshold (SMWS) and wet stress rate (HWS) for wet stress (WS) were set to 1.6 and 0.001 (EPPO, 2010), respectively. WS was accumulated if the soil moisture level (SM) exceeds the SMWS. The difference between SMWS and the SM is multiplied by the HWS to obtain the resultant WS.

Dry stress (DS) accumulates when the soil moisture level falls below the dry stress threshold (SMDS) (Kriticos et al., 2015). The difference between SMDS and weekly soil moisture level was multiplied by the dry stress rate (HDS) to give the resultant DS for the week. The SMDS and HDS were to 0.1 and -0.03 as suggested by De Villiers et al. (2016), respectively. The HDS = -0.0001 of Sridhar et al. (2014) is too low so that highly dry areas can be classified as suitable region.

2-2-3. Selection of validation sites for the parameter fitting

CLIMEX models can be used by both approaches of inductive and deductive methods, although it is basically deductive model (Kriticos et al., 2015; Villiers et al., 2016). In CLIMEX modeling, inductive approach is additionally applied to fit parameters belongs to climatic stress functions for defining the limits of species distribution range by adjusting parameter values until the model outputs include known species distribution or phenological data (Vera et al., 2002; Kriticos et al., 2005; Sutherst and Maywald, 2005; De Villiers et al., 2012; Kriticos et al., 2015).

It is very important to find the distribution boundary in the present distribution range of *B. dorsalis* in order to evaluate the potential distribution in Jeju area, Korea, because Jeju area may be included in the distribution boundary of this fruit fly. Thus, the following regions were selected for the parameter fitting based on the previous records including phenology (no. of generations per year) data as summarized in Table 6, SD Fig. 1 and 2.

Wuhan in Hubei province, the central and northern China.

The distribution area of *B. dorsalis* in China has extended to the north since its invasion, as reported by Wang (1996), Han et al. (2011) and Wan et al. (2011). Wan et al. (2011) evaluated the origin and gradual inland range expansion using the samples of *B. dorsalis* from 12 locations covering the entire distribution range in China between Wenchang, Hainan and Wanzhou, Chongqing. They suggested the species originated in the coastal region facing the South China Sea and gradually expanded to colonize mainland China. Also, their demographic analysis indicated *B. dorsalis* underwent a recent population expansion in the central China.

Wuhan region is characterized as a subtropical climate with hot and wet summer, but it has freezing cold winter. *B. dorsalis* is known to be first reported in this area in 2004, and it has become widespread and economically important in Wuhan, Hubei Province, central China since its introduction (Han et al., 2011). The population of *B. dorsalis* occurs seasonally between early July and late December with peak abundance during the period of October and early November, indicating approximately four generations per year (Han et al, 2011; data in a citrus orchard).

Some reports regarded the records of *B. dorsalis* in the central and northern China as that may represent ephemeral populations (De Villiers et al., 2016). Namely, populations migrating from the permanent habitat in the south just build up its populations during favorable seasons in northern areas. But this hypothesis may not be able to fully explain the widespread and economical damage on fruits and vegetable crops in Wuhan, with population persistent in several successive years (Han et al., 2011; Hong et al., 2015). Hong et al. (2015) used the phenology data of *B. dorsalis* obtained in Wuhan during 2007 to 2009 seasons to validate their generic plant pest forecast system. Furthermore, Han et al. (2011) reported that all the pupae placed in the field soil in mid-November being able to successfully overwinter in Wuhan. And they suggested that a small proportion of overwintering pupae may bridge the gap between winter and next spring, and lead to a small initial number of adults early in the season. Consequently, it may be more reasonable that Wuhan area can be regarded as seasonal distribution area of *B. dorsalis*, and suitable area for overwintering in some years with mild winter. Thus, the area may be the best validation site of the parameters fitting to include the northern distribution limit of *B. dorsalis*.

Consequently, we selected the test points that were sampling sites of *B. dorsalis* by previous researchers, Wan et al. (2012), Han et al. (2011) and Schutze et al. (2015b), for fitting the parameters of CS (see Table 6 for details). In Wuhan, we assumed that *B. dorsalis* can persistent in years with mild winter, but non-persistent in normal years (see below for details).

Wuxi in southern Jiangsu province, China

Wuxi city is located in southern Jiangsu province in China. This area is hot and humid in summer, and chilly and damp in winter, with an average annual temperature of 18 °C and very occasional snow (National Meteorological Information Center of China, http://data.cma.cn/).

In Sanguo Film and Television city of Wuxi district of Jiangsu province, *B. dorsalis* was first found in 2003 (Luo et al., 2009), and caused serious economic damage in citrus orchards due to a high population density (Qi et al. 2008), which seasonal populations occurred from June, peaked in September to October, and ended in November. In the region, it was observed that *B. dorsalis* pupae could overwinter successfully with showing a 35% of mortality during the winter in 2005 to 2006 (Qi et al. 2008). Also, Wang et al. (2014) reported that the northern marginal population

(31.6°N, Wuxi) had higher cold tolerance than southern populations (23.1°N and 24.3°N, Guanzhou and Xiamen, respectively) of *B. dorsalis*. Thus, the marginal population of *B. dorsalis* might have evolved a new biotype with better adaption to low temperature since its invasion into new area (Wang et al., 2014).

Consequently, the region of Wuxi was regarded as having newly invaded and established populations of *B. dorsalis* with seasonal occurrence in the year. In Wuxi, we assumed also that *B. dorsalis* can persistent in years with mild winter, but non-persistent in normal years (see below for details).

Baoshan in western Yunnan province, China

Baoshan in Yunnan province is bordered to Burma and the Hengduan Mountains in side of the west and south, respectively, and it is characterized by the Longitudinal Range-Gorge Region of China including a high plateau with an elevation of 1,700-2,300 m a.s.l., which has the south-west subtropical plateau monsoonal climate (Chen and Ye, 2007).

Probably because of cold weather caused by high altitude of Baoshan, *B. dorsalis* occurs seasonally from April to November with peak in August and no flight activity in the period between December and the next March in the area (surveyed for 4 years from 2003 to 2006 by Chen and Ye, 2007). But *B. dorsalis* occurs throughout years in Lujiangba (N 24°58′, 695 m), which is located at a similar Latitude and just away 30 km west from Baoshan (N 25°09′) (Chen and Ye, 2008).

The populations of *B. dorsalis* in Baoshan may not be formed yearly by migrant populations from the region where it occurs during whole seasons such as Lujiangba. That is, the genetic structure of Yunnan populations shows that Baoshan populations was not originated from Lujiangba due to the geographical isolation by mountain chains, the Biluoxue Mountains (average elevation: 2,500 m) (Chen and Ye, 2008).

Consequently, the region of Baoshan was regarded as persistent populations of *B. dorsalis* with seasonal occurrence in the year. This area is highly elevated and has a relatively cold climate, so it would be suitable for regarding as the northern limit.

Accordingly, we selected a total two sites where the phenology was monitored (Chen and Ye, 2007) or specimens were collected for the analysis of genetic variation (Chen and Ye, 2008) of *B. dorsalis*.

Ruili in western Yunnan province, China

Ruili is located in western Yunnan province with the southern sub-tropical damp monsoon climate. Its annual mean temperature and annual mean rainfall are 21℃ and 1,397 mm, respectively; and this area is one of the major regions in Yunnan infested throughout the year by *B. dorsalis*, with five generations per year (Chen et al., 2006).

According to the genetic diversity of *B. dorsalis* in Ruili (Shi et al., 2005; Chen and Ye, 2008), the population was significantly isolated from the central Yunnan, probably because of geographic barriers to gene flow. Instead the population seemed to be in a contact zone with flies originating from surrounding regions such as Burma, where the most divergent haplotypes are more common (Shi et al, 2005).

Consequently, we selected three sites for model validation: Huomen, Liaochengzi and Jieziang where flight activity of *B. dorsalis* was observed during full seasons (Chen et al., 2006).

Kunming in eastern Yunnan province, China

Kunming is located in eastern Yunnan province in southwest China, characterized by short, cool dry winters with mild days, and long, warm and humid summers with the southern sub-tropical damp monsoon climate (an annual mean temperature of 15.52 °C). This area has been classified by seasonally occurred zone of *B. dorsalis* (Ye, 2001), occurring May to December with two or two to three generations per year (Zhang et al., 1995; Ye, 2001; Ye and Liu, 2005).

According to the haplotype network of *B. dorsalis* populations in Yunnan, the intraspecific variability was very high, suggesting either a longer residence of this fly in Yunnan than recognized previously or a recurrent colonization process from different origins (Shi et al., 2005). The prevailing air currents originating in the Bengal fjord which flow from southwest to northeast (Chao, 1987) could play an important role in inter-population gene exchange (Shi et al., 2005). But the genetic diversity in Kunming was higher (i.e. no founder effect) than in Huanian, which is located further southwest and in which *B. dorsalis* is constantly present. Thus, an assumption should be forcedly accepted to understand the genetic diversity in Kunming: “Kunming flies originate from several surrounding southwestern locations and are dispersed over long distances through air currents and fruit exchange (Shi et al., 2005)”. Such genetic exchange must be occurred every year in Kunming, if we deny persistent Kunming populations of *B. dorsalis* that successfully overwinter. But this region has been regarded as non-persistent and re-colonized area yearly by immigrant populations of *B. dorsalis* from southern Yunnan (Ye, 2001; Ye and Liu, 2005), although the population status has not been experimentally examined.

Consequently, we selected four validation sites to evaluate the possibility of persistent establishment of *B. dorsalis* in Kunming: a point monitored by Zhang et al. (1995) and three points monitored by Ye and Liu (2005).

Jammu and Kashmir in the northern India

Jammu and Kashmir (N 32°73´ E 74°87´) is a state in northern India, which is located mostly in the Himalayan mountain, and shares borders with the states of Himachal Pradesh and Punjab to the south. This region has a humid subtropical climate (Köppen: Cwa) (Peels et al., 2007) with extreme hot summer (a maximum 46 °C), and temperatures in the winter months occasionally drops to 2 °C. This state consists of three regions: Jammu, Kashmir and Ladakh. In Jammu region, which includes Udahampur, Udheywala and Marh (see level altitude between 200 and 400 m), it is known that *B. dorsalis* occurs throughout the year on various fruit crops such as guava, ber, mango, citrus and phalsa except cooler months in December and

January (Rai et al., 2008; Bhagat, 2014). Also, an extensive survey for fruit flies in two districts of Srinagar and Budgam in Kashmir region showed that *B. dorsalis* was recorded as predominant species after *B. cucurbitae* (Coquillett) (Ganie et al., 2013a). However, *B. dorsalis* was seasonally observed during the period of July to October. Therefore, we regarded Jammu region as suitable area, and Kashmir region as marginal or seasonal occurrence area (namely, non-persistence in normal years) of *B. dorsalis* for the comparison of CLIMEX outputs to evaluate the parameters.

In Kashmir, finally, we selected Batmaloo, Shalimar, and Dal in Srinagar district, and Chadoora, Narkara and Bugam in Budgam district, where the survey was carried out by Ganie et al. (2013). In Jammu, also, Sher-e-Kashmir University of Agricultural Sciences and Technology of Jammu (SKUAST-Jammu) studied by Rai et al. (2008), and regions of Samba, Udahampur, Udheywala and Marh monitored by Tara and Gupta (2016) were selected as validation sites.

Sakishima, Okinawa and Amami, Japan

The first observation of *B. dorsalis* in Japan was recorded in 1919 at Kadena, Okinawa Islands. In more northern areas of Japan, namely Amami and Ogasawara Islands, the first records were in 1929 and ca. 1925, respectively. The early invasions in Sakishima Islands, Okinawa Islands, Amami Islands and Ogasawara Islands were eradicated by 1986 (Nakamori et al., 1991). After that, monitoring traps captured more than 300 flies between 1987 and 2008 in the areas, showing that frequent re-invasion has occurred (Ohno et al., 2009). Recently, 531 adults of *B. dorsalis* were trapped in Amami Oshima Island between 1 September and 30 October 2015 (FAO, 2016).

Although the frequent re-invasion can be highly related with a long-range dispersal of adult flies from southern countries such as the Philippines or human-induced introduction such as international trade (Ohno et al., 2009), some areas of Sakishima and Okinawa may be suitable consistently for the establishment of *B. dorsalis* (Koidsumi and Shibata, 1964a). Also, Amami is regarded as marginal or seasonal occurrence area of *B. dorsalis* (Koidsumi and Shibata, 1964a; Fujisaki, 2016). The evaluation for the distribution suitability of *B. dorsalis* in the Okinawa Islands may provide a window to understand its risk in Jeju areas, Korea. According to Ushio et al. (1982), *B. dorsalis* had occurred year round since 1974 in Amami main Island, Kikai, Tokunoshima, Yoron and Okinoerabu until its eradication in 1979. Consequently, we selected test sites in the northern region of Kikai and Amami.

Peshawar valley and Foot-hills, Pakistan

Rawalpindi region including Haripur and Dargai (foot-hills) and the Peshawar valley (Peshawar and Kohat) is located at the highest latitude among the distribution areas of *B. dorsalis*. The average air temperatures of these areas are kept in 10 to 15 ℃ in the winter, probably resulting in successful survival of this fruit fly. Thus, Syed et al. (1970) reported that *B. dorsalis* attack is almost cease in winter, but the population can maintained. In these areas, generally, the flight activity of *B. dorsalis* is stopped when air temperatures dropped below 12.78 ℃ in the late season, and they start to attack host plants when it increase to 19.4 ℃ in the following spring, March. Finally, we selected test sites at Dargai, Haripur and Kohat in Pakistan.

2-2-4. Meteorological data sets

For running CLIMEX simulation, it is required 5 meteorological data includes monthly minimum and maximum temperature (℃), total precipitation (mm), and relative humidity (%) at 09:00 and 15:00. We obtained weather variables of China and India for fitting species parameters of CLIMEX simulation from the current climate data sets of WorldClim Version 2.0 (http://worldclim.org/; Fick and Hijmans, 2017). These datasets estimated from 9,000-60,000 weather station records of worldwide aggregated from 1970 to 2000, providing high resolution (0.5-10 arc min, which is the same scale with 0.85 and 16.92 km, respectively) of global meteorological information: average monthly climate data for minimum, mean and maximum temperature, precipitation, solar radiation, wind speed and water vapor pressure (Fick and Hijmans, 2017). These averages of 30 years were regarded as weather variable in normal years. We used dataset with a resolution of 2.5 arc min because altitude gradient of the test areas were highly drastic especially in Yunnan, China and Jammu & Kashmir, India. This resolution corresponds with 4.63 km at the equator, 3.77-4.60 km in India (N 6°42' to N 35°31'; Global Administrative Areas (GADM, http://gadm.org/)) and 2.42-4.40 km in China (N 18°10' to N 58°34'; GADM). While dataset with higher resolution of 30 arc sec were available in WorldClim 2.0, precision of coordinates of each test sites were less accurate, expressed with minutes or obtained from centroid of the locality, so we didn't concern of these dataset. Relative humidity at 09:00 were calculated using the monthly average temperature and vapor pressure of Worldclim 2.0 dataset and the formula given by Fick and Hijmans (2017), then multiplied by 0.85 to obtain relative humidity at 15:00 (Kriticos et al., 2015). The datasets with GeoThiff type (.tif) were converted to meteorological data file (.mm) with Qgis 2.18.0 (https://www.qgis.org/it/site/) and CLIMEX MetManager application.

The meteorological data sets in Korea were obtained from Epinet Inc. (R&D Center, EPINET Co., Ltd, Anyang 14056, Korea). The simulated climates of current (2011-2020 average), 2050S and 2090S were used to project the suitability of *B. dorsalis* in Korea including Jeju. The weather data sets were based on the RCP (Representative Concentration Pathway) 8.5 climate change scenario provided by the Climate Change Information Center (CCIC, http://www.climate.go.kr) of the Korea Meteorological Administration. The original data sets were down scaled to a high resolution of 36 arc sec ≈1 km). This resolution corresponds with 1,111 m at the equator, 869-931 m in Korea (N 33°11' to N 38°61'; GADM).

Observed actual climatic variables of Wuhan in Hubei and Wuxi in Jiangsu for the past 33 years (1985-2017) were purchased from meteoblue®. These datasets are based on the weather simulation data with a high spatial resolution of 4-30 km and temporal resolution hourly. In Jeju, the weather variables for the period of 1985 to

2017 were obtained from the Jeju weather station.

Also, an irrigation scenario was applied. Natural precipitation is used to estimate soil moisture in CLIMEX modeling. And the soil moisture level can affect critically EI values through DS and MI. In our preliminary simulation, the region of India and Senegal was evaluated as $GI_w = 0$ when abundant season of *B. dorsalis*. Thus, we applied the scenario of 2.5 mm top-up irrigation during the year-round suggested in Africa areas by De Villiers et al. (2016).

2-2-5. Parameter fitting process based on CS and model validation

The CLIMEX model can be run in three different modes: Compare Locations (1 species or multiple species), Compare Years and Compare Locations/Years (Kriticos et al., 2015). We used Compare Locations (1 species), in which the response of a species to the long-term average climates of different locations is compared and it is normally the most frequently used of the CLIMEX applications. Also, parameters related with RI (radiation), LI (light), SVI (substrate), DI (diapause), BI (biotic), SXI (Stress Interaction Index) were not included.

For the purpose of CS parameter fitting to include the northern distribution limit of *B. dorsalis*, two regions were first tested by Compare Years module: Wuhan (N 30˚27′34.69″, E 114˚20′55.71″) and Wuxi (N 31˚29′00.96″, E 120˚13′55.20″) in China. These regions have been known as seasonal or temporary occurrence area, but the records for successful overwintering are getting accepted (Qi et al., 2008; Han et al., 2011) as described above. Thus, two scenarios were adopted under an assumption for the establishment ability of *B. dorsalis*. The first scenario was based on the observation that *B. dorsalis* could successfully overwinter in Wuhan in 2009, China. Accordingly, the parameters of DTCS and DHCS were adjusted to satisfy CS value ≈ 21 in Wuhan in 2009, because the mortality of overwintering *B. dorsalis* pupae was estimated to be 21 % from the experiment of Han et al. (2011). In the second scenario, the DTCS and DHCS were fitted to satisfy CS value ≈ 35. This criterion was originated on the mortality of 35 % in overwintering *B. dorsalis* pupae in Wuxi in 2006 (Qi et al., 2008). Also, CS values were compared during the period from 1985 to 2017 in two regions above.

Adverse condition such as drying can also affect survival of pupae of *B. dorsalis* (Vargas et al., 1987). However, in the case of Wuhan, all of the pupae survived from November to the following spring (Han et al., 2011), and in the case of Wuxi, the experiment was done in the citrus orchards (Qi et al., 2008). So it was assumed that the mortality rate of both experiments was not effected by drying. Accordingly, our outputs may slightly overestimate the effect of cold. And it would better to avoid the controversy that the results of this model are too generous to include the Jeju areas.

We compared CS values among selected all validation sites by Compare Locations module to check the robustness of selected parameters using weather data sets in normal years. Populations of *B. dorsalis* were assumed not to be persisted in the regions of Wuhan, Wuxi, Srinagar and Budgam in normal years (30-yr average from 1975 to 2000) as described above. Finally, we discussed on the most suitable parameters, which satisfy the scenarios and include successfully the distribution range of *B. dorsalis* in the validation sites, by ensuring CS <100 (persistent) or CS > 100 (non-persistent).

Model validation with the number of generations

CLIMEX generates Generation index, the number of generations per year using the parameters of PDD and DV0 as described earlier. This index is very useful to evaluate the robustness of CLIMEX model by comparing model outputs (i.e. Generation index) with observed values. The known number of generation times of *B. dorsalis* in each region was obtained from published literatures, and summarized in Table 6: Kunming (Zhang et al., 1995; Ye and Liu, 2005), Ruili (Chen et al., 2006), Wuhan (Han et al., 2011), Guangnan (Ye, 2001), Hekou (He et al., 2002), Jinghong (Ye, 2001), Qujing (Ye, 2001), Fujian (Wang et al., 2014) and Guangzhou

(Wu et al., 2007).

The prediction accuracy of the model (predictability for the number of generations) was tested by a Chi-squared test using the discrepancy between the predicted and observed values of CLIMEX model. The statistic for the Chi-squared test was approximated as [(Observed - Predicted generations)^2/Mean] (Sokal and Rohlf, 1981). The degree of freedom was applied by n-2 (n indicates sample size, that is, the number of regions included).

Model validation with weekly growth index (GI_w)

CLIMEX calculates weekly growth index (GI_w) using the weekly temperature, moisture indices, etc. as described earlier. The seasonal phenology was compared graphically with the GI_w values from the model outputs as recommended by De Villiers et al. (2016). The phenology data sets in each region were obtained from published literatures: Ruili (Chen et al., 2006), Wuhan (Han et al., 2011), Baoshan (Chen and Ye, 2007), Kunming (Ye and Liu, 2005), Jiansui (Lin'an, Nanzhuang and Qinglong) (Zhang et al., 2005) and Suzhou (Meng et al., 2008), China; Ludhiana (Mann, 1996), Dharwad (Ravikumar and Viraktamath, 2006), Nadia (Mohanpur and Jaguli) (Das et al., 2017), India; Rawalpindi (Chaudhry et al., 2000) and Peshawar (Khattak et al., 1990) Pakistan; Miyako is. and Yaeyama is. (Iwahashi, 1984), Japan. For the purpose of comparison, the numbers of *B. dorsalis* were scaled to a ratio against the peak occurrence in pheromone traps after combining monthly total values.

2-2-6. Application to Korean regions

We applied the final parameters to predict the distribution potential of *B. dorsalis* in Korea. Also, CS values were examined during the period from 1985 to 2017 in Jeju areas (Jeju city, Seogwipo city, Gosan and Seongsan). The EI values were classed by the suggestion of Sutherst et al. (2004): 0 - 0.49 = unsuitable, 0.50 − 9.99 = marginal, 10 − 19.99 = suitable, > 20 = optimal and 100 = perfect.

2-3. Results

2-3-1. Adjusted parameters of CLIMEX model and its validation

The parameter DHCS was determined to -0.0035 and -0.0006 week-1 that satisfied the scenario 1 and 2, respectively (The value of DTCS was fixed to 8 DD in advance). As well as this adjusted parameter value, other CLIMEX parameters were determined accordingly based on the previous reports with considering the annual climate and the phenology of *B. dorsalis* in the validation sites (Table 5 and 6, see SD Fig. 3 and 4 compared with known distribution).

When parameter DHCS was set to -0.0035 week-1 (Scenario 1), the values of CS were below 100 in a 40% years during the period of 1985 to 2017 in Wuhan (Fig. 4A). But *B. dorsalis* could survive only in 1999 and 2007 in Wuxi during the same period (Fig. 4B). The values of CS were kept all below 100 during the years of 1985 to 2017 in Wuhan and Wuxi region, when it was set to -0.0006 week-1 (Scenario 2).

Based on the adjusted CS-parameter, calculated CS values with previous CLIMEX models and our Scenarios using weather data sets of normal years are presented in Table 7. The model parameters of Scenario 1, Kriticos et al. (2007), De Villiers et al. (2016) and Hou and Zhang (2005) were fitted well to our general assumption which indicates non-persistent populations of *B. dorsalis* in the regions of Wuhan, Wuxi, Srinagar and Budgam in normal years. But the model of Hou and Zhang (2005) was failed to fit in Wuxi in 2006 (namely, should be CS > 100). The results of Scenario 2 showed very low CS values in all validation sites, thus resulting in successful persistence in four non-persistent regions, which was similar to the models of Wang et al. (2010) and Sridhar et al. (2014). The prediction by EPPO (2010) overestimated largely CS values in most regions.

In Kunming, which region has been regarded as non-persistent area by previous researchers, CS values were below 100 in all models except of EPPO (2010) model, indicating successful survival of overwintering populations. The CS values by our Scenario 1 was ranged a 15 to 39 in Kunming (Table 7).

The predicted number of generations per year by CLIMEX model was not significantly different with the observed values in the models of present study and Kriticos et al. (2007) (Table 8). But the prediction by Hou and Zhang (2005), Wang et al. (2010), Sridhar et al. (2014), EPPO (2010) and De Villiers et al. (2016) was significantly different with actual observation at P = 0.05 or 0.001.

Weekly GI (GI_w) values predicted by the model are provided in Figs. 5 to 8, comparing with the actual seasonal phenology data in various regions. The predicted GI_w was generally fitted well with the observed phenology in China; showing a low value in the winter and increasing in the spring. But the GI_w was kept low during summer in most areas except of Wuhan and Suzhou, in spite of high level of the fly abundance (Fig. 5). Such discrepancy was also found in Dharwad of Karnataka in south India, and Nadia of West Bengal in northwestern India (Fig. 6). The low values of GI_w during summer in the outputs of model was mostly caused by adverse MI values (data are not provided).

The large decline of GI_w values during summer in the model was also observed in Ludhiana region in india and Rawalpindi region of Peshawar in Pakistan (Fig. 7). In this case, the TI (exactly, the maximum temperature) affected largely the population abundance of *B. doralis*. On the other hand, the GI_w values by the outputs of model were kept as low as 0.1 to 0.3 during the year in Japan (Fig. 8) and this was mainly because of high MI values except for the winter season (data are not provided).

2-3-2. Projection of climate suitability in Korea

The changes of CS values for 30 years from 1985 to 2017 in four regions of Jeju are provided in Fig. 9, when the parameters of Scenario 1 and 2 were applied. The outputs by Scenario 2 showed that *B. dorsalis* populations could successfully overwinter in all years and Jeju regions, since CS values were below 100. However, CS values were kept above 100 in Jeju, Gosan and Seongsan region when Scenario 1 was applied, indicating extinction during winter season. And overwintering populations could survive partially in years with warm winter in Seogwi: 1990, 1992, 1998, 1999, 2002, 2004, 2007 and 2009.

The projected climate suitability for *B. dorsalis* by RCP 8.5 weather scenario in Korea is presented in Fig. 10 and 11 for Scenario 1 and 2, respectively. In Scenario 1, most areas in Korea were subjected to unsuitable climate (EI < 0.5) in 2010s; with marginally suitability (EI = 0.50 − 9.99) in few sites in Seogwipo-city (Fig. 9). In the 2050s with the same Scenario, however, the southern coastal part on Jeju Island fell into the climatically suitable zone (EI = 10 − 19.99). Further, the suitable zone was extended to whole costal area on Jeju Island in the 2090s; with optimal zone (EI > 20) was appeared in the southern area.

In Scenario 2, all except mountainous areas in Korea were included into marginal zone, and the southwestern part of Jeju Island and Daegu area were evaluated as suitable zone in 2010s. The optimal zone started to appear from the 2050s in Jeju and from the 2090s in the mainland of Korea. Further, most of the lowlands were simulated as suitable zone in the 2090s. The major factor that *B. dorsalis* can not establish in Korea region is the CS shown as SD Fig. 5 and 6.

2-4. Discussion

2-4-1. Selected parameters

The parameters for temperature index (TI)

The high threshold temperature of *B. dorsalis* has been known to be a 35℃ in the laboratory rearing studies (Wu et al., 2000; Rwomushana et al., 2008; Danjuma et al., 2014). Thus, DV3 (limiting high temperature) = 35 has been frequently used in CLIMEX modeling (Rwomushana et al., 2008; Danjuma et al., 2014). However, the populations of *B. dorsalis* rapidly increased during hot season in India and Pakistan where air temperatures reached 39.7℃ in Jammu, 40.3℃ in Ludhiana and 41.1℃ in Peshawar (Worldclim ver. 2.0 in 1985) (Khattak et al., 1990; Mann, 1996; Rai et al., 2008), as well as in hot regions of Wad Madani and Singa in Sudan, Africa (De Villiers et al., 2016). The TI value is set to zero when maximum air temperatures are over DV3; therefore, DV3 of 35℃ does not explain well the current distribution of *B. dorsalis* in hot regions.

Insect species have good behavioral ability for thermoregulation to maintain their body temperature stable as known as moving into shaded areas in hot environment (Fletcher, 1987). Thus, this fly adults seem successfully to survive in air temperatures over known high threshold temperature. Actually, the known distribution areas of *B. dorsalis* in hot tropical countries were simulated as suitable regions by setting DV3 to 42℃ (De Villiers et al., 2016). Consequently, we accepted 42℃ for the parameter of DV3 in this study.

We applied parameter values for DV0 (limiting low temperature) to 9.5℃ and PDD (degree-days per generation) to 717 DD. These values were derived form combined data sets of temperature-dependent development of *B. doralis* complex that were obtained form actual development experiments worldwide (see SD Table 2 for the comparison) and it was largely different from the parameters of previous researchers. For example, DV0 was set to 13 in the model of Kriticos et al. (2007), and to 11.8 in Hou and Zhang (2005), Wang et al. (2010) and Sridhar et al. (2014). Syed et al. (1970) reported that reproduction of B. dorsalis is inactivated at least below 12.78 ℃, and in the temperature-dependent total fecundity model estimated in Ch.1 of this study, reproduction of *B. doraslis* would be activated above 14 ℃. In this respect, setting the DV0 to 9.5 may not seem right because it was interpreted as the population can develop even if the constant temperature of 10 ℃. However, these condition can not exist in temperate regions such as Korea. Longevity of adults is prolonged at low temperatures for more than 100 days, sometimes for more than a year (Koidsumi and Shibata, 1964b), and it is long enough for them to encounter a favourable temperature for reproduction. It is reported that not only the adults but also immature stages could develop under varying temperature condition, and low temperature is higher than 9 ℃. (Koidsumi and Shibata, 1964b). Therefore, The DV0 of 9.5 were applied to indicate that these populations could survive and develop (GI> 0) at temperatures between 9-10 ℃. The PDD is an important parameter to determine the persistence of a species in selected region, because EI is set to '0' when accumulated degree-days during a year are smaller than PDD. As incorporated as the biological details of *B. dorsalis* in our parameters, the predicted generation times per year was not significantly different with actual observations (Table 8). Thus, our new parameters will be useful for CLIMEX modeling or population models in other regions.

The parameters for moisture index (MI)

Moisture index affects directly on EI value in CLIMEX modeling, since population growth becomes zero at MI = 0. The zero MI occurs when soil moisture (SM) is kept below SM0 (limiting low soil moisture) or above SM3 (limiting high soil moisture threshold). As seen in Table 5, various combination of SM2 and SM3 was applied in previous CLIMEX models.

The values of SM2 = 1.8 and SM3 = 2 were determined to improve the modeled GI_W in Ziguinchor (Senegal) during August when soil moisture levels reached a maximum value of 1.97 (De Villiers et al., 2016). Also, SM3 = 2 was used to predict the potential distribution of *B. dorsalis* in China (Hou and Zhang, 2005) and India (Sridhar et al., 2014).

The soil moisture level of SM > 1 indicates a runoff, a water content greater than the soil holding capacity (Kriticos et al., 2015), which may cause the death of pupae in the flooded soil. Thus, the values of SM2 = 1 and SM 3 = 1.6 (EPPO, 2010) can be more reasonable biologically, although GI_W falls to zero in rainy season during which fly adults are captured in regions such as Senegal (De Villiers et al., 2016).

Many empirical observations showed that high SM values induced the decline of *B. dorsalis* populations. For example, Vayssieres et al. (2014) found that the population abundance peaked in June by following the decline when SM increased over 1.7 during July to August in Ziguinchor, Senegal. In Ruili of China, also, a similar phenomenon was reported (Chen et al., 2006): the population of *B. dorsalis* started to drop sharply with SM value of 1.6 to 1.7 after peak abundance in mid June. EPPO (2010) determine SM of 1.6 based on the fitting ability to the distribution areas of *B. dorsalis* in Bhutan. Consequently, we used biologically valid value of SM2 = 1 and SM3 = 1.6 as recommended by EPPO (2010).

2-4-2. Model validation

Weekly growth rate (GI_w)

In the outputs of CLIMEX simulation with SM3 = 2.0 (namely the model of De Villiers et al., 2016), GI_w values were not changed sensitively by soil moisture during the summer in many cases (Fig. 5, 6 and 8). On the other hand, the results with SM3 = 1.5 (Kriticos et al., 2007) and 1.6 (scenario 1 and 2 in the present study) showed dynamical response of GI_w values with soil moisture, although the changes were not consistent always with actual phenology data in some cases (Fig. 5, 6 and 8). But we think such inconsistency may be caused by two factors. The first factor can be caused in the computational process of CLIMEX. The discrepancy was mostly due to overestimated MI values in rainy season. The MI affects the survival of pupal stage in the life cycle of *B. dorsalis*, and that is immediately reflected into GI_w values. The phenology data were based on adult populations. Therefore, a time lag could be occurred between predicted GI_w value and actual phenology as seen in Fig. 5. Also, the abundance of adult populations might not be largely affected by pupal mortality because of the long longevity of adults (Vargas et al., 2000; Ekesi et al., 2006). The second factor can be caused by overestimated pupal mortality without a consideration for the presence of heterogeneous pupation sites. In other words, mature larvae of *B. dorsalis* seek actively pupation site to increase their survival chance (Aloiykhin et al., 2001). So, all pupae might not be subjected to death due to flooded level of soil moisture. In the model, however, the GI_w values were fell out to zero because MI was calculated to zero when the soil moisture was over 1.6 (SM3). The reason why the fly adults were continuously trapped in spite of the GI_W values falling to zero in rainy season in some countries (Drew et al., 2007; De Villiers et al., 2016) seems to be caused by the combination of those two factors above. And so high pupal mortality was computationally compensated by setting SM3 as 2.0. However, SM3 = 2.0 is non-valid value biologically and hydrology in soil as described earlier. So, we used SM3 = 1.6 which is valid logically. And this parameter value (SM3 = 1.6) may not critically affect EI in Korea, because year round average GI is used to calculate EI, and rainy season is not lasted long time.

Cold stress value (CS)

We have suggested two parameter values of -0.0035 and -0.0006 week^{-1} for DHCS in the present study, which can explain the distribution of *B. dorsalis* in Wuhan and Wuxi in China, respectively. The Wuhan-based model (Scenario 1) showed reasonable CS values that well described the known distribution regions of *B. dorsalis* in the northern limit (Table 7). In the Wuxi-based model (Scenario 2), however, CS values were accumulated less than 100 in non-persistent regions (or specific years) of *B. dorsalis*.

The Wuxi-based model should be justified by empirical observations to be accepted, because it highly overestimated the survival of overwintering *B. dorsalis* pupae than that we had known. Wang et al. (2014) provided very important results for the cold hardiness of *B. dorsalis* that the marginal populations in northern limit might have evolved a new biotype with better adaption to low cold temperature as described earlier. They showed that the Wuxi populations (31.6N) had lower activities of enzymes (superoxide dismutase, catalase, peroxidase, and alcohol dehydrogenase) than those of the southern Guangzhou (23.1N) and Xiamen (24.3N) populations, and also had lower body water and higher total sugar and glycerol contents, which are all known as the parameter for increasing cold tolerance in insects. Especially, the cold hardiness of pupal stage was the most high, as some individuals survived when treated at -10℃ for 24 h. Accordingly, applying the parameter values of -0.0035 and -0.0006 week^{-1} should be valuable to evaluate distribution suitability of *B. dorsalis* in Korea.

2-4-3. Application to Korean areas

The validation technology of the error matrix has been applied to evaluate the performance of model output in CLIMEX modeling, which uses the combination of true positive, false negative, false positive and true negative (Stehman, 1977). In this study, we adjusted model parameters to include the northern limit using CS values, and the overall performance of model outputs was evaluated in terms of generation times and weekly growth rate. Since our strategy for the model parameter fitting was to include the northern limit of *B. dorsalis*, its application to Korean regions will provide useful information for the distribution suitability in risky area such as Jeju.

Wuhan-based model (Scenario 1) showed that most areas in Korea were climatically unsuitable for *B. dorsalis* in 2010s (RCP 8.5) except limited areas in

Jeju where this fly was marginally suitable. But *B. dorsalis* was optimally suitable to establish its population currently even though in Daegu according to the Wuxi-based model, when the cold tolerance was assumed. The Wuxi-based model is adventurous yet. We firstly provided CLIMEX parameters that can include relatively warm Wuxi region in the present study. Thus, these parameters should be further evaluated in other climatically similar regions in the future. In the quarantine policy, however, conservative approach is required to prevent invasive pests. Such approach may be accepted currently, since high cold tolerance of *B. dorsalis* has been realized in the laboratory and field experiments (Qi et al., 2008; Han et al., 2011; Wang et al., 2014). Further, the actual settlement capacity will be higher due to the heterogeneity of pupation sites (Aloiykhin et al., 2001), even if we accept the Wuhan-based model.

Wang et al. (2014) proposed a life cycle of *B. dorsalis* in temperate zone: pupal stage enters overwintering and they may be emerged to adults from June of the next year, so that adult populations can not be found during a long time of overwintering. This life cycle model will be applied if this fly is invaded and settled in Jeju area. Then the seasonal abundance and persistence will be eventually determined by the availability of host plants as suggested by Tan and Serit (1994) and Peng et al. (2011). In the next Chapter, consequently, we will examine the establishment ability of *B. dorsalis* with considering the temporal distribution of host plants in a selected area in Jeju, Korea.

Our CLIMEX model in the current form should be useful to concentrate or distribute the monitoring efforts of *B. dorsalis* on the risk area in Korea. The invasion route of this species is known classically as the import of fruit containing larvae, either as part of cargo, or through the smuggling of fruit in airline passenger baggage (CABI, 2018). Recently, wind-borne long distance immigration of *B. dorsalis* using air currents from origin countries is highly accepted in Okinawa Islands, Japan (Otuka, 2016; Otuka et al., 2018). Such invasion by air currents can become an another serious risk to Jeju area, Korea. When *B. dorsalis* is introduced, the settlement probability will be primary depended on the cold temperature in winter (namely cold stress, CS values). Therefore, yearly risk mapping is required to facilitate monitoring strategy for early detection against a possible founder population. Our CLIMEX model should be useful for the purpose of such risk mapping until further improved models are available.

Table 5. CLIMEX model parameters for *B. dorsalis* or its species group in previously published literatures, and parameter values adjusted in this study

Parameter name	Code	Hou and Zhang (2005)	Kriticos et al. (2007), Stephens et al. (2007)	Wang et al. (2010)	EPPO (2010)[a]	Sridhar et al. (2014)	De Villiers et al. (2016)[a]	Values adjusted in this study
Limiting low temperature (℃)	DV0	11.8	13	11.8	9	11.8	9	9.5
Lower optimal temperature (℃)	DV1	22	25	22	30	22	25	25
Upper optimal temperature (℃)	DV2	29	33	28	35	28	33	33
Limiting high temperature (℃)	DV3	35	36	35	39	35	42	42
Limiting low soil moisture	SM0	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Lower optimal soil moisture	SM1	0.5	0.25	0.8	0.25	0.5	0.25	0.25
Upper optimal soil moisture	SM2	1.75	1	1.5	1	1	1.8	1
Limiting high soil moisture	SM3	2	1.5	2	1.6	2	2	1.5
Cold stress temperature threshold (℃)	TTCS	-	2.5		6	-	2.5	0
Cold stress temperature rate	THCS	-	-0.012		-0.001	-	-0.012	0
Minimum degree-day cold stress threshold (DD)	DTCS	22	8	11.8	8	10	12	8
Degree-day cold stress rate (week^{-1})	DHCS	-0.0003	-0.002	-0.0004	-0.002	-0.00025	-0.002	-0.0035, -0.0006
Cold stress average temperature threshold (℃)	TTCSA	-	-	-	-	-	-	0
Cold stress accumulate rate	THCSA	-	-	-	-	-	-	0
Heat stress temperature threshold (℃)	TTHS	35	36	-	39	35	42	42
Heat stress temperature rate	THHS	0.0002	0.005	-	0.001	0.0002	0.005	0.005
Heat stress degree-day threshold (DD)	DTHS	-	-	-	-	-	-	0
Heat stress accumulate rate	DHHS	-	-	-	-	-	-	0
Dry stress threshold	SMDS	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Dry stress rate	HDS	-0.006	-0.024	-0.001	-0.03	-0.0001	-0.03	-0.03
Wet stress threshold	SMWS	2	1.5	2	1.6	2	-	1.6
Wet stress rate	HWS	0.002	0.007	0.002	0.001	0.009	-	0.001
Developmental temperature threshold for cold stress (℃)	DVCS	11.8	10	11.8	15	11.8	9	10
Developmental temperature threshold for heat stress (℃)	DVHS	35	36	35	39	35	42	42
Degree-days per generation (DD)	PDD	358	470	358	450	358	380	717

[a] Parameters for *B. invadens.*

Table 6. Selected sites to evaluate the cold stress (CS) values and generation times in outputs of CLIMEX simulation, in which *B. dorsalis* populations are persistent or non-persistent

Country	Location	Coordinates		Eleva-tion (m)	Occurrence (Phenology)	Generation per year	Reference	Population status	Tested index
		Latitude	Longitude						
China	Baoshan	N 25°10′00.00″ (A)[1]	E 99°13′00.00″	1,825	Seasonal (Apr. to Nov.)		Chen and Ye, 2007	Persistent	CS
		N 25°07′00.00″ (A)	E 99°09′00.00″	1,655	Seasonal (Apr. to Oct.)		Chen and Ye, 2007	Persistent	CS
	Guangnan	N 23°54′00.00″ (A’)	E 105°20′00.00″	1,160	Seasonal (no information)	3-4	Ye et al., 2001	Non-persistent	Gen
	Hekou	N 22°31′45.49″ (B)	E 103°56′04.79″	-	Seasonal (Apr. to Dec.)	5	He et al., 2002	Persistent	Gen
	Jinghong	N 22°00′00.00″ (A)	E 100°46′00.00″	550	Year-round	4	Ye et al., 2001	Persistent	Gen
	Kunming	N 24°56′00.00″ (A)	E 102°29′00.00″	1,850	Seasonal (May to Sep.)	3	Zhang et al., 1995	Non-persistent	CS, Gen
		N 24°40′00.00″ (A)	E 102°20′00.00″	1,804	Seasonal (May to Dec.)	2~	Ye and Liu, 2005	Non-Persistent	CS, Gen
		N 24°41′00.00″ (A)	E 102°23′00.00″	2,000	Seasonal (May to Dec.)	2~	Ye and Liu, 2005	Non-Persistent	CS, Gen
		N 24°42′00.00″ (A)	E 102°22′00.00″	1,980	Seasonal (May to Dec.)	2~	Ye and Liu, 2005	Non-Persistent	CS, Gen
	Ruili	N 24°00′46.47″ (B)	E 97°51′03.40″	-	Year-round	6	Jiang et al., 2001	Persistent	CS, Gen
		N 24°01′00.00″ (C)	E 97°51′00.00″	907	Year-round	5	Shi et al., 2005	Persistent	CS, Gen
		N 23°55′00.00″ (A)	E 97°44′00.00″	750	Year-round		Chen et al., 2006	Persistent	CS
		N 23°59′00.00″ (A)	E 97°49′60.00″	757	Year-round		Chen et al., 2006	Persistent	CS
		N 24°01′00.00″ (A)	E 97°53′00.00″	760	Year-round		Chen et al., 2006	Persistent	CS
	Qujing	N 25°21′00.00″ (A)	E 104°23′00.00″	2,000	Seasonal (no information)	1~2	Ye et al., 2001	Non-persistent	Gen
	Fujian	N 26°00′00.00″ (C)	E 119°18′00.00″	-	No information	5-6	Wang et al., 2014	Persistent	Gen
	Guangzhou	N 23°20′24.18″ (B)	E 113°32′13.50″	-	Year-round	7	Wu et al., 2007	Persistent	Gen
	Wuxi	N 31°29′00.96″ (B)	E 120°13′55.20″	-	Seasonal (Jun. to Dec.)		Qi et al., 2008	Persistent in 2005-2006	CS
	Wuhan	N 30°27′34.69″ (B)	E 114°20′55.71″	-	Seasonal (Jun. to Dec.)	4	Han et al., 2011	Persistent in 2008-2009	CS, Gen
India	Budgam	N 33°56′05.48″ (B)	E 74°38′16.04″	-	Seasonal (Jul. to Oct.)		Ganie et al., 2013b	Non-persistent	CS
		N 33°56′43.65″ (B)	E 74°47′39.85″	-	Seasonal (Jul. to Oct.)		Ganie et al., 2013b	Non-persistent	CS
		N 34°02′05.98″ (B)	E 74°44′26.35″	-	Seasonal (Jul. to Oct.)		Ganie et al., 2013b	Non-persistent	CS
	Marh	N 32°54′01.19″ (B)	E 74°49′20.57″	-	No information		Tara and Gupta,	Persistent	CS

						2016		
	Samba	N 32°32′50.99″ (B)	E 75°05′29.89″	-	No information	Tara and Gupta, 2016	Persistent	CS
	SKUAST Jammu	N 32°39′18.00″ (B)	E 74°48′25.20″	-	Year-round	Rai et al., 2008	Persistent	CS
	Srinagar	N 34°03′52.54″ (B)	E 74°47′32.17″		Seasonal (Jul. to Oct.)	Ganie et al., 2013b	Non-persistent	CS
		N 34°06′38.66″ (B)	E 74°51′57.67″		Seasonal (Jul. to Oct.)	Ganie et al., 2013b	Non-persistent	CS
		N 34°09′06.14″ (B)	E 74°52′26.75″		Seasonal (Jul. to Oct.)	Ganie et al., 2013b	Non-persistent	CS
	Udahampur	N 32°54′57.07″ (B)	E 75°08′01.62″	-	No information	Tara and Gupta, 2016	Persistent	CS
	Udheywala	N 32°44′39.70″ (B)	E 74°48′27.19″	-	No information	Tara and Gupta, 2016	Persistent	CS
Japan	Amami	N 28°22′43.85″ (B)	E 129°29′29.47″	-	Year-round	Ushio et al., 1982	Persistent	CS
	Kikai	N 28°19′26.10″ (B)	E 129°58′09.18″	-	Year-round	Ushio et al., 1982	Persistent	CS
Pakistan	Dargai	N 34°10′48.01″ (B)	E 71°53′08.78″	-	Seasonal (Apr. to Dec.)	Syed et al., 1970	Persistent	CS
	Haripur	N 33°59′38.06″ (B)	E 72°54′28.53″	-	Seasonal (Apr. to Dec.)	Syed et al., 1970	Persistent	CS
	Kohat	N 33°35′21.31″ (B)	E 71°26′26.00″	-	Seasonal (Mar. to Nov.)	Syed et al., 1970	Persistent	CS

* precision of coordinates represented by; A: the monitoring points (mentioned in reference) / B: the location point (plain, resident area) in google map / C: the sampling points for genetic analysis (mentioned in reference)

Table 7. Comparison of cold stress (CS) values in various CLIMEX parameters for *B. dorsalis*.

Module	Country	Location	No. of points	Hou and Zhang, 2005	Kriticos et al., 2007	EPPO, 2010	Wang et al., 2010	Sridhar et al., 2014	De Villiers et al., 2016	Scenario 1	Scenario 2	Desired value
Compare Years	China	Wuxi (in 2006)	1	70	190	270	52	23	238	202	35	CS≈35
		Wuhan (in 2009)	1	60	34	220	22	6	38	21	4	CS≈21
Compare Locations	China	Baoshan	2	50-64	0-3	369-418	16-25	7-11	1-5	0-5	0-1	CS < 100
		Kunming	4	78-96	9-22	402-611	34-46	14-20	16-30	15~39	3-7	CS > 100[1]
		Ruili	5	0	0	0	0	0	0	0	0	CS < 100
		Wuxi	1	143	492	540	102	48	595	410	70	CS > 100
		Wuhan	1	110	204	405	77	36	297	239	41	CS > 100
	India	Badgam	3	115-159	838-999	555-679	67-89	34-45	892-999	169-308	29-53	CS > 100
		Marh	1	6	0	15	0	0	0	0	0	CS < 100
		Samba	1	3	0	9	0	0	0	0	0	CS < 100
		SKUAST Jammu	1	3	0	7	0	0	0	0	0	CS < 100
		Srinagar	3	114-121	786-907	474-549	60-65	30-33	837-965	175-196	30-34	CS > 100
		Udahampur	1	6	0	19	0	0	0	0	0	CS < 100
		Udheywala	1	3	0	8	0	0	0	0	0	CS < 100
	Japan	Amami	1	2	0	0	0	0	0	0	0	CS < 100
		Kikai	1	0	0	0	0	0	0	0	0	CS < 100
	Pakistan	Dargai	1	15	83	102	1	0	83	0	0	CS < 100
		Haripur	1	11	3	63	0	0	3	0	0	CS < 100
		Kohat	1	6	0	13	0	0	0	0	0	CS < 100

In scenario 1 and 2, DHCS values were adjusted to reach CS = 21 in Wuhan in 2009 and CS = 35 in Wuxi in 2006, respectively; resulting in DHCS = -0.0035 in Wuhan and DHCS = -0.0006 in Wuxi.

[1] In Kunming, CS > 100 that indicates non-persistent of *B. dorsalis* was assumed according to previous reports (Ye, 2001; Ye and Liu, 2005).

Table 8. Comparison of χ^2-test statistic1 for the generation times per year of *B. dorsalis* among different regions

Location	No. of points	Observed no. of generations	Predicted no. of generations by various CLIMEX models				
			Hou and Zhang (2005), Wang et al. (2010), Sridhar et al. (2014)	Kriticos et al. (2007)	EPPO (2010)	De Villiers et al. (2016)	Present study
Fujian	1	5.5	8.7	5.8	9.0	10.6	5.4
Guangzhou	1	7	10.3	7.0	7.0	12.4	6.3
Wuhan	1	4	7.2	4.9	7.3	8.7	4.4
Guangnan	1	3.5	7.2	4.7	7.8	9.2	4.6
Hekou	1	5	11.7	8.0	11.6	13.7	7.0
Jinghong	1	5	11.6	7.9	11.5	13.6	7.0
Kunming	3	2	4.4	2.7	5.3	6.3	3.1
Qujing	1	1.5	4.3	2.7	5.2	6.1	3.0
Ruili	2	5	9.6	6.5	9.9	11.7	6.0
$\Sigma\ \chi^2$			40.3172	5.7869	46.6269	86.3060	4.4775
$P > \Sigma\ \chi^2$			0.0171	0.8792	0.0114	0.0001	0.9418

[1] The statistic of χ^2-values were approximated as [(Observed - Predicted generations)^2/Mean] (Sokal and Rohlf, 1981).

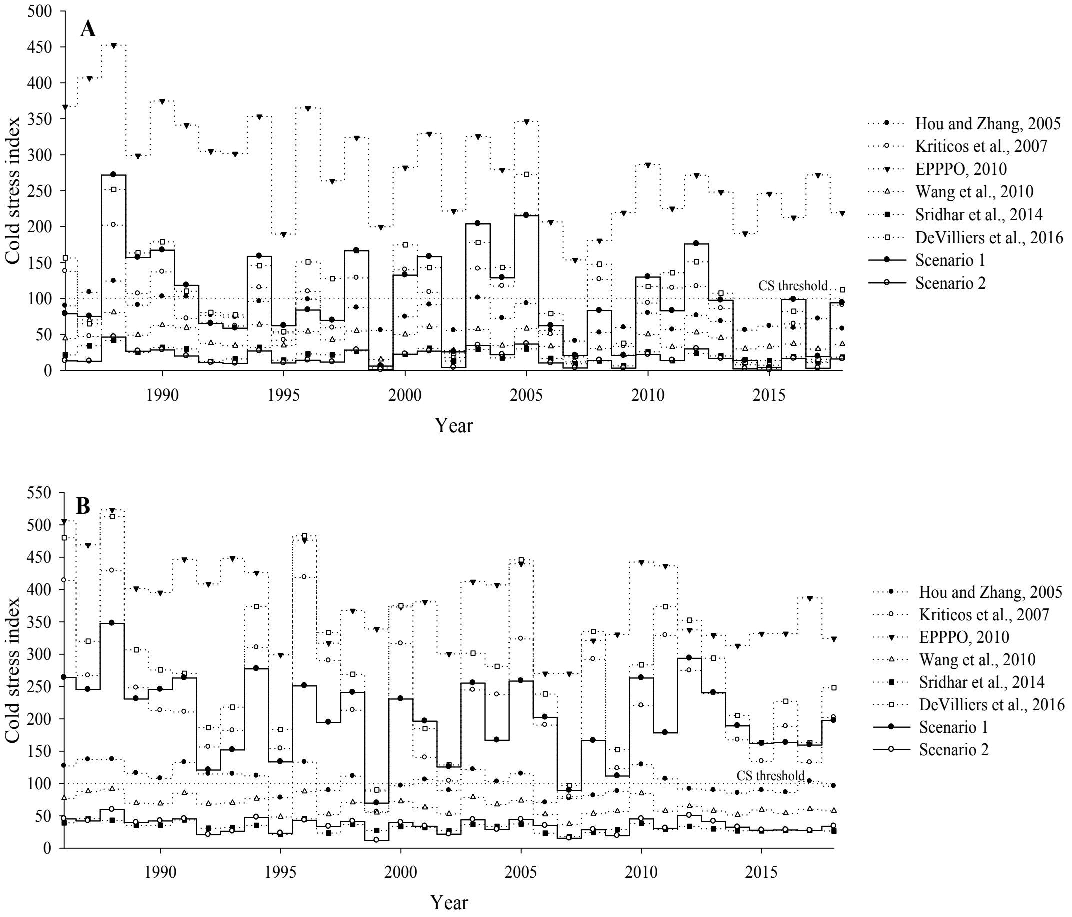


Fig. 4. Yearly variations of cold stress (CS) values calculated by the Compare Years module of CLIMEX model using various parameters in Wuhan (A) and Wuxi (B) in China. The CS-values by Scenario 1 (DHCS = -0.0035 week-1) and 2 (DHCS = -0.0006 week-1) in the present study were compared to evaluate the robustness of adjusted CS-parameters.

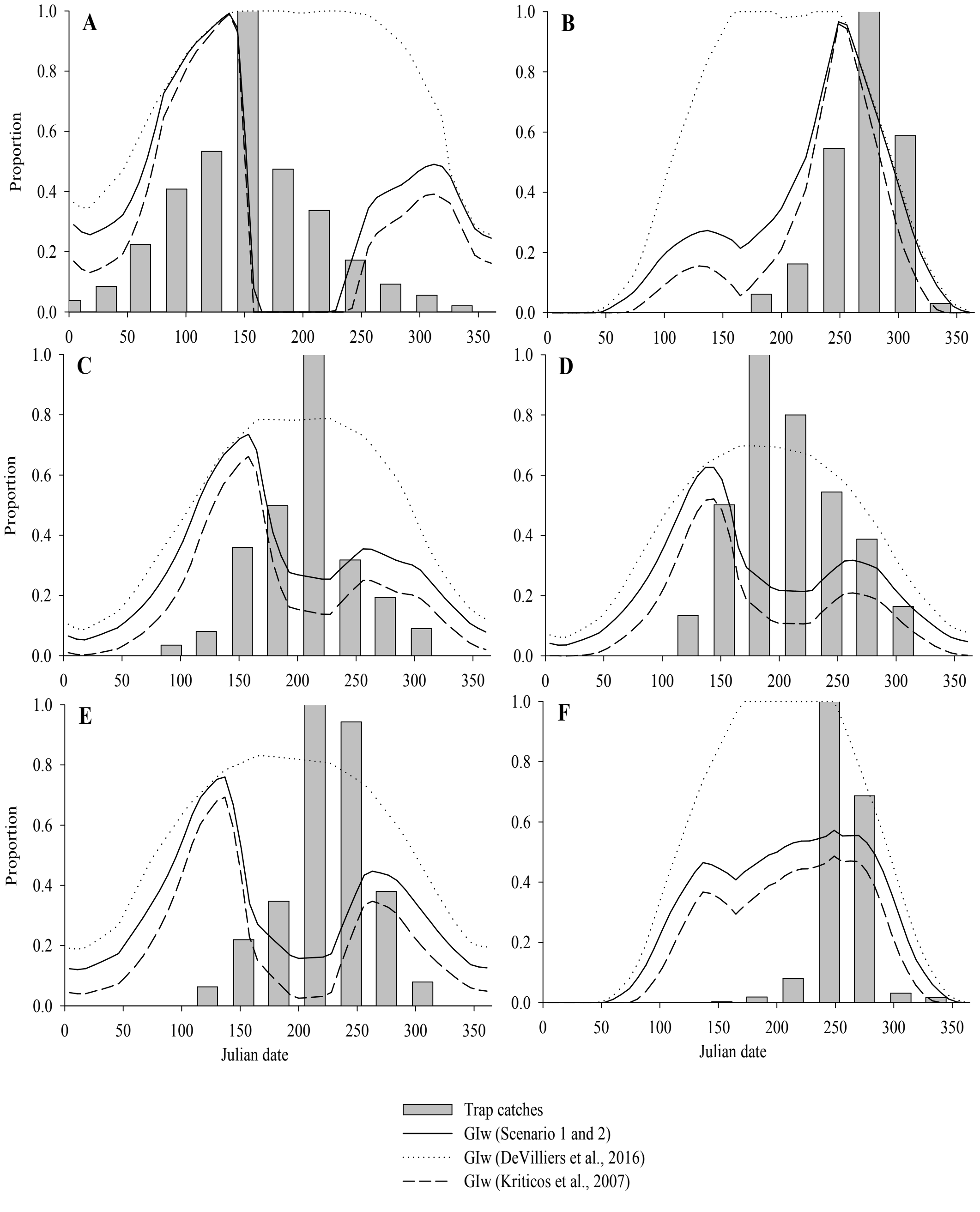


Fig. 5. Comparison of weekly growth index (GI_w) between actual phenology of *B. dorsalis* adults and CLIMEX results. The phenology data were obtained from published literature (Ye and Liu, 2005; Zhang et al., 2005; Chen et al., 2006; Chen and Ye, 2007; Meng et al., 2008; Han et al., 2011): Ruili (A), Wuhan (B), Baoshan (C), Kunming (D), Jiansui (E) and Suzhou (F).

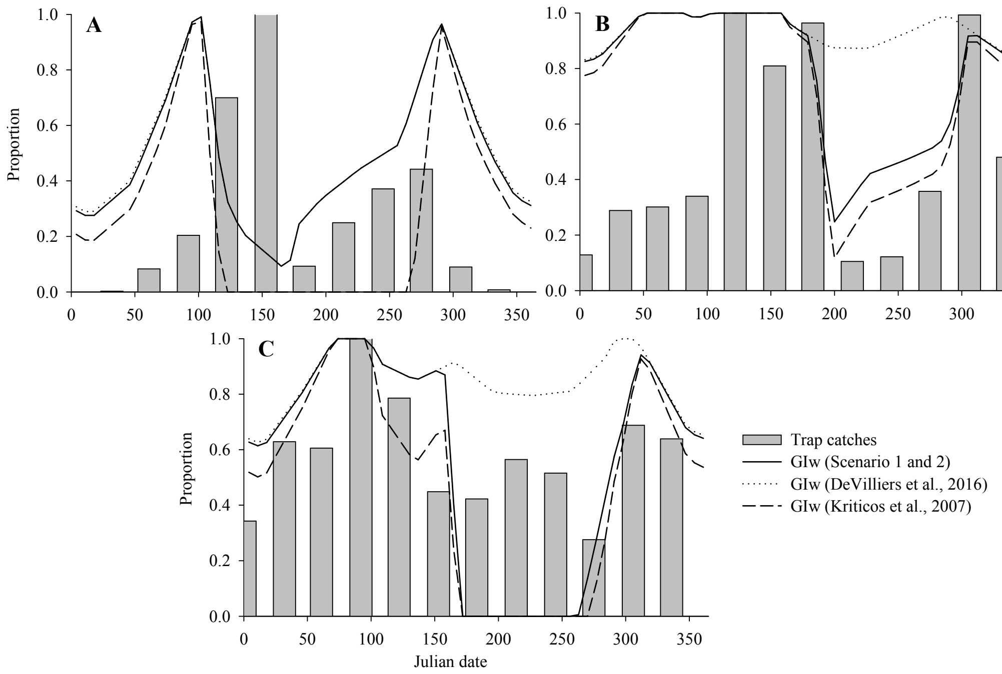


Fig. 6. Comparison of weekly growth index (GI_w) between actual phenology of *B. dorsalis* adults and CLIMEX results. The phenology data were obtained from published literature (Mann, 1996; Ravikumar and Viraktamath, 2006; Das et al., 2017): Ludhiana (A), Dharwad (B) and Nadia (Jaguli and Mohanpur) (C) in India.

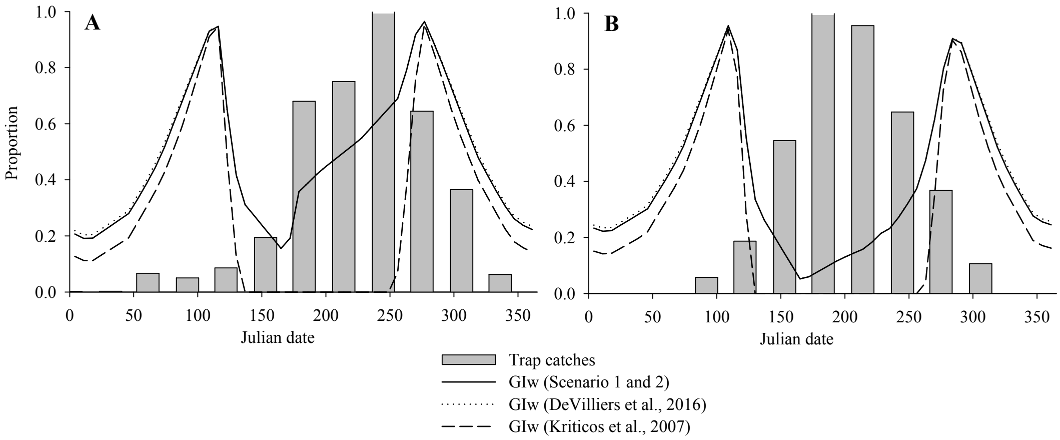


Fig. 7. Comparison of weekly growth index (GI_w) between actual phenology of *B. dorsalis* adults and CLIMEX results. The phenology data were obtained from published literature (Khattak et al., 1990; Chaudhry et al., 2000): Rawalpindi (A) and Peshawar (B) in Pakistan.

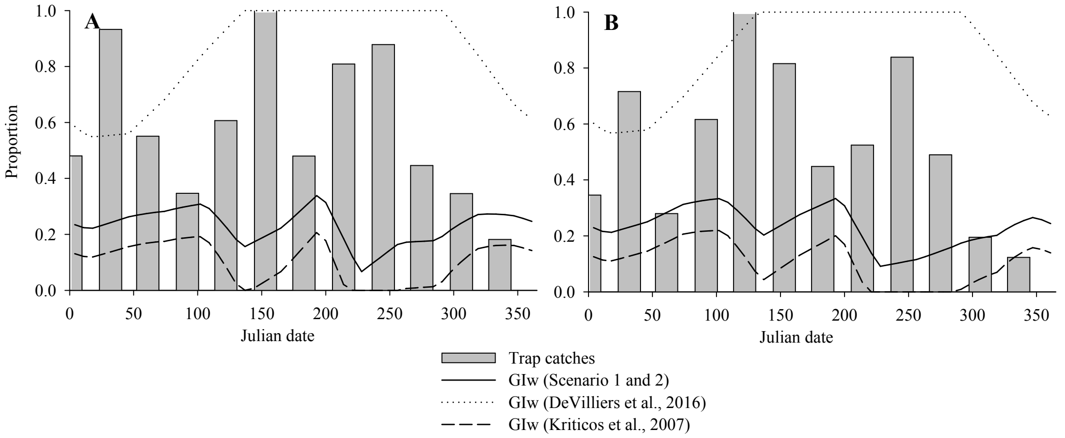


Fig. 8. Comparison of weekly growth index (GI_w) between actual phenology of *B. dorsalis* adults and CLIMEX results. The phenology data were obtained from published literature (Iwahashi, 1984): Miyako (A) and Yaeyama (B) in Japan.

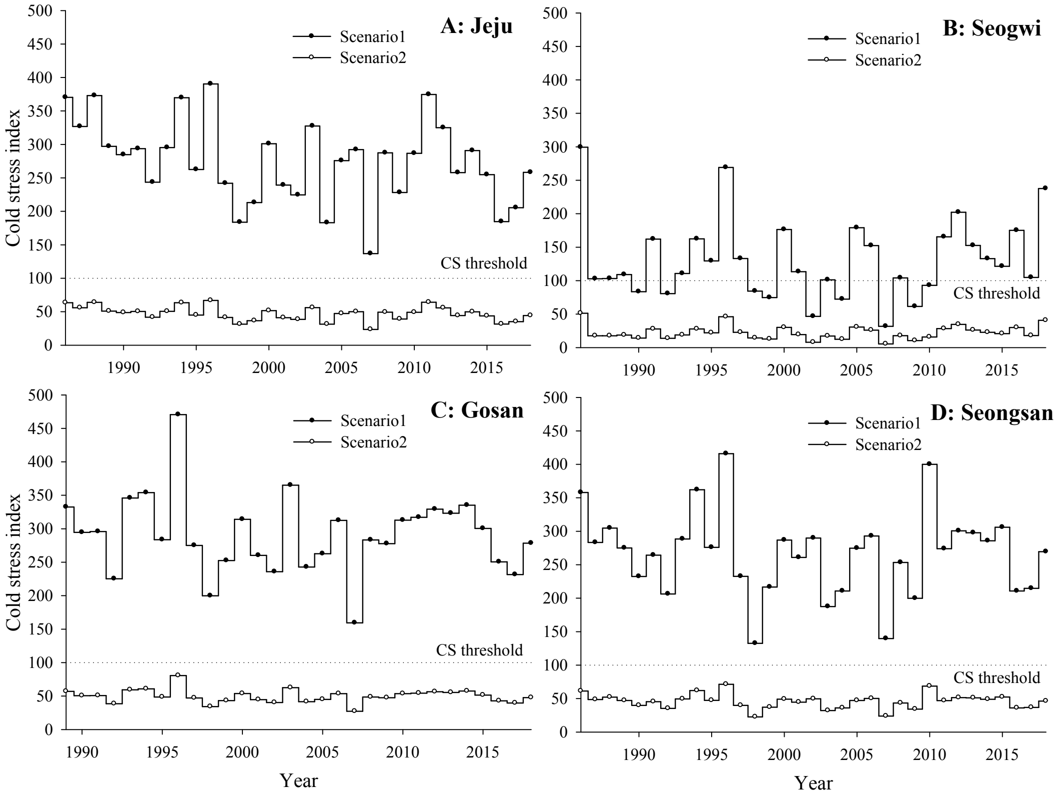
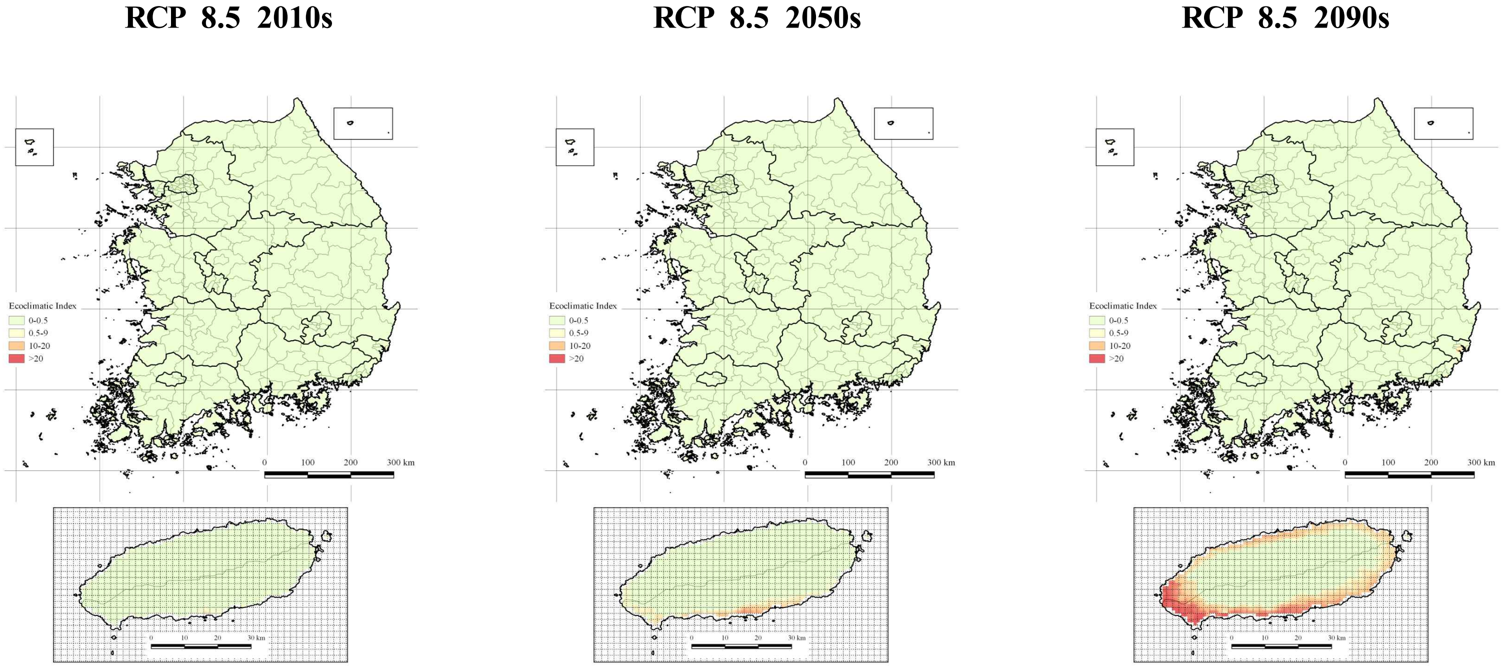


Fig. 9. Yearly variations of cold stress (CS) values calculated by the Compare Years module of CLIMEX model in Jeju, Korea. The CS-values by Scenario (DHCS = -0.0035 week-1) and 2 (DHCS = -0.0006 week-1) in the present study were compared.


RCP 8.5 2010s

RCP 8.5 2050s

RCP 8.5 2090s

Fig. 10. The projected climate suitability for *B. dorsalis* by RCP 8.5 weather scenario in Korea with enlarged in Jeju area, based on parameters of Scenario 1. In Scenario 1, the DHCS of CS parameter was adjusted to satisfy CS value ≈ 21 in Wuhan, China in 2009 (i.e. DHCS = -0.0035 week-1). The criteria of suitability suggested by Sutherst et al. (2004) was applied: unsuitable, EI = 0 − 0.49; marginal, EI = 0.50 − 9.99; suitable, EI = 10 − 19.99; optimal, EI >20; and perfect, EI = 100.

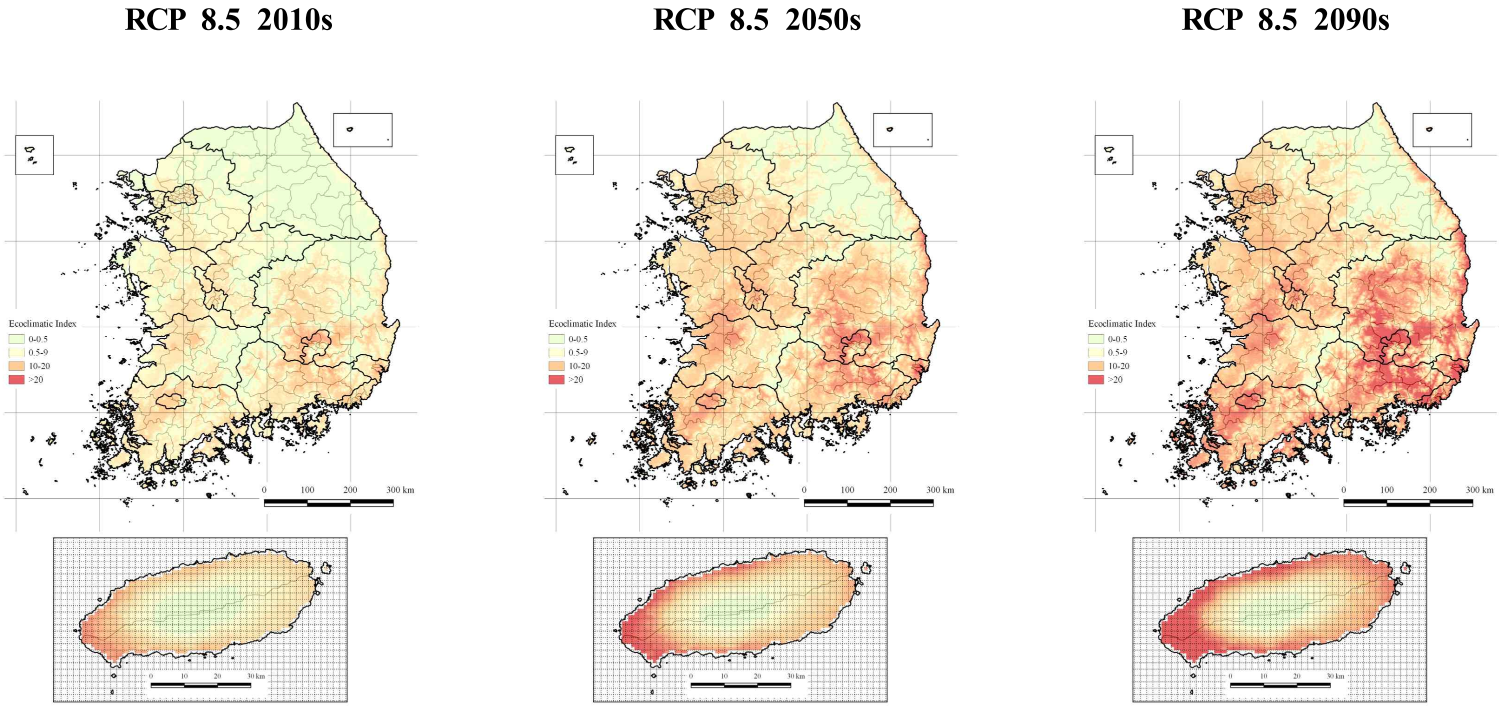


Fig. 11. The projected climate suitability for *B. dorsalis* by RCP 8.5 weather scenario in Korea with enlarged in Jeju area, based on parameters of Scenario 2. In Scenario 2, the DHCS of CS parameter was adjusted to satisfy CS value ≈ 35 in Wuxi, China in 2006 (i.e. DHCS = -0.0006 week-1). The criteria of suitability suggested by Sutherst et al. (2004) was applied: unsuitable, EI = 0 - 0.49; marginal, EI = 0.50 − 9.99; suitable, EI = 10 − 19.99; optimal, EI >20; and perfect, EI = 100.

3. A tentative evaluation for population establishment of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) based on the population modeling: considering the temporal distribution of host plants in a selected area in Jeju, Korea

3-1. Introduction

The potential distribution of *B. dorsalis* into new regions has been evaluated mainly based on climatic matching using technologies of GARP, MAXENT, CLIMEX, etc. (Kriticos et al., 2007; De Meyer et al., 2010; Sridhar et al., 2014) as described earlier Chapters. However, the settlement of invasive species may be highly affected by various external factors such as host plants and natural enemies, except for weather variables. Among them, the availability of host plants can be a key factor for settlement, because they provide a basic resource for survival. The temporal distribution of the available hosts can largely affect the survival and population dynamics in the nutritional ecology of insects (Scriber and Slansky, 1981; Kim and Lee, 2010).

This study was conducted to evaluate the effect of host plants distributed temporally on the population development of *B. dorsalis*. In this way, we will be able to predict whether *B. dorsalis* can settle down permanently in a specific region and to improve our knowledge for evaluating the potential distribution of this fruit fly. We investigated the abundance of the host plants of *B. dorsalis* in a selected site in Jeju and parameterized them in terms of the temporal availability. Also, a simple population model of *B. dorsalis* was newly constructed by using previous temperature-dependent bionomic data, to evaluate the host plant effect on the population development of *B. dorsalis*.

3-2. Construction of population model

3-2-1. Model overview

A population model of *B. dorsalis* was constructed with five developmental stages (Fig. 12): overwintered pupa, egg, larva, pupa, and adult. The model starts at overwintered pupal stage consisted of a single cohort in identical physiological age, because pupae are possible overwintering stage in Jeju area as described in Wuhan, Hubei Province, central China where temperate climate prevails, and the survival of *B. dorsalis* pupae was observed during the winter in an experiment (Peng et al., 2011). The developmental rates of pupae were accumulated daily above the low-threshold temperature, 8.6 °C. Other stages were divided into daily separate cohorts of individuals that entered the stage on the same day, and they were treated as different age groups in the stage, as suggested by Curry and Feldman (1987) and Kim and Lee (2010).

At any given time, each daily cohort is characterized by two state variables as the methods of Shaffer and Gold (1985) and Kim and Lee (2010): $a_{ij}(t)$, the physiological age of cohort j within stage i at time t and $N_{ij}(t, a)$, the number of individuals in the cohort which are of physiological age a at time t. The output of the model is $N_i(t)$, the total number in stage i at time t, which is obtained simply by summing of all the cohorts. Thus, the computations of the model are updated using the results in a daily time-step (24 h).

Daily mean air temperature and soil temperature at 5-cm depth were only considered in the model as meteorological factors. Other meteorological variables such as soil moisture and relative humidity can affect the survival of pupae in the soil. However, it was not included, because extreme dry does not occur in normal years in Jeju. The simulation of the model was conducted using the POPMODEL 1.5 (Choi and Kim, 2016), which is a non-commercial modeling tool designed specifically to project insect populations with the patent technology of “Integrated system and method for optimizing a calculation of userdefined formula (Patent IPC Registration No.: 1015784210000)”.

3-2-2. Parameterization for the temporal distribution of host plants in a selected area

A total of 471 species of plants is known as the host plants of *B. dorsalis* (see SD Table 3). These hosts are distributed temporally in terms of the availability (food resources) by *B. dorsalis*. This fruit fly lays eggs mostly in mature fruits of host plants (Steiner et al., 1957; Liquido et al., 1995). Thus, the phenology of fruit development of host plants determines the timing of food resource availability. Consequently, we modeled the curve of host availability using an SDS (symmetric double sigmoid) equation (Jandel Scientific, 2002) that has four parameters with biological interpretation.

$$K=\frac{a[1+\exp(-c/2d)][1+\exp(c/2d)]\exp(-((x-c)/d))}{\left[1+\exp(-((x-b+\frac{c}{2})/d))\right]\left[1+\exp(-((x-b-\frac{c}{2})/d)\right]} \qquad \text{Eq. 17}$$

where *K* is the carrying capacity for *B. dorsalis* at Julian date *x*, *a* is the amount of food resource, *b* is mid-point between the fruit ripening start time and the end of harvest time in Julian date, *c* is period in mature fruit, and *d* is the steepness of the curve. The parameter *d* indicates the speed how fast fruits approach maximum maturity.

The host plants of *B. dorsalis* were surveyed in a selected area of 1.6 × 1.6 km in Jeju, Korea (N 33°30′13.38″, E 126°33′12.05″ at the focal point), compared with host lists of USDA (US Dept. of Agriculture) (Liquido et al., 2015). The square grid of 1.6 × 1.6 km is regarded as unit area for setting monitoring traps in delimiting survey when one or more *B. dorsalis* is detected in an area in the standard grid system of 14.4 × 14.4 km in Korea (APQA, 2016), which originated from the monitoring system of United States (Jeffrey, 1989).

The fruiting phenology of host plants was obtained from open Webbased Data Bases in the various organization (see SD Table 5): The fruit ripening start time, the end of harvest time in Julian date, etc. The parameter *b* was determined by calculating the mid-point as "(the end of harvest time - the fruit ripening start time in Julian date)/2" for each host plant. The period to obtain mature fruit (parameter *c*) was approximated by "(the end of harvest time−the fruit ripening start time in Julian date)×3/4". Fallen fruits or over-ripened fruits were not considered since the oviposition of *B. dorsalis* can occur mostly on mature fruits hanging on fruit trees (Liquido et al., 1995).

The parameter *a* that indicates the total amount of food resource availability can be directly converted to the carrying capacity for supporting larval populations of *B. dorsalis*. First, we estimated the amount of fruits (g) that is required for complete development of single fruit fly larva by using field survey datasets reported previously by Harris and Lee (1987), Verghese et al. (2002), Mwatawala et al. (2004), Ekesi et al. (2006), and Rwomushana et al. (2008). An average number of *B. dorsalis* emerged from 1 kg of fruits were 132.5 flies, resulting in 7.54 g per fruit fly (see SD Table 6). Finally, parameter *a* was calculated by "(Yield per tree×No. of trees×Weight value)/7.54" for each host plant. Where the weight value is: 1.0 for USDA category P, 0.1 for U; also, 0.1 was assigned for non-preferred host plants that were not found in USDA category (Liquido et al., 2015; see SD Table 5). Consequently, the sum of carrying capacity of each host plant temporally represents the distribution curve of food availability in the defined area.

The parameter *d* may be host plant-specific. But we applied 1.5 for all cases indicating transition time from an immature state to the maximum maturity in 15–30 days, because of no available data.

3-2-3. The computational method of process modules

Stage transition of each stage

This module calculates the proportion of individuals that shift from one stage to the next stage using two major temperature-dependent models: the development rate model (Table 2) and distribution model of development time (Table 3). In the computation, the development rate function determined the mean (or median) rate of development per day at a given temperature, and the distribution function determined the cumulative proportion of cohort development at a given accumulated development rate (Wagner et al., 1985; Kim and Lee, 2010).

The models for eggs, larvae, and pupae estimated above were integrated to simulate transition to each stage. The proportion of the cohort shifted during the physiological age interval of a stage between i and $i+\Delta i$ was calculated by subtracting the cumulative proportion of the cohort shifted at i from the cumulative proportion of the cohort shifted at $i+\Delta i$ (Kim et al., 2001).

Adult reproduction

The oviposition model of insect species can consist of three temperature-dependent models: temperature-dependent total fecundity $f(T)$, age-specific cumulative oviposition rate $p(px_i)$, and agespecific survival rate $s(px_i)$ (Table 4) (Curry and Feldman, 1987; Kim and Lee, 2003). Where the adults' physiological ages px_i are obtained by accumulating the adult aging rates to time i using Eq. 4. Finally, the number of eggs laid by a female during the physiological age interval between px_i and px_{i+1} was calculated using the following equation (Kim and Lee, 2003):

$$A_{rp}(T;px) = f(T) \bullet [p(px_{i+1}) - p(px_i)] \bullet \frac{s(px_i) + s(px_{i+1})}{2} \qquad \text{Eq. 18}$$

Availability of host plants

The combined carrying capacity curves produce total available food resources for *B. dorsalis* at a given time, which is expressed by the carrying capacity K. The K is changed with times because *B. dorsalis* infests continually fruits and the fruits are not available by later emerging flies. The changing K was updated daily and reflected the population density of *B. dorsalis*. We assumed that the standing K affects directly the oviposition of *B. dorsalis* in a density dependent manner. A weight value W_i was calculated by following equation:

$$W_i = K_i / KN_i \qquad \text{Eq. 19}$$

where, K_i = available K at time i, KN_i = newly laid eggs converted to K for supporting the equivalent larvae, and $W_i = 1$ when $KN_i < K_i$. thus, the number of eggs survived (larvae) was calculated as $f(T) \cdot W_i$.

3-2-4. Other factors and assumption.

The soil moisture and texture may affect the survival of Tephritid fruit fly pupae (Eskafi and Fernandez, 1990; Hennessey, 1994; Hou et al., 2006). But datasets to parameterize the effects of various soil conditions are not yet available. So, we included just the natural mortality of the pupal stage in the soil. The survival rate of pupae was reported to be 96.2% in normal soil moisture in the laboratory (Hou et al., 2006). And Serit and Tan (1990) found that 77.8% of the mortality incurred during the life cycle of *B. dorsalis* in the field soil. Vargas et al. (2000) reported a 66% survival in semi-field condition. Therefore, the average pupal mortality 38.5% (survival 61.5%) was applied in the model. This survival value was a little lower than the 73.5% averaged across all temperatures in the laboratory (SD Table 2). The overwintered pupal mortality was not included, and a constant number of this stage was just provided as the initial population in the model. The egg mortality is not easy to be investigated in the field condition. Several egg hatch rate datasets have been reported to date under laboratory conditions for *B. dorsalis* complex. So, we used the average hatch rate (survival rate) across all temperatures (87.4%, SD Table 2). The average survival rate of larvae was calculated to be 77.5% under laboratory condition (SD Table 2). But the survival rate was not incorporated into the model because density-dependent mortality was already applied in the model, as described above.

The sex ratios of *B. dorsalis*, expressed by the number of females per male, were various in the laboratory and the field condition showing an average 0.99 between 17 and 33 °C in China (Luo et al., 2009) and 1.38 to 1.78 in Côte d'Ivoire (Melinand et al., 2016), respectively. We applied average sex ratio of 1.58 obtained from the later example.

We assumed that the emigration or immigration of *B. dorsalis* adults does not occur in the defined area. Also, *B. dorsalis* adults immediately find host fruits without time lags. And no population reduction by natural enemies was premised, because the effects of natural enemies against *B. dorsalis* cannot be specified in a newly established area. The model starts from the overwintered pupal stage with an arbitrarily defined number of individuals. Model computations used a daily timestep, with the assumption that all mortality occurred at the transition to the next stage (Kim and Lee, 2010).

3-2-5. Model simulation

Daily average air temperatures and soil temperatures were obtained from the Jeju weather station. The soil temperature was measured at a depth of 5 cm, and it was only available in 2015. Thus, weather data of 2015 in Jeju were used for the model simulation with the initial population of 100 pupae.

We ran the model by removing one by one the group of host plants (in Family) to evaluate the effects of the temporal distribution of host plants.

3-3. Results

3-3-1. Temporal distribution of host plants and its parameterization

The host lists found in the survey area are provided in Table 9, with the estimated parameters for the model of host availability as well as the abundance in the number of trees. The temporal distribution of food resource for each group of host plants (grouped in Family) is presented in Fig. 13. The carrying capacity (see x-axis) was expressed as the equivalent unit of fruit weight (g) to the number of larvae of *B. dorsalis*. Most of food resources was formed by Rutaceae species plants (namely *Citrus* sp.), especially after 300 Julian date in the late season. The period between 220 and 300 Julian date just before Rutaceae, Moraceae (*Ficus* spp., fig fruits) and Ebenaceae (mainly persimmon fruits) were important food resources. During the period between 160 and 220 Julian date in which host availability was relatively low, Rosaceae (*Prunus* spp.) plants were mainly served as food resources for *B. dorsalis* partially with Moraceae plants. There was an absolute shortage of food between 125 and 145 Julian date, and the fruits of Opuntiaceae (a cactus sp. *Opuntia ficus indica*) became an important food resource. Minor host plants were distributed as follows: Amaryllidaceae (a crinum fruits, *Crinum asiaticum*) between 260 and 320 Julian date, Lauraceae (a silver magnolia fruits, *Machilus thunbergii*) between 190 and 240 Julian date, Punicaceae (a pomegranate fruits, *Punica granatum*) between 250 and 300 Julian date, Rhamnaceae (a jujube fruits, *Ziziphus jujuba*) between 250 and 295 Julian date, Solanaceae (mainly egg plants, *Solanum melongena*) between 190 and 290 Julian date, and Vitaceae (a grape fruits, *Vitis vinifera*) between 220 and 270 Julian date.

The plots of host plants on the lower graph in Fig. 13 are fractionated from host plants and belong to Rosaceae. This group of host plants served as the food resources for *B. dorsalis* in spring and early summer; mainly *Eriobotrya japonica* between 145 and 180 Julian date, *Prunus mume* between 145 and 210 Julian date, *Prunus persica* between 200 and 260 Julian date, and *Pyrus communis* between 190 and 290 Julian date.

3-3-2. Typical model outputs

Simulation outputs with the standard run (that is, including whole host plants) showed total 4 times of adult generations in the selected area (Fig. 14a). The 1st-generation adults that originated from overwintered pupae started to emerge at the end of March, and the emerged adult population survived until mid-August. The 2nd-, 3rd- and 4th adult generations began to occur from mid-June, late July, and late September, respectively. As the generations progressed, adult populations largely increased. The 3rd and 4th adult generation emerged partially because of probably cool weather condition in late season. The 3rd generation adults synchronized well with the availability of Moraceae and Ebenaceae (see Fig. 13 and Fig. 14a). The 4th generation adults increased abruptly as early cultivars of mature *Citrus* fruits.

The contribution of host plants for population growth of *B. dorsalis* in the selected site was different according to the group of host plants. When host plants belong to Moraceae were removed in the simulation, *B. dorsalis* population largely decreased by 93% (Figs. 14B and 15). This phenomenon was because of the reduction of the 2nd-generation larvae between 240 and 270 Julian date caused by the shortage of food resources. However, other groups of host plants have a trivial effect on the buildup of *B. dorsalis* in the selected area (Fig. 15).

About 97% of the population was decreased compared to that of the standard run when the major host plant of *Citrus* spp. was removed. Interestingly, *B. dorsalis* was able to establish its population without citrus fruits using other food sources in the selected area, although population size was largely decreased (Fig. 15).

3-3-3. The effects of individual host plants on model outputs

The response of model outputs was evaluated by the change of included host plants. This analysis was to assess the relative importance of host plants on population growth of *B. dorsalis* in the defined area. The host plants of *O. ficus indica* (cactus plant), *E. japonica* (loquat plant), *P. mume* (Japanese apricot), *P. persica* (peach plant), *Ficus carica* (fig plant) and *Diospyros kaki* (persimmon plant) were individually combined with the group of Rutaceae (*Citrus* spp.) to simulate the model, which are main host plants temporally distributed in the selected area. For comparison, a quantity corresponding to 5% of the total amount of Rutaceae was assigned to each host plant combination in each simulation.

The host plants of *D. kaki* did not affect the adult population of *B. dorsalis* (Fig. 16A), since the temporal availability of this plant completely overlapped with Rutaceae plants in the selected area (Fig. 13). Also, the host plants of *O. ficus indica* failed to connect *B. dorsalis* populations with Citrus plants in the late season, probably because these food sources disappeared too early in the system (*O. ficus indica* plants were available 65 between and 145 Julian date). But this host plants would be able to connect with *E. japonica*, *P. mume*, *P. persica*, or *F. carica* in the establishment of *B. dorsalis* population if they had combined each other to simulate the model.

The loquat plants (*E. japonica*) could establish successfully *B. dorsalis* population by combining with citrus plants (please see the scale of Y-axis in Fig. 13B). The host plants of *P. persica*, *F. carica*, and *P. mume* in the order were a very contributing factor to population abundance of *B. dorsalis* in the selected area (Figs. 16B, C).

3-4. Sensitivity to parameter changes

We tested the sensitivity of the parameter changes of population model. The parameters were changed by increasing or decreasing each parameter values by 10%. For sensitivity analysis, the average effect and non-linearity index suggested by Shaffer and Gold (1985) and applied by Kim and Lee (2010) were used:

$$\text{Average effect} = 0.5[F(1.1po) - F(0.9po)] \qquad \text{Eq. 20}$$

$$\text{Non - linearity} = 0.5[F(1.1po) + F(0.9po)] - F(po) \qquad \text{Eq. 21}$$

where F(p) is the model output with th e parameter at a given value p, and po is the original run value of the parameter. The average (linearity) and non-linearity effect were well defined by Shaffer and Gold (1985): which means proportional to a numerical approximation of the partial first derivative of the output with respect to the parameter and an approximation of the partial second derivative, respectively.

The changes of model parameters showed little effect on peak dates in generations (Table 10). In adult abundance, the non-linearity was smaller than the average effect (in absolute value) in most cases, indicating a largely linear relationship between the parameter changes and the simulation outputs. The negative average values means that the model outputs decrease with increasing parameter values, while the negative non-linearity values imply a convex curve relationship between the parameters and outputs (Shaffer and Gold, 1985). When a negative average effect and negative non-linearity were combined, the outputs decrease along the track of a convex curve with increasing parameter values (Shaffer and Gold, 1985). In the results of our sensitivity analysis as seen in Table 10, the changes of model parameters influenced the model outputs in a complex manner, since both average and non-linearity effects are found.

The role of the parameters in the distribution model of development time is regulating the transition time of a stage to the next stage. But the parameter changes did not affect the peak date of each generation in the both of average and nonlinearity effects, while just having low or moderate effect on adult abundance. The parameter changes for larvae and pupae showed a strong negative effect on the 4th adult abundance. It seems that the delay of transition center (the increase of parameter α) and the decline in the number of transition (the increase of parameter β) lead to a lower population size in cool autumn season.

The parameter changes of oviposition component models had a large effect on adult abundance linearly or nonlinearly with more effect in latter generations. The two parameters of female aging model have opposite effects each other on the outputs of population simulation. Female aging rates increase with decreasing δ and increasing ϕ which results in shorter longevity because of accelerating female physiological age. The change of these parameters showed a strong nonlinearity effect on the adult abundance in the 3rd generation. Also, these parameters are most influencing one on the peak time among other parameters, like as the parameter a of survival rate model.

The change of parameter β in oviposition rate model had different average effect on adult abundance according to the generations. The increase of β induces larger oviposition in early and late female age, while smaller oviposition in mid-age. The larger oviposition in early age can drive larger population abundance, because more adult females are alive in the period of early age. But negative average effects were observed in 2 and 4 generations as seen in Table 10, and it might be because reduced oviposition caused by the cool seasons of spring and autumn for the 1st and 3rd generation adults, respectively. Similarly, the increase of parameter λ of survival rate model resulted in a negative average effects on adult abundance, because it induced higher mortality in early and late ages.

On the other hand, the parameter a of the survival rate model showed a negative average effect only in the 4th adult generation, which was unexpected considering that the adult longevity increases by the increase of the parameter and it increases the abundance of existing population. Such phenomenon was caused by the decrease in the larval population of 3rd generation followed by the pupal population, because the increase of existing adult population in the previous generations depleted rapidly the carrying capacity of available fruits for egg laying and larval survival. But this phenomenon may not be detectable in the actual field environment, since adult populations of different generations are highly overlapped in the fields, and any generation do not have preoccupancy on food resources. The negative average effect was just occurred by the mechanism of programming process that adopted sequential preoccupation of food sources by the order of generations for the purpose of calculation. In actual population including all generations, total adult abundance was increased by the increase of parameter a in the survival rate model.

3-5. Discussion

The frequency distribution of insect development times is not symmetrical and commonly skewed rightward (Wagner et al., 1984). We estimated the parameters of distribution model of eggs, larvae, and pupae with the assumption of symmetry characteristic, namely normal distribution. Therefore, the transition centers may be slightly advanced compared to biological estimations of the original curve. In general, however, paramete *r* changes for the distribution model of development time had a slight effect on the peak dates in the population model of insects (Shaffer and Gold, 1985; Kim and Lee, 2010). Therefore, it is expected that the parameters of the distribution model estimated by the simple method in this study did not have a great influence on the outputs of the population model of *B. dorsalis*. Rather, the estimation method using mean and standard deviation can be suggested as an alternative method of finding the parameters of the distribution model quickly.

Any model is a simplified description of the full system it represents, and a model should capture the essence of the system when the model assumption is not broken as the concept of the model by Jeffers (1982). Therefore, the model presented in this study needs to be interpreted only within the range assumed by the model.

In the present study, the carrying capacity of food resources of *B. dorsalis* was obtained by combining all the host plants in the selected area. And the elimination of food resources was calculated in units consumed by a single larva (7.54 g per larva); so, all food resources were used by *B. dorsalis* without losses in the model. However, a part of unused food resources by *B. dorsalis* can be removed in the field conditions, because the infested fruits fall to the ground even if the larvae are not infested with a saturated state, and the fruits are not available to further by the adults. Therefore, our model may underestimate the density-dependent mortality of *B. dorsalis*, resulting in somewhat conservative conclusion. In the risk assessment for quarantined pests, conservative judgments can be helpful for the prevention of pests' invasion. For the parameterization of the host availability exactly, the distribution characteristic of eggs on various fruit sizes should be examined based on behavioral studies of *B. dorsalis*. Unfortunately, few datasets are available at present, and further studies are required in the future.

Although our population model of *B. dorsalis* simplified largely the system with many assumptions, the essential modules were obtained from actual experimental data in the laboratory or field. Especially, the real temporal distribution of host plants was incorporated into the model. So, simulation results of our model, as much as incorporating biological aspects of *B. dorsalis* and reality, will give us understanding of the system behavior of *B. dorsalis* in a new area. Also, our approach may be the only effective method to evaluate foreign pests in our country, since we cannot introduce and release quarantine pests such as *B. dorsalis*.

Bactrocera dorsalis is a subtropical or tropical species, and their available host plants are distributed constantly in the origin areas. When this species invaded into new regions where it is temperate or partially subtropical, host plants cannot be available during a part of seasons. In this study, as expected, the populations of *B. dorsalis* were greatly affected by the temporal distribution of host plants in the selected site. The population abundance decreased apparently in later seasons when the spring host plants were lacking. *B. dorsalis* was completely disappeared in the system with only citrus trees (see Fig. 16A, Rutaceae only). This is because of that the longevity of *B. dorsalis* females emerged from overwintered pupae is ended in mid-August before the availability of citrus fruits in the selected site. Therefore, host plants that serve as a stepping stone to the host plants in late season are required for permanent settlement of *B. dorsalis*. In the actual systems in Jeju, various host plants like a stepping stone (see Table 9, Fig. 13) distribute heterogeneously in wild habitats or private houses. As the results in Fig. 13 showed, the host plants during mid-season become a key factor for the establishment of *B. dorsalis*, although the low winter temperature should be considered in the future. Peng et al. (2011) have found a host shift pattern that affecting the population fluctuations of *B. dorsalis* in China: pear (*Pyrus communis* L.), jujube (*Zizyphus jujuba* L.), persimmon (*Diospyros* *kaki* L.), and sweet orange (*Citrus unshiu* Marcor). Also, Tan and Serit (1994) reported that the most important component of the environment affecting adult populations of *B. dorsalis* was the availability of suitable host fruits, even in the tropics. Consequently, a seasonal management strategy against *B. dorsalis* can be suggested by considering the availability of host plants and the biology of this fruit fly, when the invasion occurred in a limited area.

The most important thing is to identify wild host plants in the target area. The major and minor host plants should be listed and evaluated by fruiting phenology. Then, various control options will be able to arranged based on a prioritization of the risk in host plants. That is, spot treatments of protein baits or male annihilation using attractant ME (methyl eugenol) (Vargas et al., 2009) can be applied sequentially on/around host plants which are temporally distributed. The strategy of attracting and kill may be useful to arrest *B. dorsalis* in a defined area because *Bactrocera* females can be highly dispersed when they cannot find host plants to lay eggs (Clarke et al., 2005).

We assumed that the adults of *B. dorsalis* could immediately find host fruits without time lags. Our simulation is limited to a small area of 1.6×1.6 km. *B. dorsalis* is a strong flier, and mature host fruits attract powerfully *B. dorsalis* (CABI, 2018). Thus, our model may not overestimate largely the actual system in the selected area. Accordingly, the spatial distribution pattern of host plants was not concerned in this study. In a larger scale of habitat, however, *B. dorsalis* adults will migrate spatially to find available host plants when they are subjected to the depletion of food fruits. Thus, the spatial pattern of host plants can be an important factor for the establishment of *B. dorsalis*.

The present study might be significant in that the temporal distribution of actual host plants was modeled and the possibility of settlement and population persistence of invasive pest was evaluated. This novel approach would be useful in the study of other pests. In addition, a database can be made by parameterizing the characteristics of the host plants in the actual system, and it can be used to create a virtual ecosystem for evaluating the establishment of invasive pests in the future.

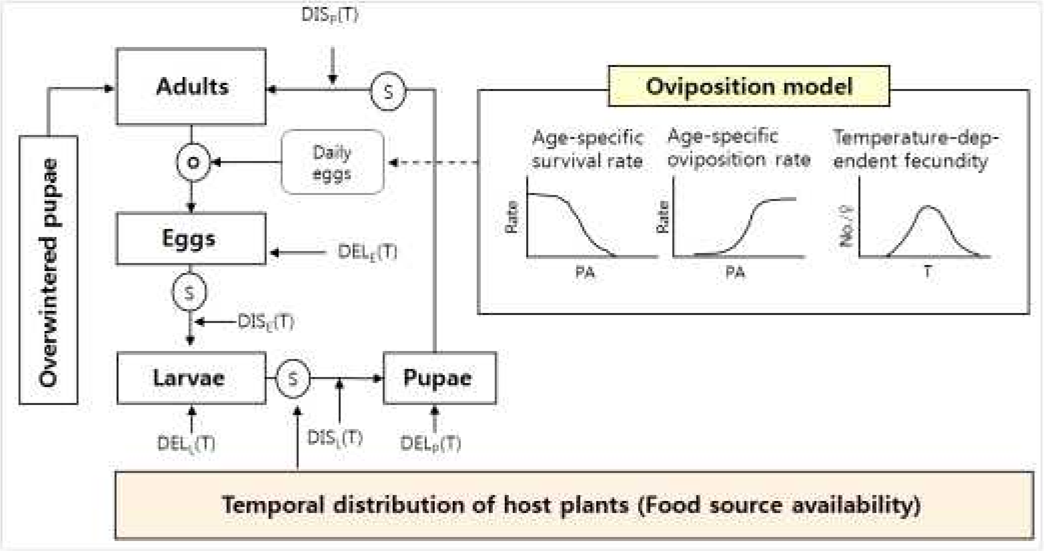


Fig. 12. The structure of population simulation model for *B. dorsalis*. DEL: development model, DIS: distribution model of development time, T: temperature, S: survival rate, O: oviposition model, and PA: physiological age. Also, E, L, and P indicate eggs, larvae, and pupae, respectively.

Table 9. Host plant lists of *B. dorsalis* found in the selected area and their estimated parameters for food availability curves

Family	Species	Plant type	No. of site found	No. of trees	Parameter			
					a	b	c	d
Amaryllidaceae	*Crinum asiaticum* L.	ornamental	6	33	9.7	289.0	67.5	1.5
Ebenaceae	*Diospyros kaki* Thunb.	ornamental	135	225	149,204.2	289.0	22.5	1.5
Lauraceae	*Machilus thunbergii* Siebold & Zucc.	ornamental, roadside tree, wild	78	93	331.4	212.5	45.8	1.5
	Neolitsea serica (Blume) Koidz.	ornamental	1	1	4.0	289.0	22.5	1.5
Moraceae	*Ficus carica* L.	commercial, ornamental, wild	30	280	422,497.2	258.5	68.3	1.5
	Morus alba L.	commercial, ornamental	3	303	16,291.5	182.0	45.0	1.5
Opuntiaceae	*Opuntia ficus-indica* (L.) Mill.	ornamental	2	10	702.6	105.5	68.3	1.5
Punicaceae	*Punica granatum* L.	ornamental	2	2	519.6	274.0	45.0	1.5
Rhamnaceae	*Ziziphus jujuba* Mill.	wild	1	1	96.3	274.0	45.0	1.5
Rosaceae	*Eriobotrya japonica* (Thunb) Lindl.	ornamental, wild	12	18	4,150.8	166.0	22.5	1.5
	Fragaria ananassa Duchesne ex Rozier	ornamental	1	40	85.5	197.0	22.5	1.5
	Malus pumila Mill.	ornamental	1	1	88.4	243.0	45.0	1.5
	Prunus mume Siebold & Zucc.	commercial, ornamental	10	254	42,289.2	182.0	45.0	1.5
	Prunus persica (L.) Batsch.	ornamental	3	4	23,361.1	232.5	45.8	1.5
	Pyrus communis L.	ornamental	1	1	8,620.7	243.0	91.5	1.5
	Pyrus pyrifolia (Burm. f.) Nakai	ornamental	2	2	1,202.2	228.0	22.5	1.5
Rutaceae	*Fortunella japonica* (Thunb.) Swingle	ornamental	3	3	1,524.4	304.0	45.0	1.5
	Citrus unshiu Marcov.	commercial (early cultinvar)	100	30,718	155,208,918.9	319.5	21.8	1.5
		commercial (extremely early)		3,414	17,245,435.4	298.5	21.8	1.5
		ornamental	35	96	485,046.8	350.0	90.0	1.5
		ornamental (overwintered)				45.0	120.0	1.5
Solanaceae	*Capsicum annuum* L.	commercial	18	1,172	15,940.9	258.5	68.3	1.5
	Lycopersicon esculentum Mill.	ornamental	1	1	236.0	212.5	45.8	1.5
	Solanum melongena L.	commercial	2	156	2,430.9	227.5	68.3	1.5
	Solanum nigrum L.	Wild	2	47	0.6	258.5	21.8	1.5
Vitaceae	*Vitis vinifera* L.	ornamental	1	1	147.8	243.0	45.0	1.5

Table 10. Results of sensitivity analysis of components models for *B. dorsalis*

Model	Stage or type	Para meter	1st generation						2nd generation				3rd generation				4th generation			
			First occurrence		Peak date		Abundance		Peak date		Abundance		Peak date		Abundance		Peak date		Abundance	
			A[1]	N[2]	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N
Distribution of development time	Egg	α	0	0	0	0	0	0	0	0	363.5	-176.5	0	0	-147	1963	0	0	36473	-57407
		β	0	0	0	0	0	0	0	0	40	1	0	0	31	254	-0.25	0.25	9672	-914
	Larva	α	0	0	0	0	0	0	1	0	-37	-9	0	0	8020	-235	0	0	-448751	117001
		β	0	0	0	0	0	0	0	0	1	-11	0	0	594.5	-55.5	0	0	-20891	1584
	Pupa	α	2.5	-0.5	1.75	-0.25	1	0	0	0	888.5	15.5	0	0	7330.5	980.5	0	0	-581264	116107
		β	1	0	-0.75	-0.25	0	-1	0	0	32	-368	0	0	769.5	2042.5	0	0	-28918.5	-614.5
Reproduction	Female aging rate	ϕ	0	0	-2.75	-0.25	0	0	-1.5	-0.5	-3036	76	-53	-53	-75416	33189	0	0	-84378.5	8614.5
		δ	0	0	7	-0.5	0	0	8.5	2.5	6059.5	-2431.5	53.5	-53.5	174928.5	129765.5	0	0	116212.5	-56861.5
	Total egg production	ω	0	0	0	0	0	0	0	0	2398.5	13.5	0	0	10981.5	1834.5	0	0	114130.5	49092.5
		ε	0	0	0	0	0	0	0.5	0.5	-1640.5	-3418.5	0	0	-3967.5	-13593.5	0.25	0.25	-1562874	-575602
		κ	0	0	0	0	0	0	0	0	163	-18	0	0	4159	981	-0.25	0.25	116004	54453
	Oviposition rate	γ	0	0	0	0	0	0	0	0	2517.5	154.5	0	0	10792.5	2330.5	-0.25	0.25	109528.5	54923.5
		η	0	0	0	0	0	0	0	0	10.5	-81.5	0	0	19548.5	-130.5	0	0	4738	-4536
		β	0	0	0	0	0	0	0	0	1672	-81	0	0	-11196	-303	0.25	0.25	123700	59167
	Survival rate	α	0	0	4.5	-1	0	0	1.5	-0.5	911.5	-274.5	53	-53	44214.5	-145.5	0.25	0.25	-10742	-8956
		λ	0	0	-1.75	-0.25	0	0	0	0	-346	-20	0	0	-2355	952	-0.25	0.25	-11211.5	-2543.5

[1] Average effect

[2] Non-linearity

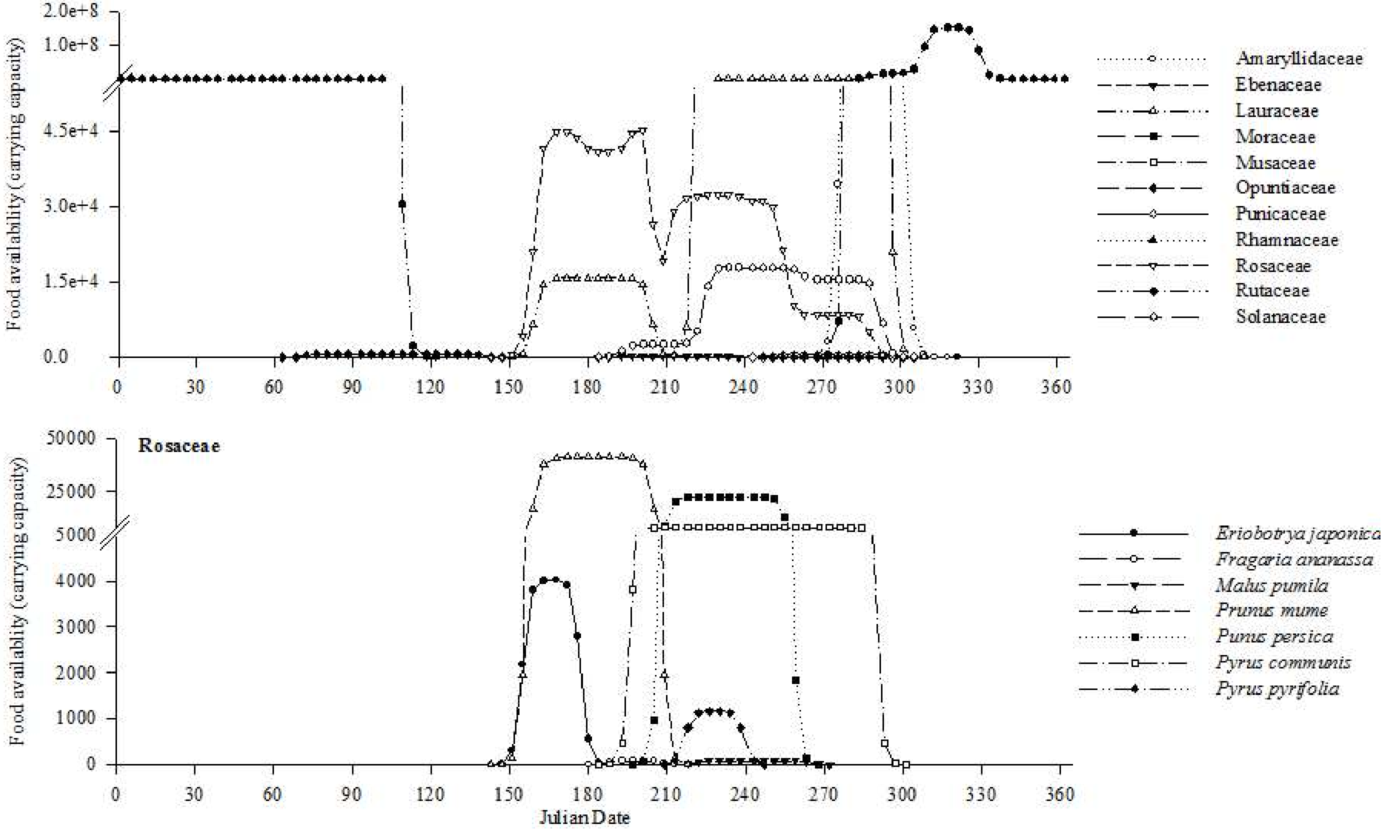


Fig. 13. Temporal distribution of host plants of *B. dorsalis* in a selected area. The carrying capacity (see x-axis) was expressed as the equivalent unit of fruit weight (g) to the number of larvae of *B. dorsalis*. The upper graph is for whole groups of host plants, and lower graph is for host plants belonging to Rosaceae.

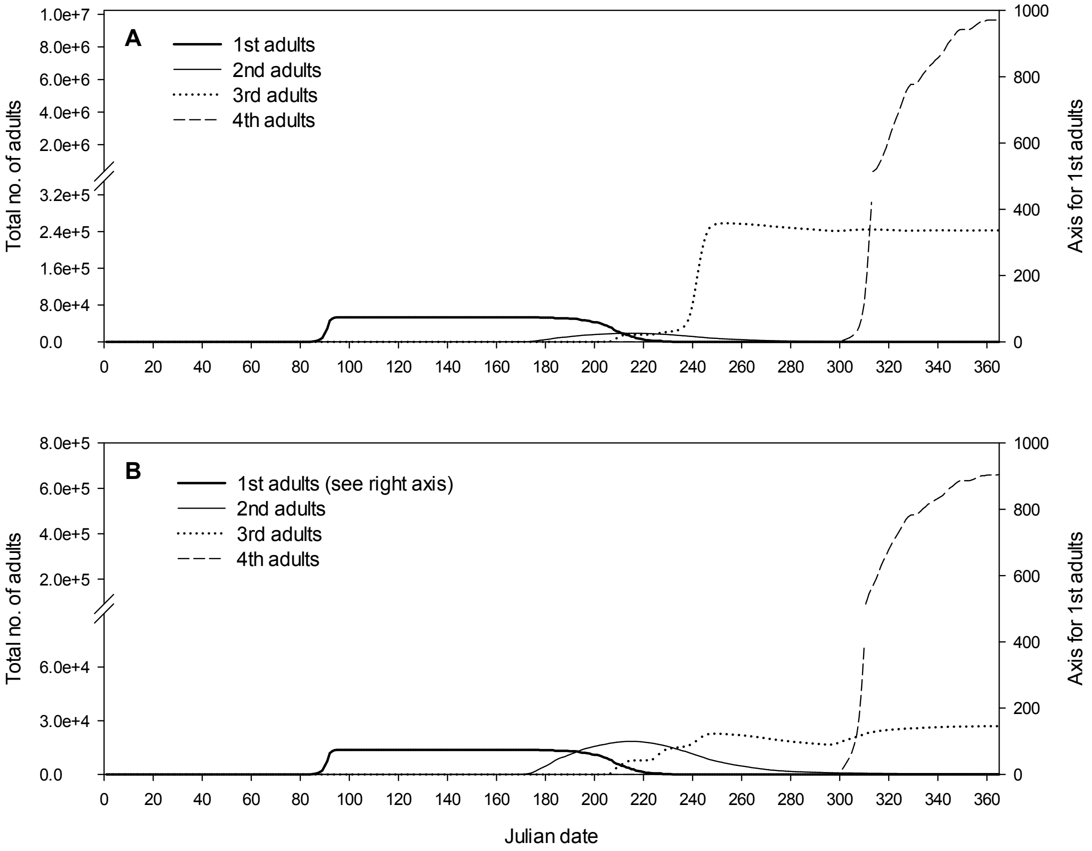


Fig. 14. The occurrence pattern of *B. dorsalis* adults in a selected area (Jeju) when whole host plants were incorporated into the population model (A). And host plants in Moraceae (*Ficus* spp., figs) were removed in the simulation. The model was simulated with an initial density of 100 pupae using driving variables of air and soil temperatures. Please see the scale of right axis for the 1st adults.

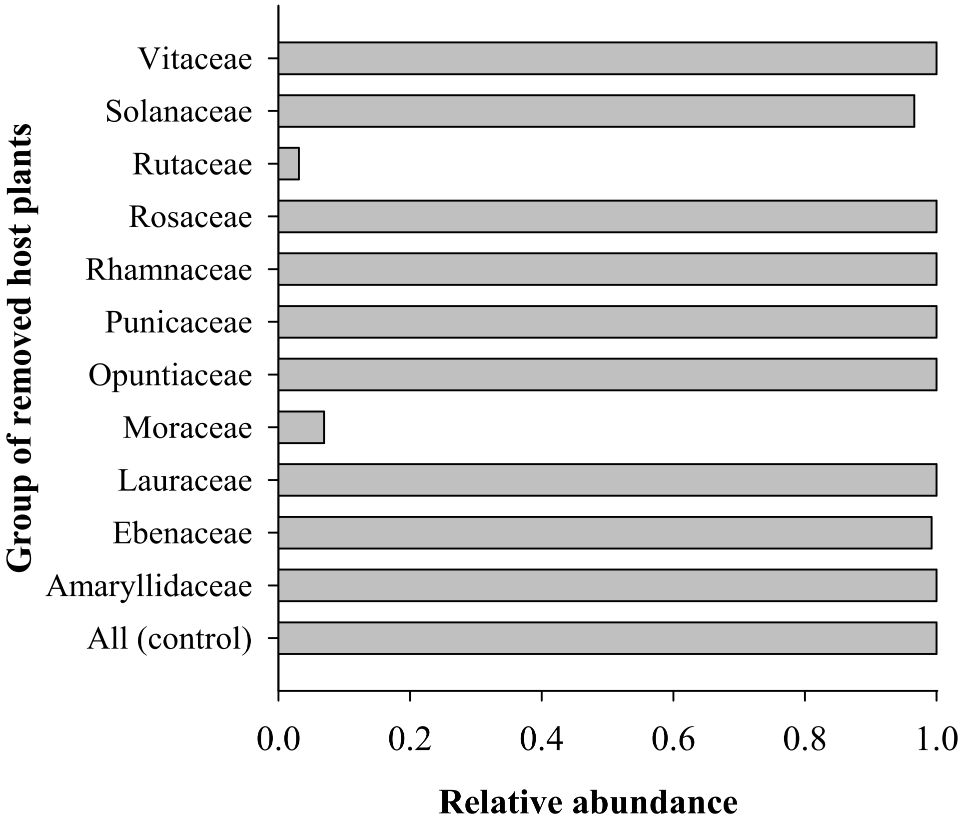


Fig. 15. Comparison of the relative abundance of adult *B. dorsalis* populations according to the removal of host plant group in model simulations. All (control) means the simulation with including all the groups of host plants.

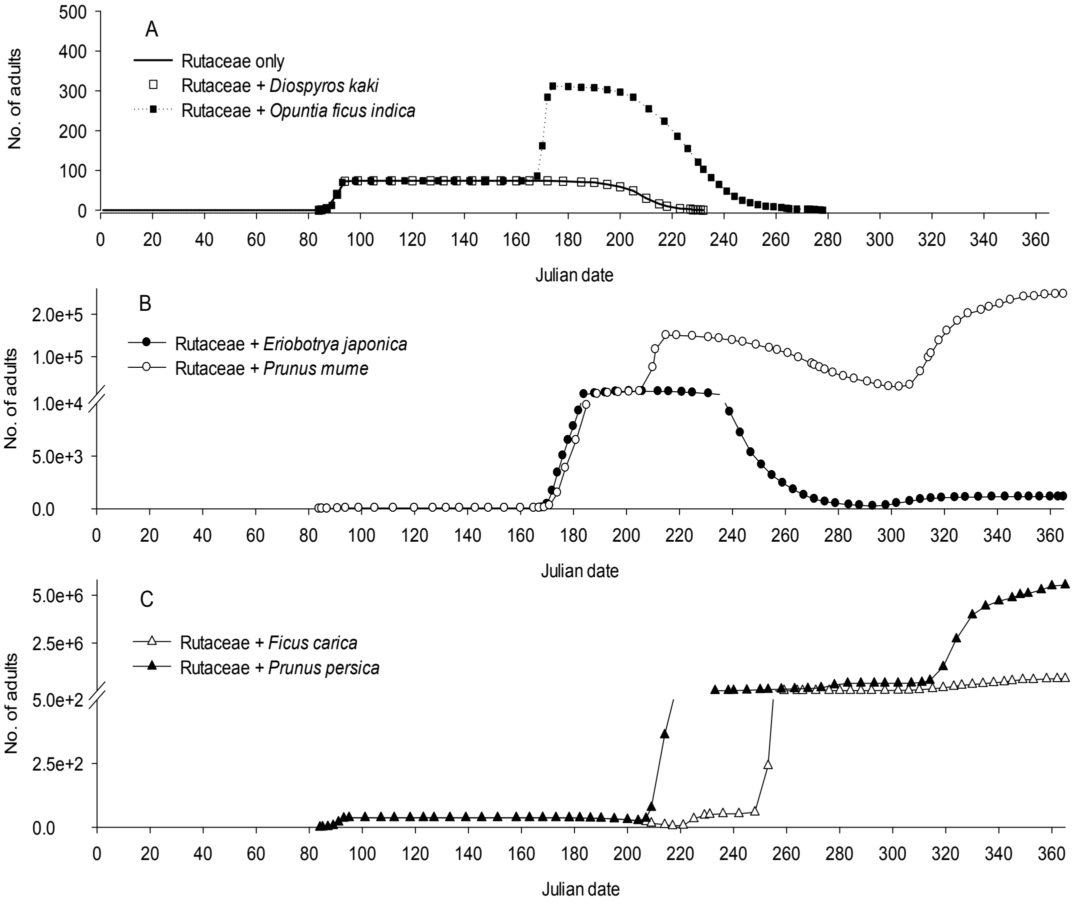


Fig. 16. The response to model outputs in the number of *B. dorsalis* adults by combining each host plant with Citrus plants (Rutaceae). For the purpose of comparison, a 5% of Rutaceae in the number of food resources was fixed for each combining host plant in each simulation. The response of model outputs was evaluated by the change of host plants included. Figures A, B, and C were separated by y-axis scale in order to make the comparison better.

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Supplementary data

SD Table 1. Distribution area of *B. dorsalis* complex in worldwide

Continent	**Country**	**Species**	**References**
Africa	Angola	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Benin	*B. invadens*	Drew et al., 2005; Vayssieres et al., 2008; De Meyer et al., 2010; Schutze et al., 2015b; Vayssieres et al., 2014
	Botswana	*B. invadens*	EPPO, 2014
	Brundi	*B. invadens*	Cassidy, 2010; Liu et al., 2011a; Drew and Romig, 2013
	Burkina Faso	*B. invadens*	Vayssieres et al., 2008; Vayssieres et al., 2014
	Cameroon	*B. invadens*	Drew et al., 2005; Abanda et al., 2008; Vayssieres et al., 2008; De Meyer et al., 2010
	Cape Verde	*B. invadens*	Ekesi and Mohamed, 2010
	Central African Republic	*B. invadens*	Goergen et al., 2011
	Chad	*B. invadens*	Vayssieres et al., 2008
	Comoros	*B. invadens*	De Meyer et al., 2010; Drew and Romig, 2013
	Congo	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Cote d'Ivoire	*B. invadens*	Vayssieres et al., 2008; De Meyer et al., 2010; Schutze et al., 2015b
	Democratic Republic of Congo	*B. invadens*	De Meyer et al., 2010; Goergen et al., 2011; Vayssieres et al., 2014
	Equatorial Guinea	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Ethiopia	*B. invadens*	De Meyer et al., 2010; Cassidy, 2010
	Gabon	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Gambia	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Ghana	*B. invadens*	Drew et al., 2005; Billah et al., 2006; Vayssieres et al., 2008; De Meyer et al., 2010; Vayssieres et al., 2014

Continent	Country	Species	References
	Guinea	*B. invadens*	Vayssieres et al., 2008; Vayssieres et al., 2014
	Guinea Bissau	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Kenya	*B. invadens*	Drew et al., 2005; Ekesi et al., 2006; Rwomushana et al., 2008; Vayssieres et al., 2008; De Meyer et al., 2010
	Liberia	*B. invadens*	Vayssieres et al., 2008
	Madagascar	*B. invadens*	EPPO, 2014
	Malawi	*B. invadens*	De Meyer et al., 2007; Oliver and Thierry., 2016
	Mali	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011;Vayssieres et al., 2014
	Mauritania	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Mayotte	*B. invadens*	EPPO, 2014
	Mozambique	*B. invadens*	Correia et al., 2008; De Meyer et al., 2010; Cassidy, 2010; Drew and Romig, 2013; Schutze et al., 2015b
	Namibia	*B. invadens*	Cassidy, 2010
	Niger	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	Nigeria	*B. invadens*	Drew et al., 2005; Vayssieres et al., 2008; De Meyer et al., 2010; Ugwu and Ojo, 2015
	Rwanda	*B. invadens*	Cassidy, 2010
	Senegal	*B. invadens*	Drew et al., 2005; Vayssieres et al., 2008; De Meyer et al., 2010; Vayssieres et al., 2014
	Sierra Leone	*B. invadens*	Vayssieres et al., 2008; Goergen et al., 2011
	South Africa	*B. invadens*	Manrakhan et al., 2015
	Sudan	*B. invadens*	Drew et al., 2005; De Meyer et al., 2010; Schutze et al., 2015b
	Tanzania	*B. invadens*	Mwatawala et al., 2007; Vayssieres et al., 2008; De Meyer et al., 2010; Drew and Romig, 2013; Geurts et al., 2014
	Togo	*B. invadens*	Drewetal.,2005; Vayssieres et al., 2008; De Meyeretal., 2010; Vayssieres et al., 2014

Continent	Country	Species	References
	Uganda	*B. invadens*	Drew et al., 2005; Vayssieres et al., 2008; De Meyer et al., 2010
	Zambia	*B. invadens*	De Meyer et al., 2010; Cassidy, 2010
	Zimbabwe	*B. invadens*	Cassidy, 2010
America	USA (Hawaii)	*B. dorsalis*	Wan et al., 2012; Barr et al., 2014
Asia	Bangladesh	*B. dorsalis*	Leblanc et al., 2013
	Bhutan	*B. invadens*	Drew et al,. 2007; De Meyer et al., 2010
	Brunei	*B. papayae*	Drew and Romig, 2013
	Cambodia	*B. dorsalis*	Drew and Hancock, 1994; Wan et al., 2012
	China	*B. dorsalis*	Drew and Hancock, 1994; Zhang et al., 1995; Jiang et al., 2001; Ye, 2001; He et al., 2002; Shi et al., 2005; Ye and Liu, 2005; Zubing et al., 2005; Chen et al., 2006; Chen and Ye, 2007; Liu et al., 2007; Wu et al., 2007; Chen and Ye, 2008; Meng et al., 2008; Qi et al., 2008; Zhao et al., 2008; Shi et al., 2010; Han et al., 2011; Li et al., 2012; Wan et al., 2012; Drew and Romig, 2013; Aketarawong et al., 2014, Wang et al., 2014; Wu et al., 2014
	Christmas Island	*B. papayae*	Drew et al., 2008; Drew and Romig, 2013
	India	*B. dorsalis*, *B. invadens*	Shukla and Prasad, 1985; Ram and Pathak, 1987; Drew and Hancock, 1994; Mann, 1996; Kumar and Agarwal, 1998; Verghese et al., 2004; Ravikumar and Viraktamath, 2006; Sithanantham et al., 2006; Rai et al., 2008; Satarkar et al., 2009; De Meyer et al., 2010; Prabhakar et al., 2012; Bhattacharya et al., 2013; Ganie et al., 2013a; Nandre and Shukla, 2014; Sathish et al., 2014; Schutze et al., 2015b; Choudhary et al., 2016; Tara and

Continent	Country	Species	References
			Gupta, 2016; Das et al., 2017; Gurung et al., 2017
	Indonesia	*B. papayae*	Drew and Hancock, 1994; Iwahashi, 2000; Drew et al., 2008; Schutze et al., 2012; Drew and Romig, 2013
	Laos	*B. dorsalis*	Drew and Hancock, 1994; Shi et al., 2010; Li et al., 2012; Wan et al., 2012; Aketarawong et al., 2014; Wu et al., 2014
	Malaysia	*B. papayae*	Tan and Lee, 1982; Rohani, 1987; Drew and Hancock, 1994; Drew et al., 2008; Schutze et al., 2012; Drew and Romig, 2013; Krosch et al., 2013
	Myanmar	*B. dorsalis*	Drew and Hancock, 1994; Shi et al., 2010; Li et al., 2012; Wan et al., 2012; Aketarawong et al., 2014
	Nepal	*B. dorsalis*	Schutze et al., 2015b
	Pakistan	*B. dorsalis*	Syed et al., 1970; Khattak et al., 1990; Chaudhry et al., 2000; Wan et al., 2012; Schutze et al., 2015b
	Philippines	*B. papayae,* *B. philippinensis*	Drew and Hancock, 1994; Iwahashi, 2000; Drew et al., 2008; Schutze et al., 2012; Drew and Romig, 2013; Wu et al., 2014
	Singapore	*B. papayae*	Drew and Hancock, 1994
	Sri Lanka	*B. invadens*	Drew and Hancock, 1994; De Meyer et al., 2010; Drew and Romig, 2013; Schutze et al., 2015b
	Taiwan	*B. dorsalis*	Drew and Hancock, 1994; Muraji et al., 2008; Schutze et al., 2012; Wan et al., 2012; Drew and Romig, 2013; Aketarawong et al., 2014
	Thailand	*B. papayae*	Drew and Hancock, 1994; Iwahashi, 2000; Krosch et al., 2013; Schutze et al., 2012; Aketarawong et al., 2014; Danjuma et al., 2014; Wu et al., 2014
	Vietnam	*B. dorsalis*	Drew and Hancock, 1994; Shi et al.,

Continent	Country	Species	References
			2010; Wan et al., 2012; Drew and Romig, 2013
Oceania	French Polynesia	*B. dorsalis*	Vargas et al., 2007; EPPO, 2014
	Papua New Guinea	*B. papayae*	Sar et al., 2001; Drew et al., 2008
	Palau	*B. philippinensis*	Drew et al., 2008; EPPO, 2014

SD Table 2. Temperature dependent development, survival, longevity and fecundity of *B. dorsalis* collected from previous reports

Temperature (°C)	Immature development (days)			Immature survival (%)			Female longevity and fecundity			Country	Food resources reared	Species examined	Reference
	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Pre-ovip. (days)	Longevity (days)	Fecundity				
15	5.71	35.95	34.08	90.67	83.54	72.16				Kenya	Carrot-based diet	*B. invadens*	Rwomushana et al., 2008
15	5.05	27.84	29.14	81.87	73.21	66.80				Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
16							31.8	133.5	175.4	Hawaii	Artificial diet	*B. dorsalis*	Vargas et al., 1997
17	3.61	23.73	25.12	85.20	71.20	24.40				China	Artificial diet	*B. dorsalis*	Luo et al., 2009
18							16.0	97.7	1479.0	Hawaii	Artificial diet	*B. dorsalis*	Vargas et al., 1997
18.5	3.20	11.10	24.90	74.00	72.00	68.00	48.4	179.8	952.1	Hawaii	Papaya fruits	*B. dorsalis*	Vargas et al., 2000
18.96	2.96	11.19	19.83							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
20	2.88	14.99	13.59	94.80	90.29	92.91				Kenya	Carrot-based diet	*B. invadens*	Rwomushana et al., 2008
20	2.70	12.16	13.19	87.20	80.79	74.35				Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
21	2.52	15.02	16.95	89.00	74.00	81.40				China	Artificial diet	*B. dorsalis*	Luo et al., 2009
23.18	1.96	9.49	12.90							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
23.5	2.00	7.30	12.20	83.00	78.00	59.00	18.2	83.6	1296.4	Hawaii	Papaya fruits	*B. dorsalis*	Vargas et al., 2000
23.92	1.16	12.02	7.03	96.03	27.48	65.41		28.19		Malaysia	Guava fruits	*B. papayae*	Mohd Noor et al., 2011
24							7.3	71.5	2682.7	Hawaii	Artificial diet	*B. dorsalis*	Vargas et al., 1997
24	2.00	7.70	12.40	85.00	83.00	66.00	37.3	93.6	1243.9	Hawaii	Papaya fruits	*B. dorsalis*	Vargas et al., 2000
24.14	1.54	7.99	11.45							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
25	1.55	12.36	11.91	92.40	85.00	88.80				China	Artificial diet	*B. dorsalis*	Luo et al., 2009
25	1.69	9.48	10.02	93.47	98.61	95.51				Kenya	Carrot-based diet	*B. invadens*	Rwomushana et al., 2008
25	1.53	7.13	9.73	85.60	85.08	80.22				Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
27	1.22	6.56	8.40	88.40	83.88	81.52				Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
28	1.20	11.10	12.40	90.00	75.60	80.90		75.1	1056.8	Kenya	Artificial diet	*B. invadens*	Ekesi et al., 2006
28.08	1.17	6.83	8.70							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
29	1.25	9.31	9.58	89.80	78.40	83.80				China	Artificial diet	*B. dorsalis*	Luo et al., 2009
29							5.7	37.8	975.4	Hawaii	Artificial diet	*B. dorsalis*	Vargas et al., 1997

29.5	2.00	7.80	10.50	75.00	65.00	44.00	21.2	49.0	396.7	Hawaii	Papaya fruits	*B. dorsalis*	Vargas et al., 2000
30	1.41	7.85	8.50	93.60	93.31	95.40				Kenya	Carrot-based diet	*B. invadens*	Rwomushana et al., 2008
30	1.11	6.51	7.16	90.93	80.09	80.01				Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
31.02	1.04	6.04	8.35							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
32							5.3	27.5	163.4	Hawaii	Artificial diet	*B. dorsalis*	Vargas et al., 1997
33	1.13	7.53	7.69	88.00	76.30	70.4				China	Artificial diet	*B. dorsalis*	Luo et al., 2009
33.56	1.00	6.38	dead							China	Artificial diet	*B. dorsalis*	Wu et al., 2000
35	1.25	6.64	dead	87.47	84.52					Kenya	Carrot-based diet	*B. invadens*	Rwomushana et al., 2008
35	1.03	5.28	dead	81.80	66.27					Thailand	Guava-based diet	*B. papayae*	Danjuma et al.,2014
Average				87.4	77.5	73.5							

SD Table 3. Reported host plant species of *B. dorsalis* and its status in Korea

Family	**Species**	**References**[1]	**Status in Korea**
Adoxaceae	*Sambucus javanica* Reinw. ex Blume	E, F	
	Viburnum japonicum (Thunb.) Spreng.	E	wild
Amaryllidaceae	*Crinum asiaticum* L.	E, F	wild (*Crinum asiaticum* var. *declinatum* (Rottb.) C.B.Clarke, *Crinum asiaticum* var. *japonicum* Baker)
Anacardiaceae	*Anacardium occidentale* L.	C, D, E, F	cultivated
	Bouea macrophylla Griff.	E, F	
	Bouea oppositifolia (Roxb.) Meisn.	E, F	
	Holigarna kurziiKing	E, F	
	Mangifera caesia Jack	E, F	
	Mangifera caloneura Kurz	E	
	Mangifera foetida Lour.	E, F	
	Mangifera griffithii Hook. f.	E, F	
	Mangifera indica L.	A, B, C, D, E, F	cultivated
	Mangifera laurina Blume	E, F	
	Mangifera longipetiolata King	E	
	Mangifera odorata Griff.	E, F	
	Mangifera pajang Kosterm.	E	
	Sclerocarya birrea (A. Rich.) Hochst.	C, D, E, F	
	Sorindeia sp.	D, E, F	
	Sorindeia madagascariensis DC.	C	
	Spondias dulcis Sol. ex Parkinson[2]	C, D, E, F	
	Spondias mombin L.	C, D, E, F	
	Spondias pinnata L.	E, F	
	Spondias purpurea L.	E, F	
Annonaceae	*Annona ×atemoya* Mabb.	E	
	Annona cherimola Mill.	A, D, E, F	
	Annona glabra L.	E, F	cultivated
	Annona macroprophyllata Donn. Sm.	E, F	
	Annona montana Macfad.	E, F	
	Annona muricata L.	C, D, E, F	cultivated
	Annona reticulata L.	E, F	
	Annona senegalensis Pers.	C, D, E, F	
	Annona squamosa L.	A, D, E, F	cultivated
	Artabotrys siamensis Miq.	E, F	

Family	Species	References[1]	Status in Korea
	Cananga odorata (Lam.) hook. f. & Thomson	E, F	
	Desmos chinensis Lour.	E, F	
	Hexalobus monopetalus (A. Rich.) Engl. & Diels[3]	E	
	Mitrephora maingayi Hook. f. & Thomson[4]	E	
	Polyalthia longifolia (Sonn.) Thwaites	E, F	
	Polyalthia simiarum (Buch.-Ham. ex Hook. f. & Thomson) Benth. ex Hook. f. & Thomson	E, F	
	Rollinia mucosa (Jacq.) Baill.[5]	E, F	
	Uvaria cordata (Dunal) Alston	F	
	Uvaria grandiflora Roxb. ex Hornem.	E, F	
	Uvariama crophylla Roxb.	E	
Apocynaceae	*Carissa carandas* L.	E, F	
	Carissa spinarum L.	E, F	
	Landolphia	F	
	Ochrosia	F	
	Ochrosia mariannensis A. DC.	E	
	Saba senegalensis (A. DC.) Pichon	C, E, F	
	Thevetia peruviana (pers.) K. Schum.	D, E, F	
	Willughbeia cochinchinensis (Pierre) K. Schum.	E	
	Willughbeia edulis Roxb.	F	
Arecaceae	*Adonidia merrillii* (Becc.) Becc.[6]	E, F	
	Areca catechu L.	A, E, F	
	Arenga engleri Becc.	A, E	
	Arenga pinnata (Wurmb.) Merr.	E, F	
	Arenga westerhoutii Griff.	E, F	
	Bactris gasipaes Kunth	E	
	Borassus flabellifer L.	E, F	
	Caryota mitis Lour.	E, F	cultivated
	Cocos nucifera L.	E	cultivated
	Jubaea chilensis (Molina) Baill.	E	
	Phoenix dactylifera L.	E	
Asparagaceae	*Dracaena draco* (L.) L.	E	cultivated
	Dracaena steudneri Schwein f. ex Engl.	E, F	cultivated
Boraginaceae	*Cordia dentata* Poir.[7]	E, F	
	Ehretia microphylla Lam.	E, F	
Bromeliaceae	*Ananas comosus* (L.) Merr.	E	cultivated

Family	**Species**	**References**[1]	**Status in Korea**
Burseraceae	*Canarium insulare*	E	
	Garuga floribunda Decne.	E, F	
Cactaceae	*Cereus aethiops* Haw.	E	
	Hylocereus undatus (Haw.) Britton & Rose	E, F	
	Opuntia ficus-indica (L.) Mill.	E	cultivated
	Pereskia grandiflora Pfeiff.	E, F	
Calophyllaceae	*Calophyllum inophyllum* L.	E, F	
	Mammea siamensis T. Anderson	E, F	
Cannabaceae	*Celtis tetrandra* Roxb.[8]	E, F	
	Capparis sepiaria L.	E, F	
	Capparis tomentosa Lam.	E	
	Maerua sp.	E, F	
	Maerua duchesnei (DeWild.) F. White	C	
Caricaceae	*Carica papaya* L.	A, C, D, E, F	cultivated
Celastraceae	*Siphonodon*	F	
	Siphonodon celastrineus Griff.	E	
Chrysobalanaceae	*Chrysobalanus icaco* L.	E	
	Parinari anamense Hance	E, F	
Clusiaceae	*Clusia rose* aJacq.	E	cultivated
	Garcinia dioica Blume	E, F	
	Garcinia atroviridis Griff.ex T. Anderson	E, F	
	Garcinia cowa Roxb. ex DC.	F	
	Garcinia dulcis (Roxb.) Kurz	E, F	
	Garcinia griffithii T. Anderson	E, F	
	Garcinia hombroniana Pierre	E, F	
	Garcinia intermedia (Pittier) Hammel	E	
	Garcinia mangostana L.	E, F	cultivated
	Garcinia mannii Oliv.	C, E, F	
	Garcinia parvifolia Miq.	E	
	Garcinia prainiana King	E, F	
	Garcinia speciosa Wall.	E, F	
	Garcinia spicata Hook. f.	A	
	Garcinia subelliptica Merr.	E	
	Garcinia xanthochymus Hook.f.	E, F	
Combretaceae	*Terminalia arenicola* Byrnes	D, F	
	Terminalia catappa L.	C, E, F	
	Terminalia chebula Retz.	E, F	
	Terminalia citrina (Gaertn.) Roxb. ex Fleming	E	

Family	Species	References[1]	Status in Korea
Convolvulaceae	*Erycibe subspicata* Wall. ex G.Don	E, F	
	Merremia vitifolia (Burm.f.) Hallierf.	E, F	
Cordiaceae	*Cordia myxa* L.[9]	D, F	
	Cordia sinensis Lam.	F	
Cornaceae	*Alangium chinense* (Lour.) Harms	E, F	
	Alangium griffithii (C. B. Clarke) Harms	E	
	Alangium salviifolium (L. f.) Wangerin	E, F	
Cucurbitaceae	*Cucurbita* spp.	A	
	Citrullus colocynthis (L.) Schrad.	C, E, F	
	Citrullus lanatus (Thunb.) Matsum. & Nakai[10]	B, C, D, E, F	
	Coccinia grandis (L.) Voigt	E, F	
	Cucumis ficifolius A. Rich.[11]	D, E, F	
	Cucumis melo L.	E, F	cultivated
	Cucumis sativus L.	C, D, E, F	cultivated
	Cucurbita maxima Duchesne	C, D, E, F	cultivated
	Cucurbita pepo L.[12]	C, D, E, F	cultivated
	Cayaponia laciniosa (L.) C.Jeffrey[13]	D	
	Diplocyclos palmatus (L.) C. Jeffrey	E	
	Gymnopetalum scabrum (Lour.) W. J. de Wilde & Duyfjes	E, F	
	Kedrostis leloja (Forssk.) C. Jeffrey	E	
	Lagenaria siceraria (Molina) Standl.	C, E, F	wild
	Luffa acutangula (L.) Roxb.	E	
	Luffa aegyptiaca Mill.	E	wild
	Momordica balsamina L.	E	
	Momordica charantia L.	C, E, F	cultivated
	Momordica cochinchinensis (Lour.) Spreng.	E	
	Sechium edule (Jacq.) Sw.	E	
	Trichosanthes boninensis Nakai	E	
	Trichosanthes cucumerina L.	E	
	Trichosanthes dioica Roxb.	E	
	Trichosanthes ovigera Blume	E, F	
	Zehneria mucronata	E	
	Zehneria wallichii	E, F	
Dilleniaceae	*Dillenia obovata* (Blume) Hoogland	E, F	
Ebenaceae	*Diospyros areolata* King & Gamble	E, F	
	Diospyros blancoi A. DC.	E, F	
	Diospyros castanea (Craib). H. R.	E, F	

Family	Species	References[1]	Status in Korea
	Fletcher		
	Diospyros diepenhorstii Miq.	E, F	
	Diospyros glandulosa Lace	E	
	Diospyros japonica Siebold & Zucc.	E	
	Diospyros kaki Thunb.	A, E, F	wild, cultivated
	Diospyros lotus L.	B	wild
	Diospyros malabarica (Desr.) Kostel.	E, F	
	Diospyros maritima Blume	E	
	Diospyros mollis Griff.	E, F	
	Diospyros montana Roxb.	C, D, E, F	
	Diospyros roxburghii Carrière	F	
	Diospyros sandwicensis (A. DC.) Fosberg	E	
	Diospyros vera (Lour.) A. Chev.	E	
Elaeocarpaceae	*Elaeocarpus hygrophilus* Kurz	E, F	
	Elaeocarpus serratus L.	E	
Ericaceae	*Vaccinium reticulatum* Sm.	E	
Euphorbiaceae	*Aporusa villosa* (Lindl.) Baill.	E, F	
	Balakata baccata (Roxb.) Esser	E, F	
	Excoecaria agallocha L.	E, F	
	Glochidion littorale Blume	E, F	
	Phyllanthus acidus (L.) Skeels	E	
	Shirakiopsis indica (Willd.) Esser	E, F	
Fabaceae	*Adenanthera pavonina* L.	E, F	
	Afzelia xylocarpa (Kurz) Craib	E, F	
	Cordyla africana Lour.	F	
	Cordyla pinnata (A.Rich.) Milne-Redh.	D, E	
	Inocarpus fagifer (Parkinson) Fosberg[14]	E, F	
	Parkia speciosa Hassk.	E, F	
	Phaseolus vulgaris L.	E, F	cultivated
	Sesbania grandiflora (L.) Poir.	E	
Fagaceae	*Castanopsis*	F	
Flacourtiaceae	*Dovyalis hebecarpa* (Gardner) Warb.	E, F	
	Flacourtia indica (Burmanf.) Merrill	D, E	
	Flacourtia rukam Zoll. & Moritzi	E, F	
Gentianaceae	*Fagraea ceilanica* Thunb.	E, F	
Hanguanaceae	*Hanguana malayana* (Jack) Merr.	E, F	
Irvingiaceae	*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill.	C, D, E, F	
	Irvingia malayana Oliv. ex A. W. Benn.	E, F	
Juglandaceae	*Juglans hindsii* (Jeps.)R.E.Sm.	E	
	Juglans nigra L.	E	cultivated

Family	**Species**	**References**[1]	**Status in Korea**
	Juglans regia L.	E	cultivated
Lamiaceae	*Callicarpa longifolia* Lam.	E, F	
	Gmelina elliptica Sm.	E, F	
	Gmelina philippensis Cham.	E, F	
	Premna serratifolia L.	E, F	
Lauraceae	*Cinnamomum tenuifolium* (Makino) Sugim.[15]	A	
	Cinnamomum yabunikkei H. Ohba	E	wild
	Lindera oxyphylla Hk. f.	E	
	Litsea glutinosa (Lour.) C. B. Rob.	E, F	
	Litsea japonica (Thunb.) Juss.[16]	A	wild
	Litsea salicifolia (J. Roxb. ex Nees) Hook. f.	E, F	
	Machilus thunbergii Siebold & Zucc.	A, E	wild
	Neolitsea sericea (Blume) Koidz.	E	wild
	Persea americana Miller	A, C, D, E, F	cultivated
Lecythidaceae	*Barringtonia edulis* Seem.	E, F	
	Careya arborea Roxb.	E, F	
	Careya sphaerica Roxb.	E	
Loganiaceae	*Fragaea berteroana* Bentham var. *sair* Gilg.&Benedict	E	
	Strychnos mellodora S. Moore	D, E, F	
Lythraceae	*Punica granatum* L.	A, E, F	cultivated
Malpighiaceae	*Malpighia emarginata* DC.	E, F	
	Malpighia glabra L.	C, E, F	
Malvaceae	*Durio zibethinus* L.	C	cultivated
	Gossypium barbadense L.	E	
	Theobroma cacao L.	E, F	cultivated
Meliaceae	*Azadirachta excelsa* (Jack) M. Jacobs	E, F	
	Chukrasia tabularis A. Juss.	E, F	
	Heynea trijuga Roxb. ex Sims	E, F	
	Lansium domesticum Corrêa	E, F	
	Lansium parasiticum (Osbeck) K. C. Sahni & Bennet	E	
	Sandoricum koetjape (Burm.f.) Merill	E, F	
Menispermaceae	*Fibraurea tinctoria* Lour.	E, F	
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	E	
	Artocarpus altilis (Parkinson) Fosberg[17]	A, E, F	
	Artocarpus chama Buch.-Ham.	E	
	Artocarpus elastica Reinw. ex Blume	E, F	

Family	**Species**	**References**[1]	**Status in Korea**
	Artocarpus heterophyllus Lam.	E, F	cultivated
	Artocarpus integer (Thunb.) Merr.	E, F	
	Artocarpus lacucha Buch.-Ham.	E, F	
	Artocarpus lanceifolius Roxb.	E, F	
	Artocarpus lanceolatus Trécul	E, F	
	Artocarpus odoratissimus Blanco[18]	E, F	
	Artocarpus rigidus subsp. *asperulus* (Gagnep.) F. M. Jarrett	E, F	
	Artocarpus sericicarpus F. M. Jarrett	E, F	
	Ficus auriculata Lour.	E, F	
	Ficus benjamina L.	E, F	
	Ficus carica L.	A, E	cultivated
	Ficus chartacea (Wall. ex Kurz) Wall. ex King	E, F	
	Ficus concatian	E	
	Ficus eligodon	E	
	Ficus erecta Thunb.	E	wild
	Ficus fistulosa Reinw. ex Blume	E, F	
	Ficus hirta Vahl	E, F	cultivated
	Ficus hispida L. f.	E, F	
	Ficus microcarpa L. f.	E, F	cultivated
	Ficus obpyramidiata	E, F	
	Ficus ottoniifolia Miq.	E, F	
	Ficus pumila L.	E	cultivated
	Ficus racemosa L.	E, F	
	Ficus religiosa L.	E, F	cultivated
	Ficus retusa L.	A	cultivated
	Ficus septica Burm. f.	E	
	Ficus sycomorus L.	C, F	
	Ficus virgata Reinw. ex Blume	E	
	Maclura cochinchinensis (Lour.) Corner	E, F	
	Morus alba L.	E, F	wild, cultivated
	Morus nigra L.	E, F	cultivated
	Streblus asper Lour.	E, F	
Muntingiaceae	*Muntingia calabura* L.	E, F	
Musaceae	*Musa* spp.	A, C, D, E, F	
	Musa ×*paradisiaca* L.[19]	E, F	cultivated
	Musa acuminata Colla	E, F	cultivated
	Musa balbisiana Colla	D, F	

Family	**Species**	**References**[1]	**Status in Korea**
	Musa troglodytarum L.	E, F	
Myricaceae	*Morella rubra* Lour.	E	wild
Myristicaceae	*Horsfieldia subglobosa* Warb.	E	
	Knema globularia (Lam.) Warb.	E, F	
Myrtaceae	*Acca sellowiana* (O. Berg) Burret	E	cultivated
	Eugenia reinwardtiana (Blume) DC.	E	
	Eugenia brasiliensis Lam.	E	
	Eugenia palumbis Merr.	F	
	Eugenia uniflora L.	E, F	
	Pimenta dioica (L.) Merrill	E	
	Plinia cauliflora (Mart.) Kausel[20]	F	
	Psidium cattleyanum Sabine var. *littorale* (Raddi) Fosberg[21]	D	
	Psidium cattleyanum Sabine[22]	A, E, F	cultivated
	Psidium guajava L.	A, B, C, D, E, F	cultivated
	Rhodomyrtus tomentosa (Aiton) Hassk.	E, F	
	Syzygium aromaticum (L.) Merr. & L. M. Perry	E, F	
	Syzygium aqueum (Burm.f.) Alston	F	
	Syzygium borneense (Miq.) Miq.	E, F	
	Syzygium cumini (L.) Skeels	D, E, F	
	Syzygium formosanum (Hayata) Mori.	E, F	
	Syzygium grande (Wight) Walp.	E, F	
	Syzygium jambos (L.) Alston	C, D, E, F	cultivated
	Syzygium lineatum (DC.) Merr. & L. M. Perry	E, F	
	Syzygium malaccense (L.) Merrill & L. M. Perry	C, D, E, F	
	Syzygium megacarpum (Craib) Rathakr. & N.C.Nair[23]	E, F	
	Syzygium nervosum DC.	E, F	
	Syzygium samarangense (Blume) Merr. & L. M. Perry	A, D, E, F	
Olacaceae	*Olax scandens* Roxb.	E	
	Schoepfia fragrans Wall.	E, F	
Oleaceae	*Chionanthus parkinsonii* (Hutch.) Bennet & Raizada	E, F	
	Myxopyrum smilacifolium Blume	E, F	
	Nestegis sandwicensis (A. Gray) O. Deg., I. Deg. & L. A. S. Johnson	E	
	Olea europaea L.	E	cultivated

Family	**Species**	**References**[1]	**Status in Korea**
Orchidaceae	*Papilionanthe hookeriana* (Rchb. f.) Schltr. × *Papilionanthe teres* (Roxb.) Schltr.	E	
Oxalidaceae	*Averrhoa bilimbi* L.	E, F	
	Averrhoa carambola L.	A, C, D, E, F	cultivated (*Averrhoa carambola* 'Ell Lin')
Pandanaceae	*Pandanus fragrans* Gaudich.	E	
	Pandanus odorifer (Forssk.) Kuntze	E	
Passifloraceae	*Passiflora edulis* Sims	A, E, F	cultivated
	Passiflora foetida L.	E, F	
	Passiflora incarnata L.	E	
	Passiflora laurifolia L.	E, F	
	Passiflora ligularis Juss.	E	
	Passiflora quadrangularis L.	E, F	
	Passiflora suberosa L.	F	
	Passiflora tripartita (Juss.) Poir. var. *mollissima* (Kunth) Holm-Niels. & P.Jørg.	E	
Phyllanthaceae	*Antidesma ghaesembilla* Gaertn.	E, F	
	Baccaurea angulata Merr.	E	
	Baccaurea motleyana (Müll. Arg.) Müll. Arg.	E, F	
	Baccaurea racemosa (Reinw.) Müll. Arg.	E, F	
	Baccaurea ramiflora Lour.	E, F	
	Bischofia javanica Blume	E	cultivated
	Breynia racemosa (Blume) Müll.Arg.[24]	E, F	
	Bridelia stipularis (L.) Blume	E, F	
	Flueggea virosa (Roxb. ex Willd) Royle	E, F	
	Sauropus androgynus (L.) Merr.	E, F	
Piperaceae	*Piper nigrum* L.	F	
Polygalaceae	*Xanthophyllum flavescens* Roxb.	E, F	
	Coccoloba uvifera (L.) L.	E	cultivated
Primulaceae	*Ardisia crenata* Sims	E, F	wild
Putranjivae	*Putranjiva roxburghii* Wall.	B	
Rhamnaceae	*Ziziphus hysudrica*[25]	B	
	Ziziphus jujuba Mill.[26]	B, E, F	wild, cultivated
	Ziziphus mauritiana Lam.	C, D, E, F	
	Ziziphus nummularia (Burm. f.) Wight & Arn.	E, F	
	Ziziphus oenoplia (L.) Mill.	E, F	
Rhizophoraceae	*Rhizophora*	F	

Family	**Species**	**References**[1]	**Status in Korea**
Rosaceae	*Eriobotrya japonica* (Thunb) Lindl.	A, B, C, D, E, F	cultivated
	Fragaria ×ananassa Duchesne ex Rozier	E	cultivated
	Fragaria chiloensis (L.) Mill.	E	
	Malus domestica Borkh.[27]	B, D, E, F	wild
	Malus sylvestris (L.) Mill.	E	
	Prunus armeniaca L.	B, E, F	wild, cultivated
	Prunus avium (L.) L.	E, F	wild, cultivated
	Prunus bokhariensis Royle ex C.K.Schneid	B	
	Prunus campanulata Maxim.	E	cultivated
	Prunus cerasifera Ehrh.	E	
	Prunus cerasoides D. Don	E	
	Prunus cerasus L.	E, F	wild, cultivated
	Prunus domestica L.	E, F	wild, cultivated
	Prunus ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr.	E, F	
	Prunus mume Siebold & Zucc.	E	wild, cultivated
	Prunus persica (L.) Batsch.	A, B, D, E, F	wild, cultivated
	Prunus salicina Lindl.	A, E, F	wild, cultivated
	Pyrus communis L.	B, E, F	cultivated
	Pyrus pashia Buch.-Ham. ex D. Don	B, E	cultivated
	Pyrus pyrifolia (Burm. f.) Nakai[28]	B, E, F	wild, cultivated
Rubiaceae	*Breonia chinensis* (Lam.) Capuron	F	
	Coffea arabica L.	D, E, F	cultivated
	Coffea canephora Pierre ex A. Froehner	D, E, F	
	Gynochthodes umbellata (L.) Razafim. & B. Bremer	E, F	
	Ixora javanica (Blume) DC.	E, F	
	Ixora macrothyrsa (Teijsm. & Binn.) R. Br.	E, F	
	Morinda citrifolia L.	E, F	cultivate
	Morinda coreia Buch.-Ham.	E, F	
	Nauclea orientalis (L.) L.	E, F	
	Neolamarckia cadamba (Roxb.) Bosser	E	
	Neonauclea purpurea (Roxb.) Merr.	F	
	Ochreinauclea maingayi (Hook. f.) Ridsdale	E, F	
	Sarcocephalus latifolius (Sm.) Bruce	C, D, E, F	
Rutaceae	×*Citrofortunella floridana* J. W. Ingram & H. E. Moore	E	

Family	Species	References[1]	Status in Korea
	×*Citrofortunella microcarpa* (Bunge) Wijnands	E, F	
	Aegle marmelos (L.) Corrêa	E	
	Casimiroa edulis La Llave &Lex.	E, F	cultivated
	Citrus ×*tangelo* J. W.I ngram & H. E. Moore	D, E	
	Citrus aurantiifolia (Christm. Swingle)	E, F	
	Citrus aurantium L.	A, D, E, F	wild, cultivated
	Citrus clementina Hort. ex Tanaka	E	
	Citrus deliciosa Ten.	E	
	Citrus depressa Hayata	E	
	Citrus hystrix DC.	E, F	
	Citrus jambhiri Lush.	E	
	Citrus keraji Hort. ex Tanaka	E	
	Citrus latifolia (Yu. Tanaka) Tanaka	E, F	
	Citrus limetta Risso	E	
	Citrus limon (L.) Burm. f.	C, D, E, F	cultivated
	Citrus limonia Osbeck	E	
	Citrus maxima (Burm.) Merrill[29]	A, D, E, F	
	Citrus medica L.	A	wild (*Citrus medica* var. *junos* Siebold)
	Citrus natsudaidai Hayata	A, E	cultivated
	Citrus nobilis Lour.	A, E	
	Citrus oto Hort. ex Yu. Tanaka	E	
	Citrus paradisi Macfady	C, D, E, F	
	Citrus reticulata Blanco	A, C, D, E, F	
	Citrus sinensis (L.) Osbeck	C, D, E, F	cultivated
	Citrus swinglei Burkill ex Harms	D, F	
	Citrus unshiu Marcow.	A, E	cultivated
	Clausena lansium (Lour.) Skeels	A, E, F	
	Fortunella japonica (Thunb.) Swingle	D, E, F	cultivated
	Fortunella margarita (Lour.) Swingle	A, D, E, F	cultivated
	Fortunella polyandra (Ridl.) Tanaka	E, F	
	Glycosmis pentaphylla (Retz.) DC.	E, F	
	Murraya exotica L.	A, E	
	Murraya paniculata (L.) Jack	E, F	cultivated
	Poncirus trifoliata (L.) Raf.	A, E, F	cultivated
	Toddalia asiatica (L.) Lam.[30]	E	
	Triphasia trifolia (Burm. f.) P. Wilson	E, F	
Santalaceae	*Santalum paniculatum* Hook. & Arn.	E	

Family	**Species**	**References**[1]	**Status in Korea**
Sapindaceae	*Blighia* sp.	C, E, F	
	Blighia sapida K .D .Koenig	D	
	Dimocarpus longan Lour.[31]	A, E, F	cultivated
	Lepisanthes alata (Blume) Leenh.	E	
	Lepisanthes fruticosa (Roxb.) Leenh.	E, F	
	Lepisanthes rubiginosa (Roxb.) Leenh.	E, F	
	Lepisanthes tetraphylla (Vahl) Radlk.	E, F	
	Litchi chinensis Sonn.	A, E, F	cultivated
	Nephelium cuspidatum Blume var. *eriopetalum* (Miq.) Leenh.	E	
	Nephelium lappaceum L.	A, E, F	cultivated
	Pometia pinnata J. R. Forst. & G. Forst.	E, F	
Sapotaceae	*Chrysophyllum albidum* G. Don	C, D, E, F	
	Chrysophyllum cainito L.	E, F	cultivated
	Chrysophyllum roxburghii G. Don	E	
	Manilkara jaimiqui (C. Wright) Dubard subsp. *emarginata* (L.) Cronquist	E	
	Manilkara sapota (L.) Van Royen	D	
	Manilkara zapota (L.) P. Royen	E, F	cultivated
	Mimusops elengi L.	E, F	
	Palaquium	F	
	Palaquium maingayi (C. B. Clarke) King & Gamble	E, F	
	Planchonella	F	
	Planchonella duclitan (Blanco) Bakh. f.	E, F	
	Pouteria caimito (Ruiz & Pav.) Radlk.	E, F	
	Pouteria campechiana (Kunth) Baehni	E, F	
	Pouteria sapota (Jacq.) H. E. Moore & Stearn	E	
	Pouteria viridis (Pittier) Cronquist	E	
	Vitellaria paradoxa C. F. Gaertn.	C, D, E, F	
Simaroubaceae	*Simarouba glauca* DC.	E	
Solanaceae	*Brugmansia ×candida Pers.*	E	cultivated (*Brugmansia* x*candida* 'Grand Marnier')
	Capsicum annuum L.	A, D, E, F	wild, cultivated
	Capsicum chinense Jacq.	E	
	Capsicum frutescens L.	A, C, D, E, F	
	Capsicum pubescens Ruiz & Pav.	E	
	Cestrum latifolium Lam.	E	

Family	Species	References[1]	Status in Korea
	Cestrum nocturnum L.	E	cultivated
	Datura stramonium L.	E	naturalized
	Lycianthes biflora (Lour.) Bitter	E	
	Nicandra physalodes (L.) Gaertn.	E	naturalized
	Nicotiana glauca Graham	E	
	Nicotiana tabacum L.	E	cultivated
	Physalis angulata L.	E, F	naturalized
	Physalis minima L.	E	
	Physalis peruviana L.	E	
	Physalis philadelphica Lam.	E	
	Physalis pubescens L.	E	
	Solanum americanum Mill.	E	naturalized
	Solanum capsicoides All.	D, E, F	
	Solanum aculeatissimum Jacq.	F	
	Solanum aethiopicum L.	E, F	
	Solanum anguivi Lam.	E	
	Solanum betaceum Cav.	F	
	Solanum donianum Walp.	E	
	Solanum erianthum D. Don	E	
	Solanum grandiflorum Ruiz & Pav.	E	
	Solanum granuloso-leprosum Dunal	E	
	Solanum hazenii Britton	F	
	Solanum incanum L.	D, E, F	
	Solanum lasiocarpum Dunal	E	
	Solanum linnaeanum Hepper & P.-M. L. Jaeger	E	
	Solanum lycopersicum L.[32]	A, D, E, F	cultivated
	Solanum macrocarpon L.	E	
	Solanum mammosum L.	E	
	Solanum mauritianum Scop.	E	
	Solanum melongena L.	E, F	wild, cultivated
	Solanum muricatum Aiton	E	cultivated
	Solanum nigrescens M. Martens & Galeotti	E	
	Solanum nigrum L.	D, E	wild, cultivated, naturalized
	Solanum pimpinellifolium L.	E	
	Solanum pseudocapsicum L.	E	
	Solanum quitoense Lam.	E	

Family	**Species**	**References**[1]	**Status in Korea**
	Solanum rudepannum Dunal	F	
	Solanum scabrum Mill.	E	
	Solanum seaforthianum Andrews	E	
	Solanum sessiliflorum Dunal	E	
	Solanum sodomeum L.	D, F	
	Solanum stramoniifolium Jacq.	E, F	
	Solanum torvum Sw.	E, F	
	Solanum trilobatum L.	E, F	
	Solanum tuberosum L.	E	cultivated
Staphyleaceae	*Turpinia ternata* Nakai	E	
Thymelaeaceae	*Wikstroemia phillyreifolia* A. Gray	E	
Tiliaceae	*Microcos tomentosa* Sm.	E, F	
Vitaceae	*Cissus repens* Lam.	E, F	
	Vitis vinifera L.	E	wild, cultivated
Ximeniaceae	*Ximenia americana* L.	E, F	
Zingiberaceae	*Alpinia mutica* Roxb.	E, F	

[1] References. A: Sakae (1968) B: Syed et al. (1970) C: Ekesi and Billah (2006), D: EPPO (2010), E: Liquido et al. (2015), F: CABI (2018)

[2] written as synonym in Ekesi and Billah (2006) and EPPO (2010); *Spondias cytherea*

[3] corrected from *Exalobus monopetalus* (Liquido et al., 2015)

[4] written as synonym in CABI (2018); *Mitrephora teysmannii*

[5] written as synonym in CABI (2018); *Rollinia pulchrinervia*

[6] written as synonym in CABI (2018); *Veichia merrillii*

[7] written as synonym in CABI (2018); *Cordia alba*

[8] corrected from *Celtis tetranda* (Liquido et al., 2015)

[9] written in EPPO (2010) as followed; *Cordia* sp. cf *myxa*

[10] written as synonym in Syed et al. (1970); *Citrullus vulgaris*

[11] written as synonym in EPPO (2010); *Cucumis figarei*

[12] written as synonym in EPPO, 2010; *Cucumis pepo*

[13] written as synonym in Sakae (1968); *Bryonopsis laciniosa*

[14] corrected from *Inocarpus fagiferus* (Liquido et al., 2015)

[15] written as synonym in Sakae (1968); *Cinnamomum japonicum*

[16] written as Hamabiwa (common name in Japanese) in Sakae (1968)

[17] written as synonym in Sakae (1968); *Artocarpus communis*

[18] written as synonym in CABI (2018); *Artocarpus nitidus*

[19] written as synonym in Sakae (1968); Musa sapientum

[20] written as synonym in CABI (2018); *Myrciaria cauliflora*

[21] written as synonym in Sakae (1968); *Psidium cattleianum*

[22] written as synonym in EPPO (2010); *Psidium littorale*

[23] written as synonym in Liquido et al. (2015); *Eugenia megacarpa*

[24] written as synonym in Liquido et al. (2015); *Breynia reclinata*

[25] corrected from *Zizyphus hysudrica* (Syed, 1970)

[26] written as synonym in Syed et al. (1970); *Zizyphus sativa*

[27] written as synonym in Syed et al. (1970); *Malus pumilla*

[28] written as synonym in Syed et al. (1970); *Pyrus sinensis*

[29] written as synonym in Sakae (1968) and EPPO (2010); *Citrus grandis*

[30] corrected from *Taddalia asiatica* (Liquido et al., 2015)

[31] written as synonym in Sakae (1968); *Euphoria longana*

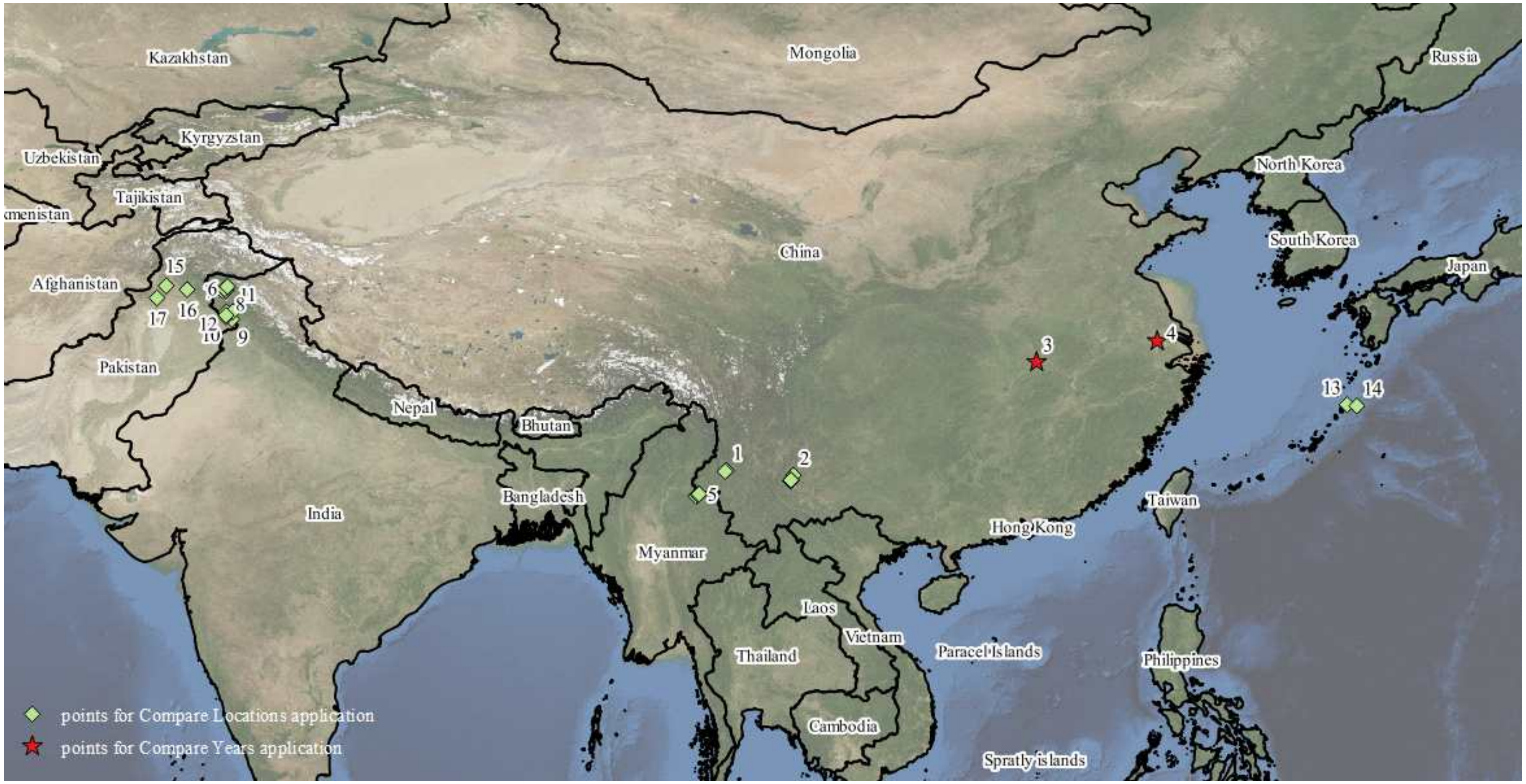
[32] written as synonym in Sakae (1968) and EPPO (2010)0; *Lycopersicon esculentum*

SD Table 4. Infestation rate in several host fruits of *B. dorsalis* complex

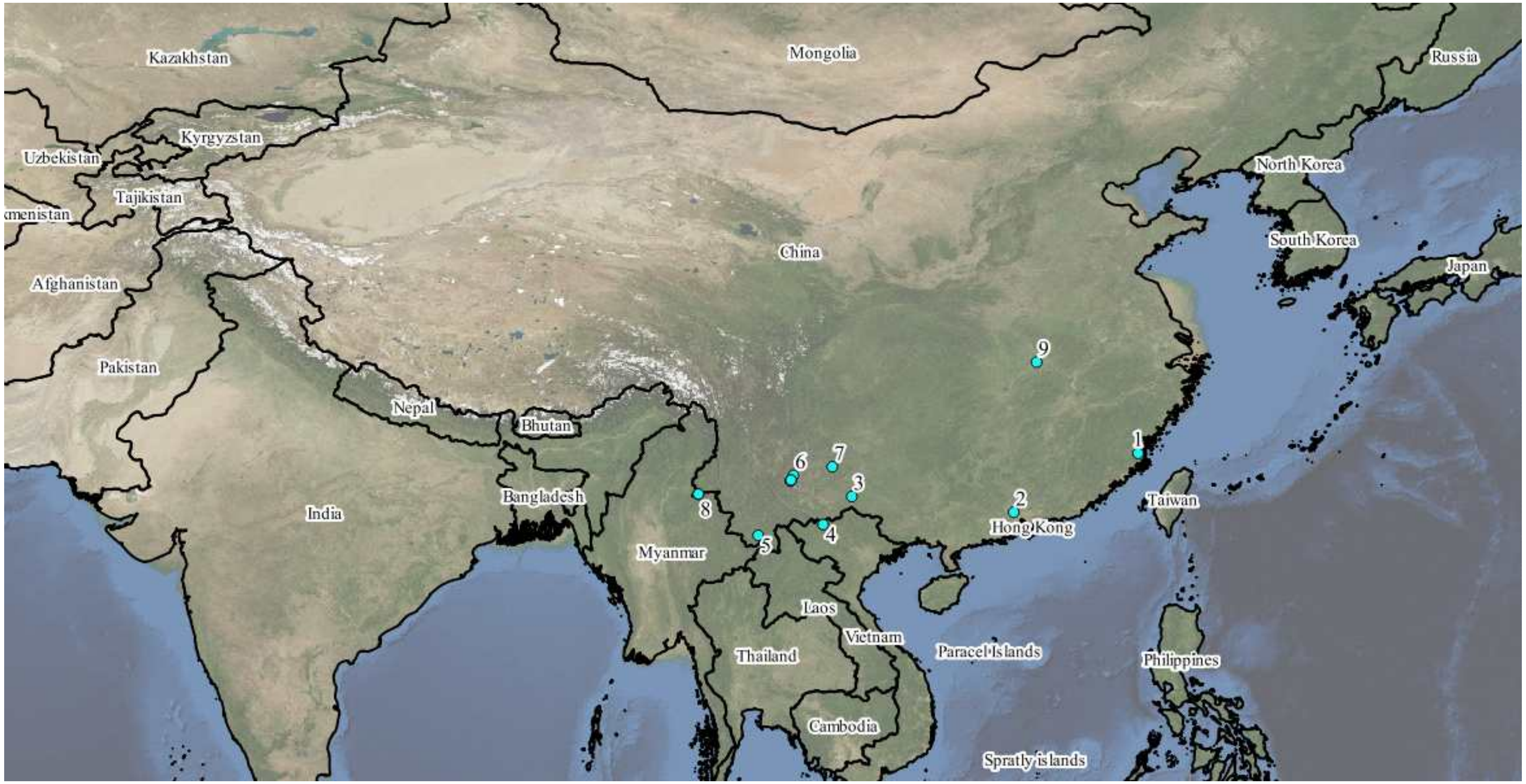
	Country, Locality	Species	% fruit infested	Reference
Annona cherimola Mill.				
	Kenya	*B. invadens*	15~50	Rwonushana et al., 2008
Annona muricata L.				
	Kenya	*B. invadens*	6~20	Rwonushana et al., 2008
Annona squamosa L.				
	Mozambique	*B. invadens*	37	Jose et al., 2013
	Kenya	*B. invadens*	54	Rwonushana et al., 2008
Capsicum annum L.				
	Japan, Okinawa	*B. dorsalis*	3	Yasuda, 1978
Carica papaya L.				
	USA, Hawaii	*B. dorsalis*	55	Clerke et al., 2005
	Japan, Okinawa	*B. dorsalis*	23	Yasuda, 1978
Citrus limon (L.) Burm. f.				
	Kenya	*B. invadens*	0~29	Rwonushana et al., 2008
Citrus reticulata Blanco				
	Kenya	*B. invadens*	10~12	Rwonushana et al., 2008
	Japan, Okinawa	*B. dorsalis*	11	Yasuda, 1978
Citrus sinensis (L.) Osbeck				
	Kenya	*B. invadens*	0~29	Rwonushana et al., 2008
Cordia myxa L.				
	Kenya	*B. invadens*	6	Rwonushana et al., 2008
Diplocyclos palmutus (L.) C.Jeffrey				
	Japan, Okinawa	*B. dorsalis*	2	Yasuda, 1978
Eriobotrya japonica (Thunb.) Lindl.				
	Pakistan	*B. dorsalis*	5~10	Syed et al., 1970
Ficus erecta Thunb.				
	Japan, Okinawa	*B. dorsalis*	2	Yasuda, 1978
Garcinia subelliptica Merr.				
	Japan, Okinawa	*B. dorsalis*	19	Yasuda, 1978
Machilus thunbergii Siebold & Zucc.				
	Japan, Okinawa	*B. dorsalis*	15	Yasuda, 1978
Mangifera indica L.				
	Kenya	*B. invadens*	1~64	Ekesi et al., 2006
		B. invadens	1~60	Rwonushana et al., 2008
	Mozambique	*B. invadens*	57	Jose et al., 2013
	Pakistan	*B. dorsalis*	100	Syed et al., 1970
	India	*B. dorsalis*	0~94	Verghese et al., 2002

Country, Locality	Species	% fruit infested	Reference
	B. dorsalis	0~87	Godse and Bhole, 2003
Mangifera indica L.			
India	*B. dorsalis*	31~88	Mann, 1996
Murraya paniculata (L.) Jack			
Japan, Okinawa	*B. dorsalis*	0.2	Yasuda, 1978
Musa sp. AAA			
Kenya	*B. invadens*	0~36	Rwonushana et al., 2008
Nephelium lappaceum L.			
USA, Hawaii	*B. dorsalis*	0.1	Clerke et al., 2005
Prunus armeniaca L.			
Pakistan	*B. dorsalis*	48	Syed et al., 1970
Prunus bokhariensis Royle ex C.K.Schneid.			
Pakistan	*B. dorsalis*	5~54	Syed et al., 1970
Prunus persica (L.) Batsch.			
Pakistan	*B. dorsalis*	5~14	Syed et al., 1970
Japan, Okinawa	*B. dorsalis*	15	Yasuda, 1978
Psidium guajava L.			
Mozambique	*B. invadens*	92.49	Jose et al., 2013
Kenya	*B. invadens*	12~34	Rwonushana et al., 2008
Pakistan	*B. dorsalis*	5~86	Syed et al., 1970
Japan, Okinawa	*B. dorsalis*	31	Yasuda, 1978
Punica granatum L.			
Mozambique	*B. invadens*	7	Jose et al., 2013
Pyrus pashia Buch.-Ham. ex D.Don			
Pakistan	*B. dorsalis*	20	Syed et al., 1970
Pyrus pyrifolia (Burm. f.) Nakai			
Pakistan	*B. dorsalis*	20~64	Syed et al., 1970
Sclerocarya birrea (A. Rich.) Hochst.			
Kenya	*B. invadens*	36~41	Rwonushana et al., 2008
Solanum lycopersicum L.			
Kenya	*B. invadens*	1~9	Rwonushana et al., 2008
Sorindeia madagascariensis DC.			
Kenya	*B. invadens*	1	Rwonushana et al., 2008
Terminalia catappa L.			
Mozambique	*B. invadens*	67.32	Jose et al., 2013
Kenya	*B. invadens*	19~83	Rwonushana et al., 2008
Japan, Okinawa	*B. dorsalis*	48	Yasuda, 1978
Toddalia asiatica (L.) Lam.			

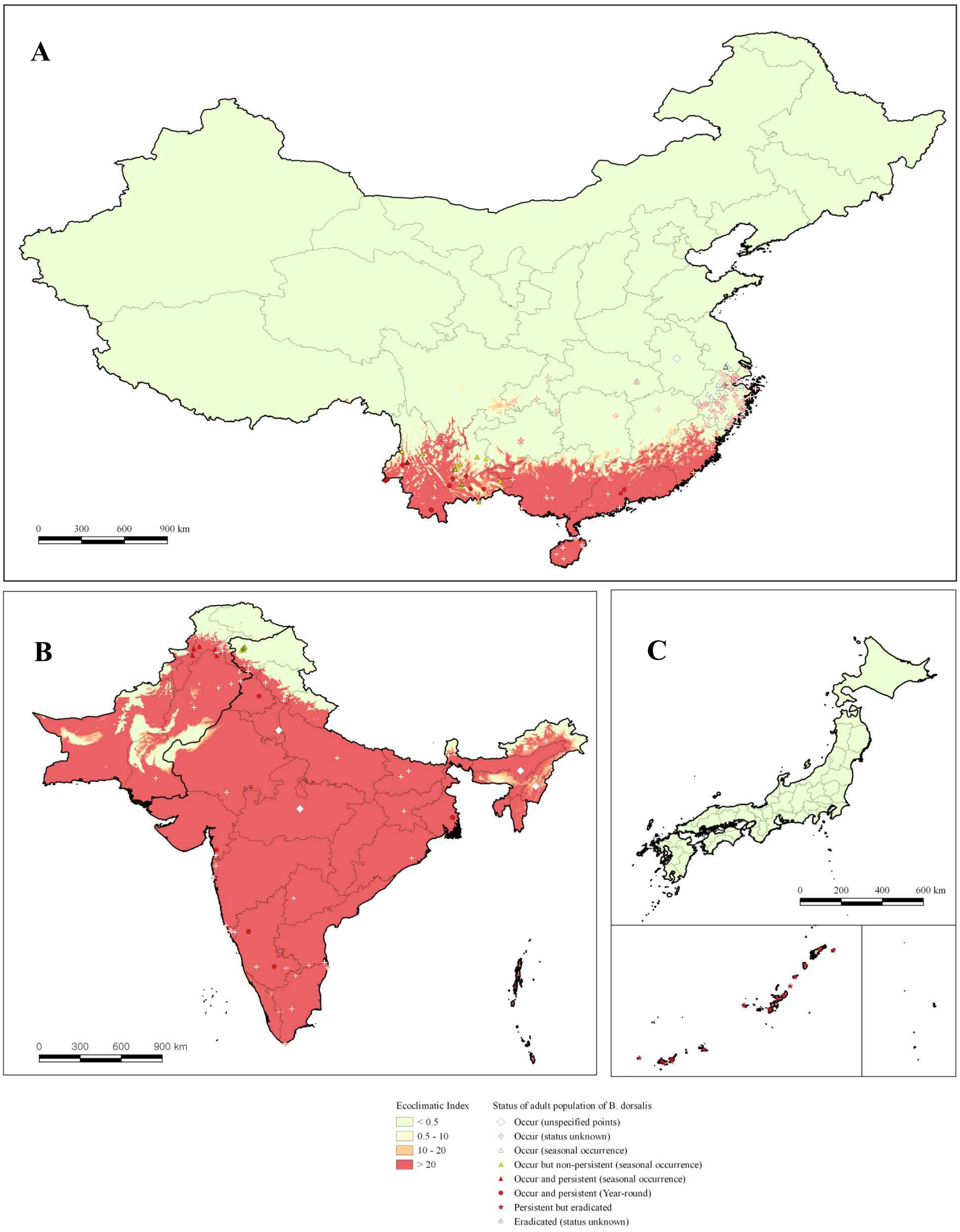
Country, Locality	Species	% fruit infested	Reference
Japan, Okinawa	*B. dorsalis*	2	Yasuda, 1978
Ziziphus jujuba Mill.			
Pakistan	*B. dorsalis*	20~50	Syed et al., 1970



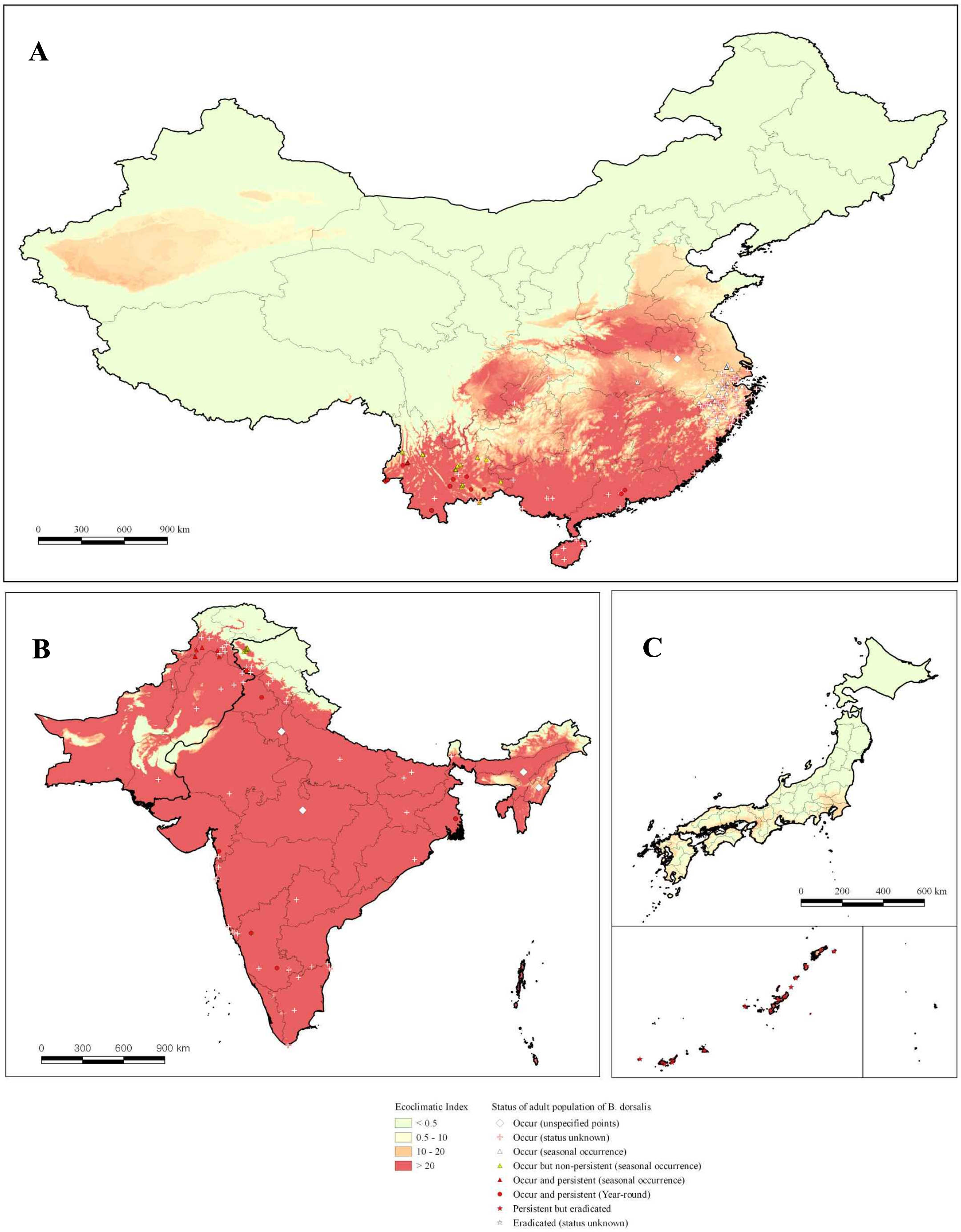
SD Fig. 1. Selected sites to evaluate the cold stress (CS) value in Asia region; (1) Baoshan, (2) Kunming, (3) Wuhan, (4) Wuxi, (5) Ruili, (6) Srinagar, (7) Budgam, (8) Marh, (9) Samba, (10) SKUAST Jammu, (11) Udahampur, (12) Udheywala, (13) Amami, (14) Kikai, (15) Dargai, (16) Haripur and (17) Kohat



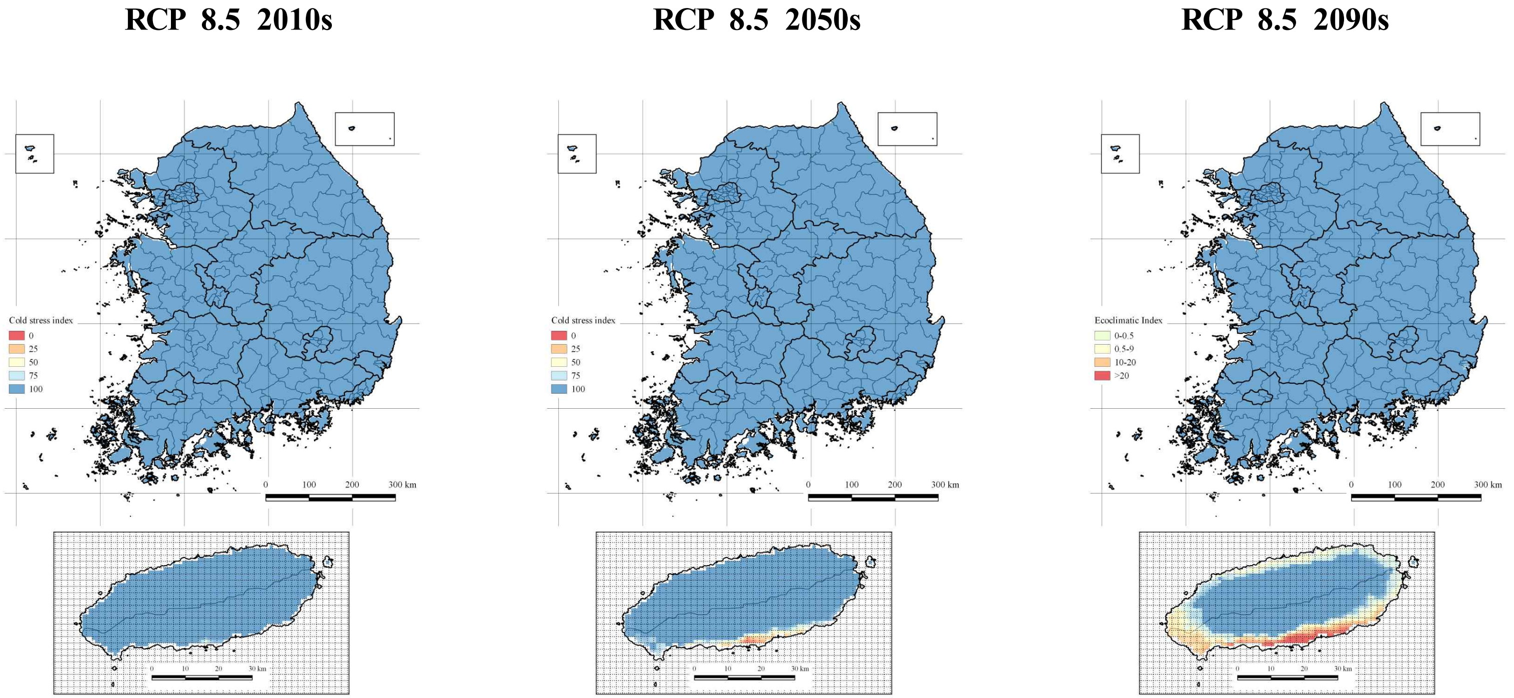
SD Fig. 2. Selected sites to evaluate the generation index (generation per year) in Asia region; (1) Fujian, (2) Guangzhou, (3) Guangnan, (4) Hekou, (5) Jinghong, (6) Kunming, (7) Qujing, (8) Ruili and (9) Wuhan.



SD Fig. 3. Comparison with occurrence status of *B. dorsalis* and model results of ecoclimatic index obtained using species parameters of Scenario 1 in China (A), India and Pakistan (B) and Japan (C).

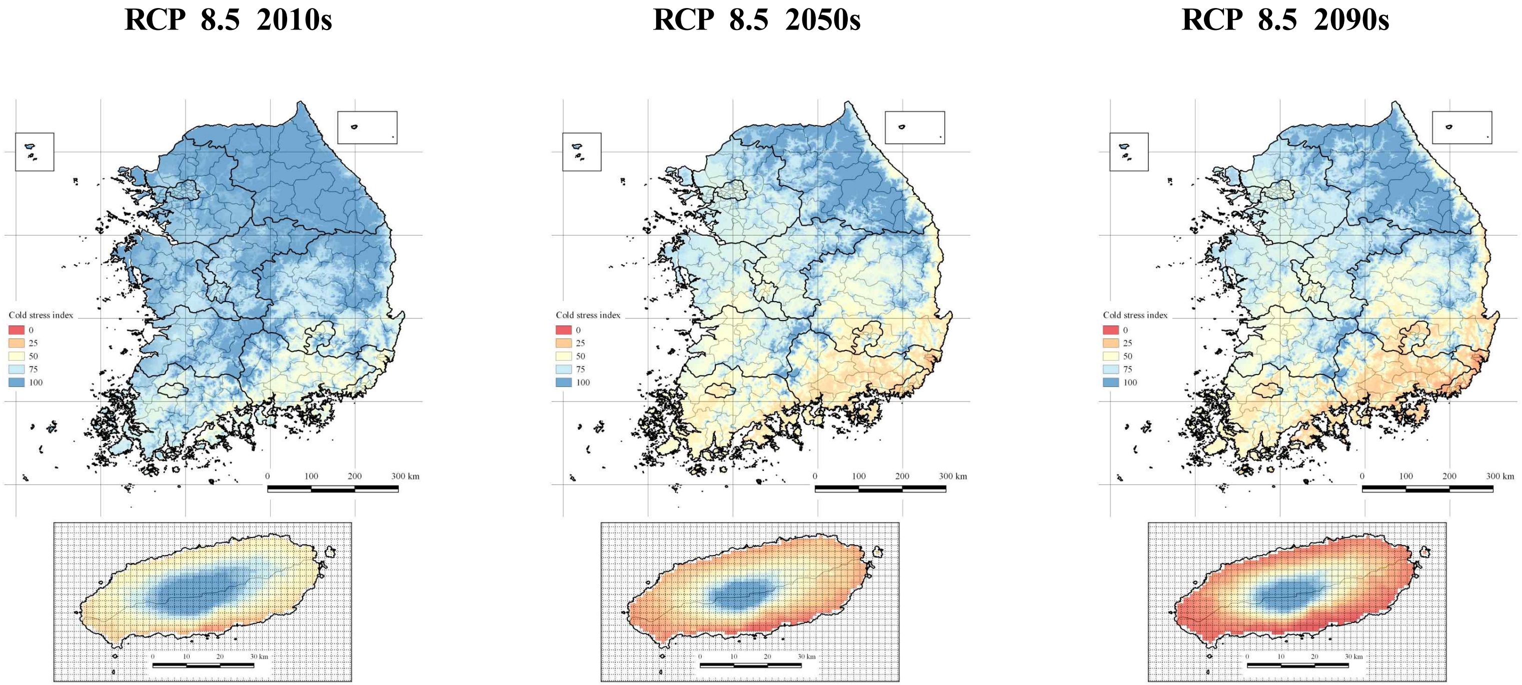


SD Fig. 4. Comparison with occurrence status of *B. dorsalis* and model results of ecoclimatic index obtained using species parameters of Scenario 2 in China (A), India and Pakistan (B) and Japan (C).



RCP 8.5 2010s **RCP 8.5 2050s** **RCP 8.5 2090s**

SD Fig. 5. The projected cold stress for *B. dorsalis* by RCP 8.5 weather scenario in Korea with enlarged in Jeju area, based on parameters of Scenario 1. In Scenario 1, the DHCS of CS parameter was adjusted to satisfy CS value ≈ 21 in Wuhan, China in 2009 (i.e. DHCS = -0.0035 week-1). The criteria of cold stress above 100 means the population can not sustained during winter in the area (Kriticos et al., 2015)



SD Fig. 6. The projected cold stress for *B. dorsalis* by RCP 8.5 weather scenario in Korea with enlarged in Jeju area, based on parameters of Scenario 2. In Scenario 2, the DHCS of CS parameter was adjusted to satisfy CS value ≈ 35 in Wuxi, China in 2006 (i.e. DHCS = -0.0006 week-1). The criteria of cold stress above 100 means the population can not sustained during winter in the area (Kriticos et al., 2015)

SD Table 5. Parameter estimation of food availability curve for each host plant of *B. dorsalis* observed in selected area of Jeju

Species	Class of host plants (preference)		Fruit phenology and general characteristic										
	USDA category[1]	Weight value[2]	Shape of fruit	Diameter	Length	No. fruit per tree	Fruit weight (g)[3]	Recommended planting density (ea/10a)	Yield per area (kg/10)[4]	Yield per tree (g)	Start maturing (Julian date)	End of harvest (Julian date)	Reference[5]
Crinum asiaticum		0.1	Flat oval	25	20	10	2.21			22.08	244	334	A
Diospyros kaki	P	1								5000.00	274	304	B
Machilus thunbergii		0.1	Spherical	11.5	11.5	1000	0.27			268.69	182	243	A
Neolitsea serica		0.1	Spherical	12	12	1000	0.31			305.28	274	304	A
Ficus carica	P	1						167	1900	11377.25	213	304	B
Morus alba		0.1						222	900	4054.05	152	212	B
Opuntia ficus-indica	P	1						9920	5255	529.74	60	151	B
Punica granatum	P	1						926	1814	1958.96	244	304	B
Ziziphus jujuba	U	0.1						42	305	7261.90	244	304	B
Eriobotrya japonica	P	1						111	193	1738.74	151	181	B
Fragaria ananassa		0.1						9000	1450	161.11	182	212	B, C
Malus pumila		0.1						260	1733	6665.38	213	273	B, C
Prunus mume		0.1						56	703	12553.57	152	212	B
Prunus persica	P	1						28	1233	44035.71	202	263	B, C
Pyrus communis	P	1								65000.00	182	304	D
Pyrus pyrifolia		0.1						56	2538	45321.43	213	243	B, C
Fortunella japonica		0.1						83	3180	38313.25	274	334	B
Citrus unshiu	P	1						83	3162	38096.39	305	334	B, C
Citrus unshiu	P	1						83	3162	38096.39	305	365	B, C
Citrus unshiu (overwintered)	P	1						83	3162	38096.39	0	120	B, C

Capsicum annuum	P	1						2857	293	102.56	213	304	B, C
Lycopersicon esculentum	P	1						3704	6590	1779.16	182	243	B, C
Solanum melongena	U	0.1						926	1088	1174.95	182	273	B
Solanum nigrum		0.1	Spherical	6.5	6.5	20	0.05			0.97	244	273	A
Vitis vinifera		0.1						137	1527	11145.99	213	273	B, C

[1] Class of host plants, USDA category (Liquido et al., 2015): P: Preferred host; U: Undetermined

[2] The weight value: 1.0 for USDA category P, 0.1 for U; also, 0.1 was assigned for non-preferred host plants that were not found in USDA category.

[3] calculated by (1/6) x (Fruit length/10) x (Fruit diameter/10)2) * 1.06 (Mutsher et al., N.D)

[4] calculrated by (Fruit weight) * (No. fruits per tree) * 1000(g/kg) or (Yield per area) / (recommended planting density)

[5] Reference for fruit phenology and general characteristic; A: http://www.nature.go.kr; Korea National Arboretum, B: http://www.nongsaro.go.kr; Korea Rural Development Administration, C: http://kostat.go.kr/; Statistics Korea, D: Álvarez-Fernández, 2011

SD Table 6. Estimation of the average no. of *B. dorsalis* adults emerged from infested host fruit (kg)

Hostplant Scientific name	Country,	Fruit fly (FF) species[1]	No. of fruits	Total weight of fruits (kg)[2]	% fruit infested	Infested weight (kg)[3]	No. of infested fruits[4]	No. of FF in infested fruits[5]	No. of FF/fruit	No. of FF/kg in infested fruits[6]	Reference[7]
Mangifera indica	Kenya	inv	113	37.8	1.2*	0.45*	1.0*	1.0		2.2	E
Mangifera indica	Kenya	inv	56	18.2	3.0*	0.55*	2.0*	2.0		3.6	E
Annona squamosa	Kenya	inv	58	13.2	54.1	7.14*	31.0*	33.0		4.6	R
Mangifera indica	Hawaii, USA	dor	84	31.8	100.0	31.75*	84.0	184.0		5.8	H
Psidium guajava	Hawaii, USA	dor	14	3.0	100.0	3.04*	14.0	20.0		6.6	H
Citrus sinensis	Kenya	inv	114	10.4	28.5	2.96*	32.0*	23.0		7.8	R
Litchi chinensis	Hawaii, USA	dor	110	1.6	100.0	1.59	110.0	13.0		8.2	H
Citrus sinensis	Kenya	inv	101	9.8	12.6	1.23*	13.0*	11.0		8.9	R
Mangifera indica	Kenya	inv	36	12.5	8.7*	1.09*	3.0*	10.0		9.2	E
Murraya paniculata	Hawaii, USA	dor	980	0.3	100.0	0.29*	980.0	3.0		10.2	H
Psidium guajava	Kenya	inv	84	9.8	31.3	3.07*	26.0*	41.0		13.4	R
Citrus reticulata	Hawaii	dor	41	4.3	100.0	4.34*	41.0	65.0		15.0	H
Citrus sinensis	Kenya	inv	224	25.6	12.7	3.25*	28.0*	49.0		15.1	R
Mangifera indica	Tanzania	dor	10	2.2	100.0	2.20	10.0	37.0		16.8	M
Mangifera indica	Tanzania	dor	5	1.1	100.0	1.10	5.0	20.0		18.2	M
Mangifera indica.	Kenya	inv	32	11.6	6.8*	0.79*	2.0*	15.0		19.1	E
Lycopersicon esculentum	Kenya	inv	123	1.2	8.7	0.10*	11.0*	2.0		19.2	R
Mangifera indica	Tanzania	dor	10	2.2	100.0	2.20	10.0	45.0		20.5	M
Mangifera indica	Kenya	inv	145	40	31.2	12.48*	45.0*	257.0		20.6	R
Mangifera indica	Tanzania	dor	8	2.4	100.0	2.40*	8.0	50.0		20.8	M
Mangifera indica	Kenya	inv	121	40.5	72.8*	29.48*	88.0*	624.0		21.2	E
Annona muricata	Kenya	inv	16	6.5	6.3	0.41*	1.0*	9.0		22.0	R
Eugenia malaccensis	Hawaii, USA	dor	360	15.7	100.0	15.72*	360.0	350.0		22.3	H
Eugenia jambos	Hawaii, USA	dor	68	1.4	100.0	1.36*	68.0	33.0		24.3	H
Mangifera indica	Kenya	inv	112	29.5	40.2	11.86*	45.0*	296.0		25.0	R
Mangifera indica	Tanzania	dor	2	0.4	100.0	0.40	2.0	10.0		25.0	M
Fortunella japonica	Hawaii, USA	dor	10	0.1	100.0	0.10*	10.0	3.0		28.8	H
Citrus sinensis	Kenya	inv	15	1.9	12.5	0.24*	2.0*	7.0		29.5	R

Mangifera indica	Kenya	inv	55	18.3	56.1*	10.26*	31.0*	303.0		29.5	E
Psidium guajava	Hawaii, USA	dor	42	2.9	100.0	2.86*	42.0	88.0		30.8	H
Mangifera indica	Tanzania	dor	10	2	100.0	2.00	10.0	64.0		32.0	M
Musa sp.	Kenya	inv	262	5.2	36.4	1.89*	95.0*	66.0		34.9	R
Mangifera indica	India	dor	100	26.0*[8]	20.0	5.20*	20.0	182.0*	1.82	35.0	V
Terminalia catappa	Hawaii, USA	dor	600	15.2	100.0	15.20*	600.0	534.0		35.1	H
Eugenia uniflora	Hawaii, USA	dor	70	0.34	100.0	0.34*	70.0	12.0		35.3	H
Citrus reticulata	Kenya	inv	46	4.8	10.3	0.49*	5.0*	18.0		36.4	R
Citrus sinensis	Kenya	inv	31	2.6	12.3	0.32*	4.0*	12.0		37.5	R
Mangifera indica	India	dor	100	26.0	5.0	1.30*	5.0	50.0*	0.50	38.5	V
Mangifera indica	India	dor	100	26.0	34.0	8.84*	34.0	352.0*	3.52	39.8	V
Citrus reticulata	Hawaii, USA	dor	52	3.4	100.0	3.41*	52.0	146.0		42.8	H
Eugenia malaccensis	Hawaii, USA	dor	7	0.3	100.0	0.34*	7.0	15.0		43.6	H
Citrus reticulata	Kenya	inv	40	4.3	12.5	0.54*	5.0*	24.0		44.7	R
Mangifera indica	India	dor	100	26.0*	8.0	2.08*	8.0	94.0*	0.94	45.2	V
Mangifera indica	Kenya	inv	92	30.8	55.8*	17.19*	51.0*	803.0		46.7	E
Mangifera indica	Tanzania	dor	10	1.9	100.0	1.90	10.0	92.0		48.4	M
Musa sp.	Kenya	inv	145	9.3	12.1	1.13*	18.0*	55.0		48.9	R
Psidium guajava	Kenya	inv	32	3.6	34.4	1.24*	11.0*	61.0		49.3	R
Mangifera indica	India	dor	100	26.0*	21.4	5.56*	21.4	286.0*	2.86	51.4	V
Terminalia catappa	Hawaii, USA	dor	1439	37.1	100.0	37.10*	1439.0	2215.0		59.7	H
Mangifera indica	India	dor	100	26.0*	4.0	1.04*	4.0	64.0*	0.64	61.5	V
Psidium cattleyanum	Hawaii, USA	dor	180	3.2	100.0	3.20*	180.0	197.0		61.6	H
Mangifera indica	Kenya	inv	454	148.6	57.5	85.45*	261.0*	5830.0		68.2	R
Mangifera indica	India	dor	100	26.0*	54.0	14.04*	54.0	1018.0*	10.18	72.5	V
Mangifera indica	Kenya	inv	204	72.9	40.2	29.31*	82.0*	2141.0		73.1	R
Musa sp.	Kenya	inv	132	2.8	10.2	0.29*	13.0*	21.0		73.5	R
Mangifera indica	India	dor	100	26.0*	2.0	0.52*	2.0	42.0*	0.42	80.8	V
Mangifera indica	India	dor	100	26.0*	6.0	1.56*	6.0	126.0*	1.26	80.8	V
Eugenia uniflora	Hawaii, USA	dor	200	0.9	100.0	0.94*	200.0	78.0		83.4	H
Mangifera indica	India	dor	100	26.0*	94.0	24.44*	94.0	2054.0*	20.54	84.0	V
Terminalia catappa	Kenya	inv	16	0.4	18.8	0.08*	3.0*	7.0		93.1	R
Mangifera indica	Kenya	inv	51	17.5	63.9*	11.18*	33.0*	1056.0		94.4	E
Annona cherimola	Kenya	inv	35	0.7	31.4	0.22*	11.0*	21.0		95.5	R
Sclerocarya birrea	Kenya	inv	154	3.1	41.3	1.28*	64.0*	123.0		96.1	R

Psidium guajava	Kenya	inv	31	3.1	12.0	0.37*	4.0*	36.0		96.8	R
Mangifera indica	India	dor	100	26.0*	18.0	4.68*	18.0	466.0*	4.66	99.6	V
Mangifera indica	India	dor	100	26.0*	14.0	3.64*	14.0	368.0*	3.68	101.1	V
Citrus limon	Kenya	inv	21	3	28.6	0.86*	6.0*	97.0		113.1	R
Mangifera indica	India	dor	100	26.0*	24.0	6.24*	24.0	710.0*	7.10	113.8	V
Annona cherimola	Kenya	inv	86	2.2	23.5	0.52*	20.0*	62.0		119.9	R
Mangifera indica	India	dor	100	26.0*	20.0	5.20*	20.0	644.0*	6.44	123.8	V
Clausena lansium	Hawaii, USA	dor	170	1.7	100.0	1.66*	170.0	209.0		125.9	H
Mangifera indica	India	dor	100	26.0*	12.0	3.12*	12.0	398.0*	3.98	127.6	V
Eugenia uniflora	Hawaii, USA	dor	62	0.23	100.0	0.23*	62.0	31.0		133.0	H
Psidium cattleyanum	Hawaii, USA	dor	521	5.0	100.0	5.01*	521.0	705.0		140.7	H
Mangifera indica	Kenya	inv	206	65.9	64.4	42.44*	133.0*	6012.0		141.7	R
Eugenia jambos	Hawaii, USA	dor	54	0.3	100.0	0.32*	54.0	47.0		146.4	H
Mangifera indica	India	dor	100	26.0*	38.0	9.88*	38.0	1640.0*	16.40	166.0	V
Annona cherimola	Kenya	inv	6	0.6	50.0	0.30*	3.0*	51.0		170.0	R
Mangifera indica	Kenya	inv	43	13.2	50.8	6.71*	22.0*	1204.0		179.6	R
Mangifera indica	India	dor	100	26.0	6.0	1.56*	6.0	322.0*	3.22	206.4	V
Eugenia uniflora	Hawaii, USA	dor	140	0.5	100.0	0.51*	140.0	106.0		207.8	H
Murraya paniculata	Hawaii, USA	dor	12458	5.3	100.0	5.25*	12458.0	1103.0		210.1	H
Mangifera indica	Kenya	inv	119	38.4	59.7	22.92*	71.0*	5004.0		218.3	R
Psidium cattleyanum	Hawaii, USA	dor	65	0.5	100.0	0.45*	65.0	112.0		246.7	H
Murraya paniculata	Hawaii, USA	dor	520	0.2	100.0	0.22*	520.0	56.0		251.1	H
Murraya paniculata	Hawaii, USA	dor	4165	1.6	100.0	1.55*	4165.0	416.0		268.4	H
Cordia myxa	Kenya	inv	33	0.6	6.1	0.04*	2.0*	10.0		273.2	R
Terminalia catappa	Kenya	inv	121	3.6	35.2	1.27*	43.0*	443.0		349.6	R
Murraya paniculata	Hawaii, USA	dor	1866	0.8	100.0	0.76*	1866.0	268.0		352.6	H
Annona cherimola	Kenya	inv	40	1.1	15.0	0.17*	6.0*	59.0		357.6	R
Murraya paniculata	Hawaii, USA	dor	3620	1.9	100.0	1.86*	3620.0	737.0		396.2	H
Musa sp.	Kenya	inv	9	0.9	33.3	0.30*	3.0*	123.0		410.4	R
Murraya paniculata	Hawaii, USA	dor	11301	4.8	100.0	4.76*	11301.0	2353.0		494.3	H
Murraya paniculata	Hawaii, USA	dor	1544	1.1	100.0	1.05*	1544.0	552.0		525.7	H
Sclerocarya birrea	Kenya	inv	127	2.5	36.2	0.91*	46.0*	597.0		659.7	R
Terminalia catappa	Kenya	inv	92	3.2	83.9	2.68*	77.0*	2089.0		778.1	R
Sorindeia	Kenya	inv	108	0.1	1.0	0.00*	1.0*	1.0		1000.0	R

madagascariensis												
Murraya paniculata	Hawaii, USA	dor	4547	1.8		100.0	1.77*	4547.0	2224.0		1256.5	H
										Average no. of FF /kg	132.54	
										Fruit wight (g)/FF	7.54	

[1] represent surveyed species as followed; dor = *B. dorsalis*, inv = *B. invadens*

[2] calculated by (Fruit weight (g)) * (No of fruits) /1000

[3] calculated by (Total weight of fruit) * (% fruit infested) / 100

[4] calculated by (No of fruits) * (% fruit infested)

[5] calculated by (No of fruits) * (No. of FF/fruit)

[6] calculated by (No. of FF in infested fruits) / (Infested weight (kg))

[7] data obtained from; H: Harris and Lee, 1987, V: Veghese et al., 2002, M: Mwatawala et al., 2004, E: Ekesi et al., 2006, R: Rwonushana et al., 2008

[8] estimated from mango weight average of other data.

* calculated value

사 사

백지와 다름없이 이곳에 들어섰습니다. 많음 배움과 많은 시행착오가 있었지만 그래도 제게 제대로 설 수 있으리라 해 주시고 부족하나마 쌓아온 것들이 결실을 맺도록 오랜 기간 동안 인내하여 지도해주신 김동순 교수님 감사드립니다.

바쁘신 와중에도 불구하고 정성들여 논문을 검토하고 부족한 부분을 지도해주신 전용철 교수님, 송정흡 연구관님, 이종호 연구관님, 박정준 교수님 큰 감사의 말씀 올립니다. 또한 많은 관심 주시고 조언을 아끼지 않으셨던 현해남 교수님, 김주성 교수님, 정용석 교수님 무척 감사드립니다. 저희 학생들을 위해 많은 지도편달 해주셨던 강열길 교수님, 송창길 교수님께도 큰 감사 올립니다. 저는 아직 부족한 것이 많습니다. 그렇지만 앞으로 더욱 정진하여 그 은혜를 갚아나가고자 합니다.

미숙한 한 사람으로써 한 편의 논문을 내기까지 많은 도움이 필요하였습니다. 시간과 노력이라는 물리적인 것들 뿐 아니라 자리와 연령을 불문한 주변의 많은 도움과 조언들이 저에게 큰 힘이 되었습니다. 노고를 같이 해주신 김용근 선생님, 권순화 박사님 마음 깊이 감사드리고 경훈, 건, 성오, 명수, 상희, 희정이, 진우 모두 많은 시간 함께 고생했고 너무 감사합니다. 그리고 신용균 선생님, 장용석 박사님, 김경범 선생님, 이영돈 선생님, 양진영 선생님께, 그리고 정훈이에게 많은 도움을 받았고 감사드립니다. 덕분에 이렇게 달려올 수 있었습니다.

더불어 모든 일에 있어서 원동력을 불어넣어주신 그리고 헤메지 않도록 모범이 되어주신 현승용 박사님, 양경식 선생님, 최경산 박사님, 좌명은 선생님, 민동원 선생님 마음 깊이 감사드립니다. 친애하는 우리 학과 선후배분들, 여학우 동기 친구들, 사대부고 자연반 친구들과 혁만 오빠, 준희 언니, 수아 항상 고맙고 감사드리며 받았던 관심과 사랑을 기반으로 스스로를 돌아보며 계속해서 앞으로도 노력해나갈 것입니다.

끝으로 지금의 저를 있게 해주신 어머니 아버지, 사랑하는 지현언니와 명지언니, 소운이, 영빈이, 그리고 은사 강현주 선생님 언제나 감사드립니다.