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Demography and Uncertainty of Population Growth of *Conogethes punctiferalis* (Lepidoptera: Crambidae) Reared on Five Host Plants With Discussion on Some Life History Statistics

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Abstract

The development, survival, and fecundity data of *Conogethes punctiferalis* (Guenée) (Lepidoptera: Crambidae) reared on chestnut (*Castanea mollissima* Blume), maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.), hawthorn (*Crataegus pinnatifida* Bunge), and apple (*Malus domestica* Miller) were collected at 25 ± 1°C and 70 ± 5% RH. Raw data were analyzed and compared by using the age-stage, two-sex life table. The mean fecundity (*F*) was the highest (282.3 eggs per female) when larvae were reared on chestnut. The lowest mean fecundity (19.2 eggs per female) occurred on apple. The net reproductive rates (R_0) were 134.52, 106.77, 30.29, 27.61, and 8.63 offspring on chestnut, maize, sunflower, hawthorn, and apple, respectively. The intrinsic rates of increase (*r*) were 0.1359, 0.1326, 0.0807, 0.0811, and 0.0448 d^{-1} on chestnut, maize, sunflower, hawthorn, and apple, respectively. Computer projections based on the age-stage, two-sex life table revealed the stage structure and variability of the population growth of *C. punctiferalis*. Our results demonstrated that although chestnut and maize were the most suitable host plants for *C. punctiferalis*, the moths were also able to develop and reproduce on sunflower, hawthorn, and apple.

Key words: *Conogethes punctiferalis*, life table, demographic characteristics, host plants

The yellow peach moth, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Crambidae), is an important polyphagous pest distributed widely throughout tropical regions of Asia from India through southeastern Asia and into Australia (Sekiguchi 1974, Waterhouse 1993, Luo 2015). It is responsible for causing serious damage to over 40 species of fruits, field crops, and forest trees, including peach, apple, plum, hawthorn, chestnut, maize, durian, citrus, papaya, maize, sorghum, sunflower, castor, masson pine, and others (Sekiguchi 1974; Waterhouse 1993; Lin et al. 1995; Wang et al. 2006).

Over the past 20 yr, *C. punctiferalis* has caused serious damage to maize in the Huang-Huai-Hai region of eastern China, one of the major maize-growing areas in the country. When feeding on maize, *C. punctiferalis* larvae generally infest the ear with many larvae clustering and damaging individual maize ears, causing serious yield loss. The damage caused by *C. punctiferalis* during the ear stage will often aggravate the occurrence of ear rot diseases, resulting in additional serious loss in yield (Yang et al. 2015, Liu et al. 2017). In recent years, as a result of adjustments to the crop system,

climatic changes, and ineffective pest management, the impact from *C. punctiferalis* has increased substantially in China, especially in the Huang-Huai-Hai region. The population and amount of damage caused by *C. punctiferalis* have surpassed those of another major maize borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), becoming the primary pest in maize fields (Wang et al. 2006).

In order to precisely predict pest population growth and coordinate the timing of control strategies in integrated pest management, it is crucial to understand the survival, development, longevity, fecundity, and other demographic parameters of the target pest under different environmental conditions. Because all of the above data can be obtained through the construction of life tables, the life table has become one of the most important tools of population ecology and pest management (Chi 1988, Huang et al. 2018). Traditional age-specific life tables (Lotka 1907, Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) deal only with female individuals while ignoring male individuals, do not consider variability in the developmental rate among individuals, and cannot precisely take into account preadult

mortality. The application of traditional female age-specific life tables to a two-sex population will inevitably result in erroneous results (Huang and Chi 2012, Huang et al. 2018), including their inability to accurately predict the growth of a population and the extent of its damage to crops (Chi 1988, Chi and Yang 2003, Chi and Su 2006). In contrast to traditional female age-specific life tables, the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) not only takes the variability in development rate among individuals into account, but also the total population (males and females, plus those that die prior to reaching adulthood). In addition, population projection can reveal the dynamics of stage structure during the growth of a population, which is essential for successful pest management (Chi 1990, Huang et al. 2018). The two-sex life table has been applied to a wide variety of insect and mite species, e.g., *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) (Hu et al. 2010), *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) (Huang and Chi 2013), *Athetis lepigone* (Möschler) (Lepidoptera: Noctuidae) (Rong 2016), and *Luciaphorus perniciosus* Rack (Acari: Pygmephoridae) (Bussaman et al. 2017).

Due to the increasing impact of *C. punctiferalis* on maize production, knowledge of its life table is needed for ecological studies and, especially, local pest management programs. Although *C. punctiferalis* is polyphagous, each individual generally feeds only on a single host plant throughout its lifespan. Therefore, it is necessary to ultimately develop life tables on different host plants. To determine the demographic characteristics and to construct a comprehensive knowledge base for *C. punctiferalis*, we collected detailed life history data on the development, survival, and reproduction of moths reared on five host plants, i.e., chestnut (*Castanea mollissima* Blume), maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.), hawthorn (*Crataegus pinnatifida* Bunge), and apple (*Malus domestica* Miller). We analyzed the life history raw data using the age-stage, two-sex life table and then used population projection to show the change of stage structure and its variability during population growth. We also discussed some commonly used life history parameters, i.e., the sex ratio, the oviposition period, oviposition days, and mean daily fecundity, and proposed several formulae for their innovative analysis and interpretation.

Materials and Methods

Insects
Individuals of *C. punctiferalis* were originally collected from an experimental field (36° 10′18″ N, 117° 09′23″ E) at Shandong Agricultural University, Tai'an, China, in August and September 2016, and subsequently laboratory reared for five generations. Larvae were reared on fruits or seeds of chestnut, maize, sunflower, hawthorn, and apple. Insects were kept in a RXZ Series Artificial Climate Box set at 25 ± 1°C, 70 ± 5% RH, and a photoperiod of 15:9 (L:D) h. Newly emerged moths were kept in nylon mesh cages (35 × 35 × 35 cm) under the above conditions and provided with a gauze-wrapped cotton-wool pad moistened with a 10% honey solution. A slice of apple wrapped with gauze was supplied for oviposition.

Host Plants (Diets)
All of the host plants involved in the study, chestnut kernel, maize kernel, sunflower seeds without pericarp, hawthorn fruit, and apple fruit, were adapted to Tai'an city, Shandong province, China.

Life-Table Study
Prior to initiating the life-table study, the larvae were reared for one generation on the different diets (chestnut kernels, maize kernels, sunflower seeds, hawthorn fruits, and apple fruits) in a RXZ Series Artificial Climate Box set at 25 ± 1°C. According to Mou et al. (2015), we used only viable eggs to precisely estimate the population parameters. The viable eggs were randomly selected according to Ai et al. (2014) for life-table analysis in each treatment. The total numbers of eggs used were 170, 106, 188, 189, and 207 eggs for chestnut, maize, sunflower, hawthorn, and apple, respectively. Eggs were kept in Petri dishes lined with a moistened filter paper until the larvae hatched. Hatched larvae were individually moved to six-well cell culture plates and supplied with fresh diet daily. Because larvae of *C. punctiferalis* feed on or in the rearing media and usually spin a silk cocoon, frequent examination would disturb their feeding and consequently slow their development, lower survival rates, and decrease fecundity. Since the body size of larvae significantly increases from the second to third instar and the stage differentiation can be easily identified during this period, we grouped the first and second instars as L1–L2 and the third to fifth instars as L3–L5 to avoid frequent disturbance. The survival of the larvae, however, was observed and recorded, daily. Emerging adults were paired and kept together in nylon mesh cages (35 × 35 × 35 cm), and provided with a gauze-wrapped cotton-wool pad moistened with a 10% honey solution. An apple wrapped with gauze was supplied for oviposition as described by Honda (1979). Because one pair of adults per cage resulted in low mating rates and fecundity in a preliminary study, five pairs of adults were kept in each cage to determine the daily fecundity. The total viable eggs produced by five females were recorded every 24 hr and the mean fecundity was assigned to each surviving female. The fecundity was checked daily until the deaths of all individuals. All experiments were conducted at 25 ± 1°C, 70 ± 5% RH, and a photoperiod L:D (15:9) h.

Life-Table Analysis
Life history data were analyzed according to the age-stage, two-sex life-table theory (Chi and Liu 1985; Chi 1988), using the computer program TWOSEX-MSChart (Chi 2017b). Following Chi and Liu (1985), the age-stage-specific survival rate (s_{xj}) (where x is the age and j is the stage), age-stage-specific fecundity (f_{xj}), age-specific survival (l_x), age-specific fecundity (m_x), and demographic parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and T, mean generation time) were calculated.

The intrinsic rate of increase (r) was estimated by using the iterative bisection method and the Euler–Lotka equation with the age indexed from 0 (Goodman 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \qquad (1)$$

The life expectancy (e_{xj}), which is the length of time that an individual of age x and stage j is expected to survive, was calculated according to Chi and Su (2006). The contribution of an individual of age x and stage j to the future population (v_{xj}) (Fisher 1930) was calculated according to Tuan et al. (2014a,b). To get stable estimates of the standard errors of the demographic parameters, we used the bootstrap technique with 100,000 replications. Differences between treatments were calculated by using the paired bootstrap test (Efron and Tibshirani 1993, Akca et al. 2015).

Population Projection

The potential growth of *C. punctiferalis* populations on the five rearing media was projected according to Chi (1990) by incorporating the life-table data into the program TIMING-MSChart (Chi 2017a). The variability of population growth was projected according to Huang et al. (2018) by using the life tables representing the 0.025th and 0.975th percentiles of the bootstrap results of the finite rate of increase.

Results

Basic Life History Statistics of *C. punctiferalis*

The developmental times for each stage are listed in Table 1. The length of the egg stage in the different treatments ranged from 4.00 to 4.28 d. The total larva duration was 15.5, 14.7, 20.4, 21.6, and 27.9 d on chestnut, maize, sunflower, hawthorn, and apple, respectively. The larval duration of *C. punctiferalis* reared on maize was significantly shorter than other treatments, while the larval duration reared on apple was significantly longer. The pupal duration in the different treatments ranged from 9.4 to 10.4 d. The pupal duration on maize was significantly shorter than it was in other treatments.

The total number of emerged adult females (N_f) was 81, 52, 54, 74, and 93 on chestnut, maize, sunflower, hawthorn, and apple, respectively, while the number of emerged male adults (N_m) was 74, 46, 50, 70, and 61. The preadult survival rates (s_a) on the above hosts were 91.2, 92.5, 55.3, 76.2, and 74.4%, respectively (Table 1). The adult longevity on maize (12.6 d) was the longest and was significantly longer than all other treatments. The insects reared on chestnuts had the second longest adult longevity (10.6 d). The total lifespan of *C. punctiferalis* reared on sunflowers was significantly shorter (35.1 d) than those reared on other hosts, while moths reared on apple had the longest (46.6 d) total lifespan. The adult

pre-oviposition period of *C. punctiferalis* was the shortest (2.3 d) when reared on chestnut and the longest (3.3 d) on apple. The total pre-oviposition period (TPOP) of *C. punctiferalis* was the shortest when reared on maize (31.9 d), while those reared on apples had the longest (44.8 d).

The mean fecundities (F) of female adults (N_f) were significantly different among all treatments. The greatest mean fecundity (282.3 eggs) was observed on chestnut and the lowest (19.2 eggs) on apple. When only reproductive females (N_{fr}), i.e., those females actually laying viable eggs, were used to calculate the mean fecundity of reproductive females (F_r), the F_r values were generally higher than F (Table 1). The number of oviposition days (O_d) on chestnut (7.8 d) and maize (8.3 d) was significantly greater than the other three treatments. The mean number of eggs laid during each oviposition day (E_d) was the greatest on chestnut (36.4 eggs), which was almost 10-fold of that on apple (3.8 eggs). The lowest proportion of females in a cohort (N_f/N) was observed when reared on sunflowers (0.287); there were no significant differences among the other four treatments (ranging from 0.392 to 0.491). Higher proportions of males in a cohort (N_m/N) were observed on chestnut (0.435) and maize (0.434) compared with percentages on the other three. In most instances, no significant differences were noted between the N_f/N and N_m/N values; the exception, however, occurred when reared on apple where the female proportion ($N_f/N = 0.449$) was significantly higher than the male proportion ($N_m/N = 0.295$). The pupal weights of *C. punctiferalis* were significantly heavier on chestnut, maize, and sunflower than those on hawthorn and apple.

Demographic Parameters

The demographic parameters, including the net reproductive rate (R_0), mean generation time (T), intrinsic rate of increase (r), and finite rate (λ) are listed in Table 2. The net reproductive rates (R_0)

Table 1. Means and SE of the developmental durations, adult longevity, APOP, TPOP, fecundity, female proportion in cohort (N_f/N), male proportion in cohort (N_m/N), and pupal weight of *C. punctiferalis* reared on five host plants

Statistics	Host plants (cohort size)				
	Chestnut (170)	Maize (106)	Sunflower (188)	Hawthorn (189)	Apple (207)
Development duration (d)					
Egg	4.28 ± 0.05a	4.09 ± 0.04cd	4.22 ± 0.04ab	4.16 ± 0.04bc	4.00 ± 0.03d
1st to 2nd instars	5.4 ± 0.1d	5.2 ± 0.1d	6.2 ± 0.1b	5.8 ± 0.1c	6.6 ± 0.1a
3rd to 5th instars	10.1 ± 0.1d	9.8 ± 0.2d	14.1 ± 0.3c	15.4 ± 0.2b	21.8 ± 0.1a
Total larval stage	15.5 ± 0.2de	14.7 ± 0.5e	20.4 ± 0.4c	21.6 ± 0.4bc	27.9 ± 0.6a
Pupa	10.4 ± 0.1a	9.4 ± 0.1b	10.3 ± 0.1a	10.2 ± 0.1a	10.2 ± 0.1a
Total preadult stage	30.1 ± 0.1c	28.6 ± 0.3d	34.9 ± 0.3b	35.3 ± 0.3b	40.9 ± 0.4a
Preadult survival rate (s_a)	0.912 ± 0.022a	0.925 ± 0.026a	0.553 ± 0.036c	0.762 ± 0.031b	0.744 ± 0.030b
Adult longevity (d)	10.6 ± 0.2b	12.6 ± 0.6a	7.6 ± 0.4c	8.3 ± 0.2c	8.4 ± 0.3c
APOP (d)	2.3 ± 0.5c	2.8 ± 0.1b	3.1 ± 0.2ab	3.0 ± 0.1b	3.3 ± 0.1a
TPOP (d)	32.2 ± 0.2c	31.9 ± 0.4c	38.6 ± 0.5b	37.6 ± 0.4b	44.8 ± 0.6a
Total life span (d)	38.6 ± 0.6c	39.8 ± 0.7bc	35.1 ± 0.8d	41.0 ± 0.6b	46.6 ± 0.8a
Fecundity (F) (eggs)	282.3 ± 11.1a	217.7 ± 17.9b	105.5 ± 12.3c	70.5 ± 6.2d	19.2 ± 1.7e
Oviposition days O_d (d)	7.8 ± 0.3a	8.3 ± 0.5a	6.1 ± 0.6b	6.1b ± 0.3b	5.7 ± 0.3b
Eggs/oviposition day (E_d)	36.4 ± 0.7a	26.7 ± 1.0b	23.0 ± 0.7c	11.8 ± 0.4d	3.8 ± 0.1e
Fecundity (F_r) (eggs)	282.3 ± 11.1a	221.9 ± 17.7b	138.9 ± 12.1c	72.5 ± 6.0d	21.5 ± 1.7e
Female proportion (N_f/N)	0.476 ± 0.038aA	0.491 ± 0.049aA	0.287 ± 0.033bA	0.392 ± 0.038aA	0.449 ± 0.035aA
Male proportion (N_m/N)	0.435 ± 0.038aA	0.434 ± 0.048aA	0.226 ± 0.032cA	0.370 ± 0.035abA	0.295 ± 0.032bcB
N_{fr}/N_f ratio	1.000 ± 0.000a	0.981 ± 0.019a	0.759 ± 0.059c	0.971 ± 0.019a	0.892 ± 0.032b
N_f, N_{fr}, N_m, N_n	81, 81, 74, 15	52, 51, 46, 8	54, 41, 50, 84	74, 72, 70, 45	93, 83, 61, 53
Pupal weight (mg)	69.8 ± 2.02a	74.22 ± 1.77a	71.59 ± 1.70a	46.80 ± 1.33b	33.06 ± 1.69c

APOP, adult pre-oviposition period; TPOP, total pre-oviposition period.

Means within a row followed by the same lowercase letter are not significantly different according to the paired bootstrap test at 5% level.

Means of the female and male proportion in the same treatment followed by the different upper-case letter denotes significant difference in proportion of sex.

were 134.52, 106.77, 30.29, 27.61, and 8.63 offspring on chestnut, maize, sunflower, hawthorn, and apple, respectively. The R_0 values on chestnut and maize were significantly higher than the other three treatments. The highest intrinsic rate of increase (r) and finite rate (λ) for *C. punctiferalis* were observed on chestnut ($r = 0.1359$ d^{-1}, $\lambda = 1.1456$ d^{-1}) and maize ($r = 0.1326$ d^{-1}, $\lambda = 1.1442$ d^{-1}), which were significantly higher than those in the other three treatments; the lowest r and λ values were observed on apple ($r = 0.0448$ d^{-1} and $\lambda = 1.0458$ d^{-1}). The mean generation time (T) ranged from the shortest (35.21 d) on chestnut to the longest (48.11 d) on apple.

The survival rate curves (s_{xj}) of *C. punctiferalis* reared on five diets are shown in Figure 1. These curves show the probability that

an egg will survive to age x and stage j. The higher curves observed in female adults show the higher proportion of N_f/N when compared with N_m/N. Due to the variable developmental rates that occur among individuals, overlapping between stages can be observed. The curves for both sexes on chestnut and maize were significantly higher those in the other three treatments reflecting the higher preadult survival rates on these hosts.

The age-specific survival rate (l_x), female age-stage-specific fecundity (f_{x5}) (the female adult being the fifth life stage), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *C. punctiferalis* reared on different diets are shown in Figure 2. The l_x is the probability that a newly laid egg will survive to age x and is calculated by pooling all surviving individuals of both sexes with those that died

Table 2. Mean (±SE) of demographic parameters of *C. punctiferalis* reared on five host plants: the net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T)

Parameters	Host plants				
	Chestnut	Maize	Sunflower	Hawthorn	Apple
R_0 (offspring)	134.52 ± 11.98a	106.77 ± 13.74a	30.29 ± 4.93b	27.61 ± 3.41b	8.63 ± 1.01c
r (d^{-1})	0.1359 ± 0.0025a	0.1326 ± 0.0046a	0.0807 ± 0.0040b	0.0811 ± 0.0033b	0.0448 ± 0.0026c
λ (d^{-1})	1.1456 ± 0.0029a	1.1442 ± 0.0050a	1.0841 ± 0.0043b	1.0844 ± 0.0036b	1.0458 ± 0.0027c
T (d)	36.06 ± 0.21c	35.21 ± 0.44c	42.26 ± 0.61b	40.93 ± 0.43b	48.11 ± 0.75a

Means within a row followed by the same lowercase letter are not significantly different according to the paired bootstrap test at 5% level.
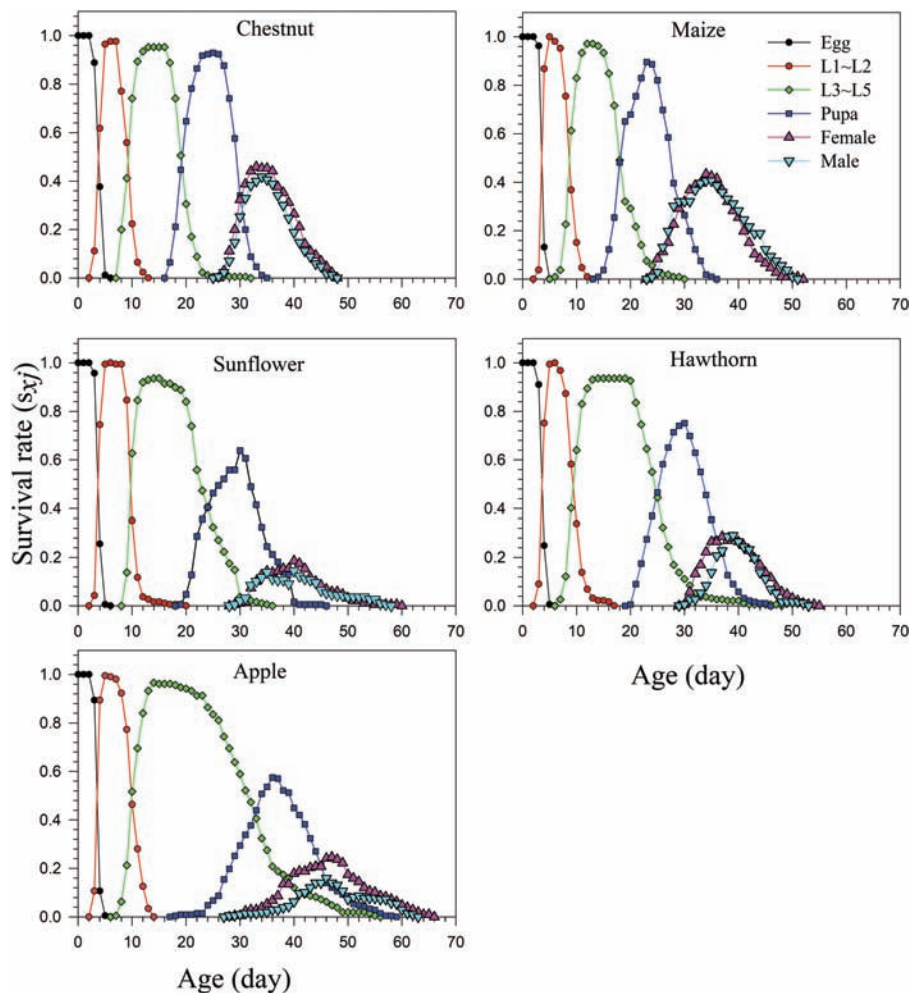
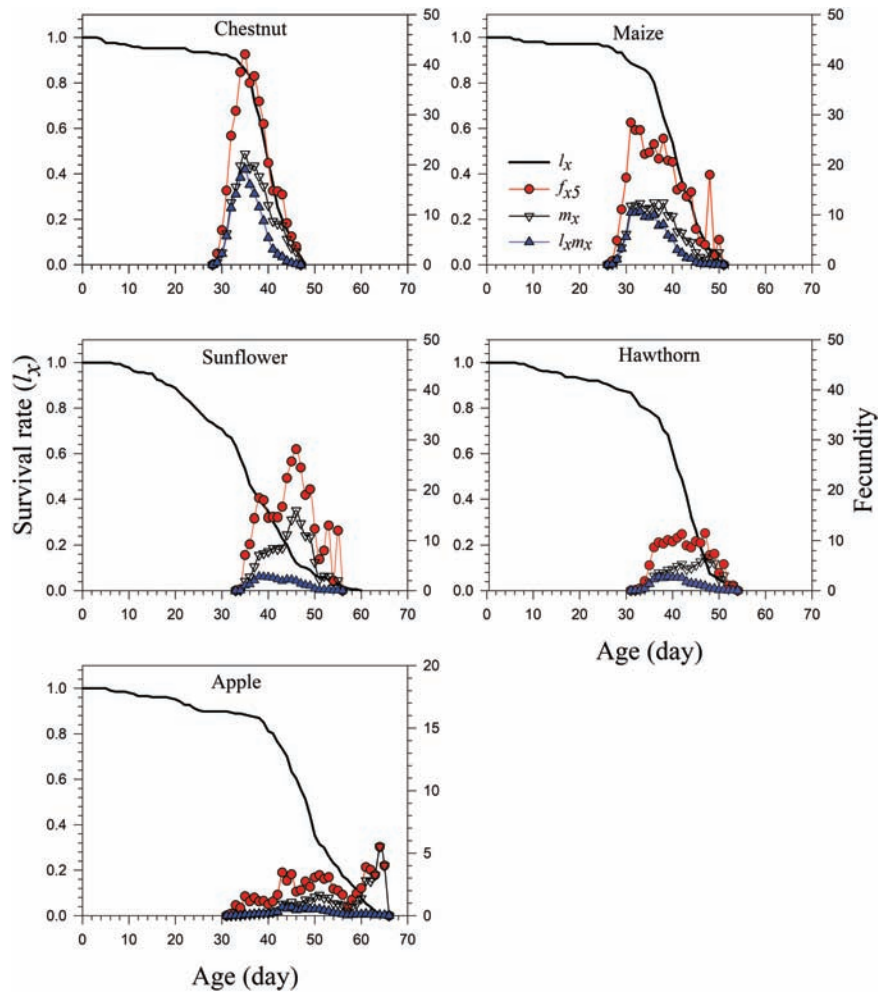**Fig. 1.** Age-stage specific survival rate (s_{xj}) of *C. punctiferalis* reared on different host plants.

Fig. 2. Age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of *C. punctiferalis* reared on different host plants.

during the preadult stages. The l_x curve is actually a simplified version of all curves in Figure 1. The female age-stage-specific fecundity (f_{x5}) is the mean number of fertilized eggs produced by the female adult at age x (Fig. 2). The peak f_{x5} values were 42.08, 28.44, 28.15, 11.27, and 5.50 eggs per day on chestnut, maize, sunflower, hawthorn, and apple, respectively. By factoring in the survival rate, the highest age-specific maternity values ($l_x m_x$) were 19.06, 10.67, 2.84, 3.12, and 0.69 offspring, respectively.

The life expectancy (e_{xj}) for each age-stage group reared on the five diets is plotted in Figure 3. It gives the expected length of time that an individual of age x and stage j will survive. The life expectancy of a newborn egg (e_{01}) is identical to the mean longevity. The life expectancy of a newly laid egg was 38.6, 39.8, 35.1, 41.0, and 46.6 d on chestnut, maize, sunflower, hawthorn, and apple, respectively (Table 1; Fig. 3).

The reproductive value (v_{xj}) gives the expected contribution of an individual of age x and stage j to the future population (Fisher 1930, Tuan et al. 2014a,b) (Fig. 4). The major reproductive curve peaks for individuals reared on chestnut, maize, sunflower, hawthorn, and apple occurred at 33 d ($v_{33,5}$ =164.59 d^{-1}), 32 d ($v_{32,5}$ =123.47 d^{-1}), 39 d ($v_{39,5}$ =85.64 d^{-1}), 36 d ($v_{36,5}$ =53.47 d^{-1}), and 43 d ($v_{43,5}$ =17.33 d^{-1}), respectively (Fig. 4). The peak reproductive values on chestnut and maize occurred earlier and were higher than other treatments.

The population growth and stage structure of *C. punctiferalis* reared on the five rearing media are shown in Figure 5. Starting with 10 eggs, the population increased much faster on chestnut and maize; while the population reared on apple would increase very slowly. The variability of the adult population size is shown in Figure 6. At the peak of adult curves at day 70, the number of adults on chestnut could hypothetically ranges from 800 to 1,100 adults and from 500 to 960 adults on maize. In addition, the adults emerged earlier on chestnut and maize than on other media. After 60–80 d, the number of adults on chestnut and maize was 10-fold greater than on sunflower and hawthorn.

Discussion

Host plants affect the development, survival, and fecundity of herbivorous insects. Shorter development times and higher reproduction rates of insects on a host indicate greater suitability of a host plant (Awmack and Leather 2002, Saeed et al. 2010). To thoroughly understand an insect population, it is necessary to include as much information as possible regarding stage differentiation, survival rate, developmental rate, and fecundity in a systematic manner. However, because there are a number of problems associated with using female age-specific life tables (Huang and Chi 2012, Huang et al. 2018), we encourage entomologists to use the age-stage, two-sex life table to correctly evaluate the effect of variable environmental and nutritional factors on the growth, survival, reproduction, and, most importantly, the increase rate of insect populations.
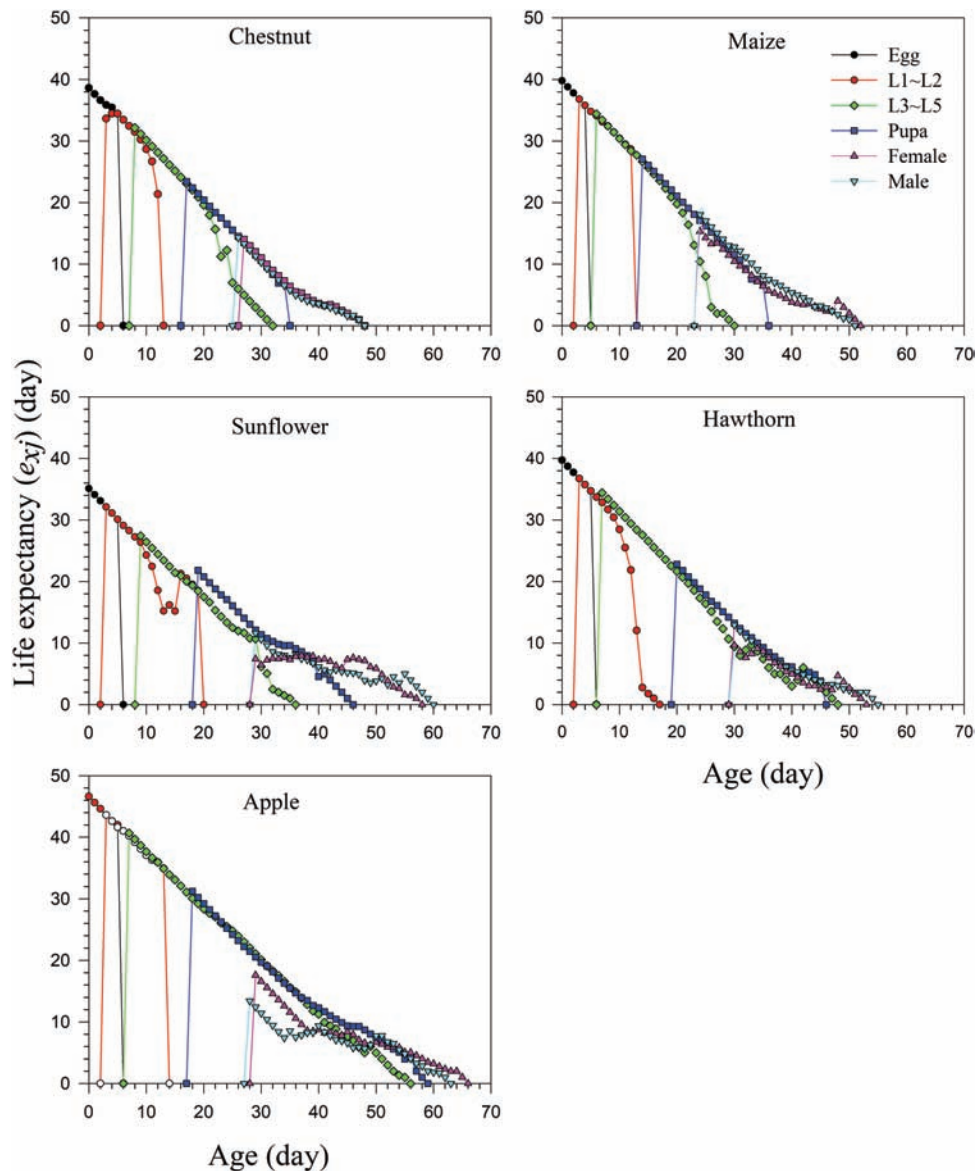
Fig. 3. Age-stage-specific life expectancy (e_{xj}) of *C. punctiferalis* reared on different host plants.

In our study, variations in the development, survival, and fecundity of *C. punctiferalis* reflect different fitness of the species on chestnut, maize, sunflower, hawthorn, and apple. The overlap in the s_{xj} curves (Fig. 1) shows the variable developmental rates in stage differentiation among *C. punctiferalis* individuals. These overlaps were present in most of the life history data. Because traditional female age-specific life tables do not consider stage differentiation, they are forced to disregard stage differentiation and these overlaps; omitting stage overlapping consequently results in errors in data analysis and subsequent applications. Similarly, the differences in life expectancy and reproductive value among individuals of the same age but different stages can be observed in the e_{xj} and v_{xj} curves (Figs. 3 and 4). The life expectancy is calculated using the age-stage survival rate (s_{xj}) without assuming that the population reaches a stable age-stage distribution. It can therefore be used to predict the survival of a population at that condition.

When reared on chestnut and maize, *C. punctiferalis* were shown to have a shorter preadult developmental time, higher preadult survival rate, shorter TPOP, longer adult longevity, higher fecundity, and

greater pupa weight compared to the other three diets (Table 1). The combined effects of these factors resulted in *C. punctiferalis* having a greater net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ) when reared on chestnut and maize compared with those reared on sunflower, hawthorn, and apple (Table 2). These demographic parameters explain the high fitness of *C. punctiferalis* being responsible for the serious damage to maize in the Huang-Huai-Hai region in China. Because *C. punctiferalis* does demonstrate this high level of fitness on chestnut and maize, we suggest that growers refrain from planting maize in areas nearby or adjacent to chestnut orchards. Moreover, control practices should be considered against *C. punctiferalis* in areas involved in hawthorn, sunflower, or apple production to take into consideration the moth's lower fitness and population growth on these host plants. All of the results in this study were consistent with the relationship between *F*, R_0, N_f, and N as proved Chi (1988).

Life-table parameters often vary with different environmental variables, host species, and myriad other factors (Atlihan et al. 2017, Özgökçe et al. 2018). In our study, the fecundity of *C. punctiferalis*
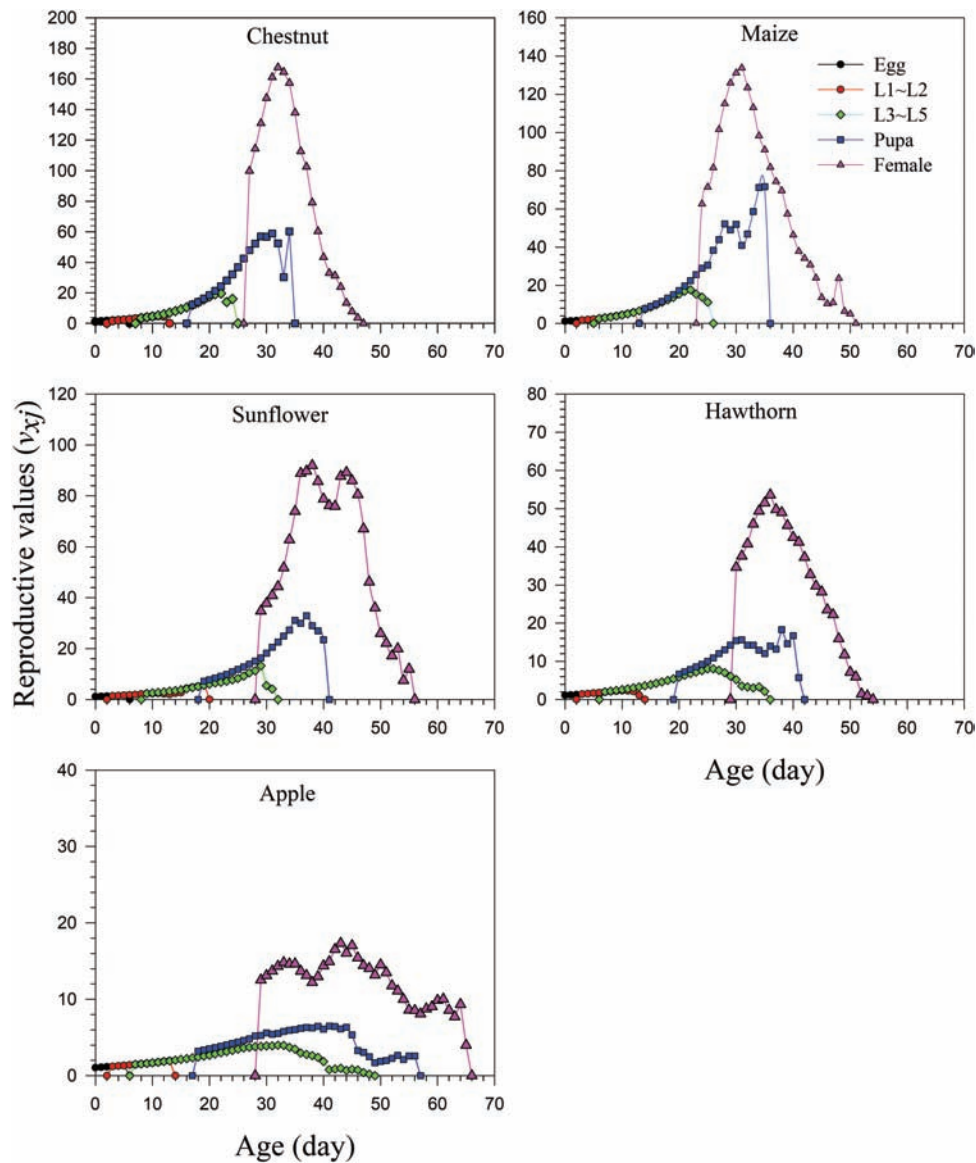
Fig. 4. Age-stage specific reproductive value (v_{xj}) of *C. punctiferalis* reared on different host plants.

on chestnut (282.32 eggs) was much higher than that reported by Du et al. (2012) (55.00 eggs at 23°C and 39.70 eggs at 27°C). The difference may be due to their daily replacement of host plants, which would likely disturb feeding by the larvae resulting in low preadult survival rates (63.56% at 23°C and 54.44% at 27°C). In this study, we grouped the larval stages into two stages (i.e., 1~2 instar and 3~5 instar) to avoid frequently disturbing the larvae. Other possible factors responsible for the difference of female fecundities might be attributed to the size of the adult cage, the number of adult pairs per cage, etc.

Life tables contain the survival rate, developmental rate, sex ratio, fecundity, etc. All of these data are closely related to each other and form a large data set. If any single parameter is isolated from the others and analyzed ignoring its interrelationship to others, it may result in a misleading and/or contradictory conclusion. The following considerations are common pitfalls:

1. *Sex ratio*: Sex ratio is a common statistic in many demographic publications. However, two populations with identical 1:1 sex ratios may exhibit entirely different fitness.

A simple female:male ratio does not necessarily reflect the difference in preadult survival rate and its consequence in population fecundity. In this study, we used the proportion of female adults (N_f/N) and male adults (N_m/N) in each cohort. The values of N_f/N and N_m/N reflect not only the common sex ratio (male:female) but also the difference in preadult survival rate. The N_f/N and N_m/N values can be used to illustrate the differences in the net reproductive rate and intrinsic rate of increase, etc.

2. If the mean fecundity is calculated based only on those females actually producing offspring, then the mean fecundity of reproductive females (F_r) is:

$$F_r = \frac{\sum_{x=1}^{N_{fr}} E_x}{N_{fr}} \tag{2}$$

where E_x is the total number of eggs laid by reproductive females and N_{fr} is the number of reproductive females. Because
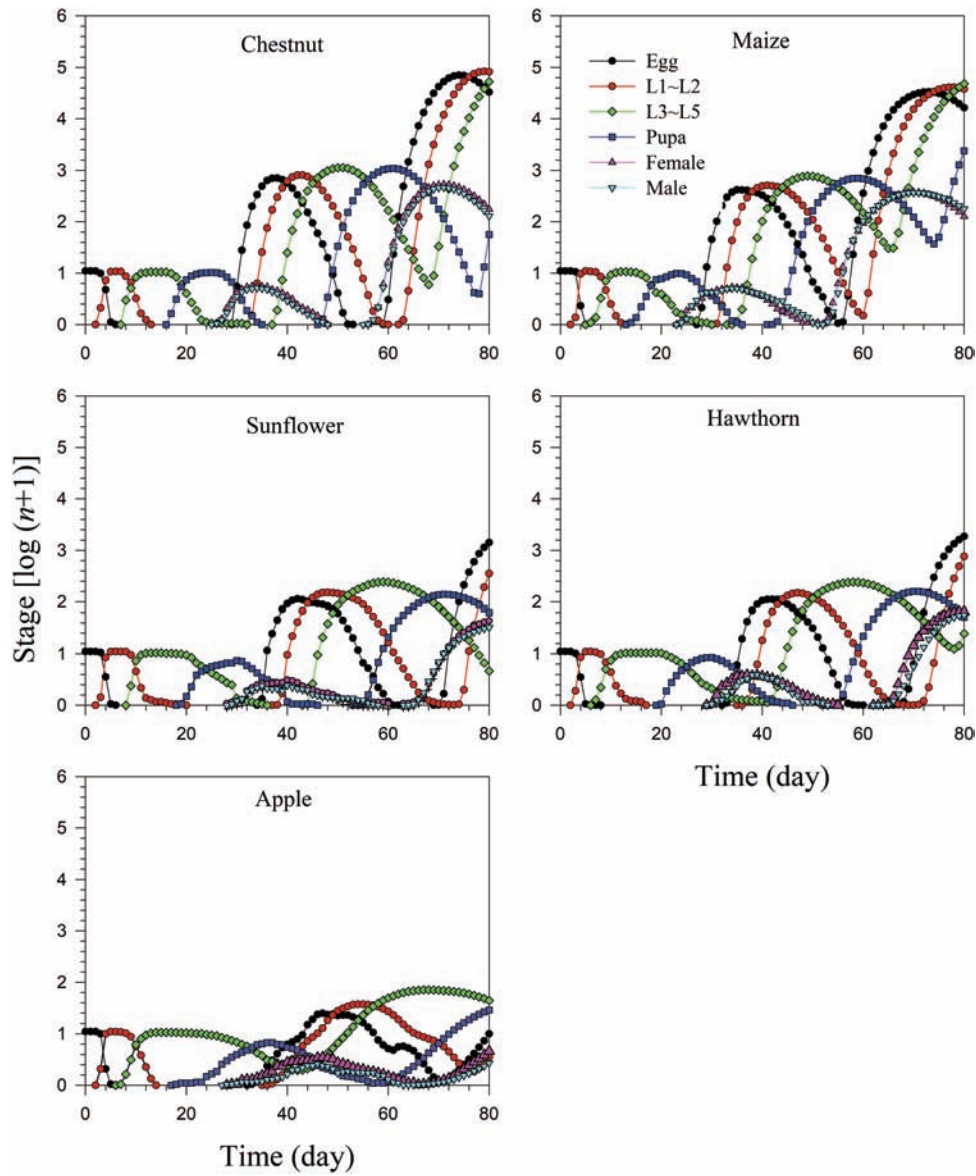
Fig. 5. Population projection of *C. punctiferalis* reared on different host plants.

$$N_f \times F = \sum_{x=1}^{N_f} E_x = \sum_{x=1}^{N_{fr}} E_x = N_{fr} \times F_r$$

the relationship between F, R_0, N_f, and N proved by Chi (1988) can also be written as:

$$R_0 = \frac{N_{fr}}{N} F_r \qquad (3)$$

In cases where substantial numbers of females did not reproduce, the values of F_r and N_{fr} and their relationship to F and N_f can be used to explain the fitness of the population.

3. *Oviposition period and oviposition days*: In general, the oviposition period is considered to be the length of time from the first to the last oviposition. However, it does not inevitably correspond to the actual number of days that an insect has produced eggs. In other words, a long oviposition period does not necessarily equal

a high fecundity. In this article, we reported the oviposition days (O_d) and eggs per oviposition day (E_d). The O_d gives the mean number of days that an insect has laid eggs, and is calculated as:

$$O_d = \frac{\sum_{x=1}^{N_{fr}} D_x}{N_{fr}} \qquad (4)$$

where D_x is the number of oviposition days of one female. The number of eggs produced during each oviposition day is calculated as:

$$E_d = \frac{\sum_{x=1}^{N_{fr}} E_x}{\sum_{x=1}^{N_{fr}} D_x} = \frac{\sum_{x=1}^{N_{fr}} E_x}{O_d \times N_{fr}} = \frac{F_r}{O_d} \qquad (5)$$

where E_d is the mean number of eggs produced on each oviposition day. The following equation can be derived from equations 9 and 11:
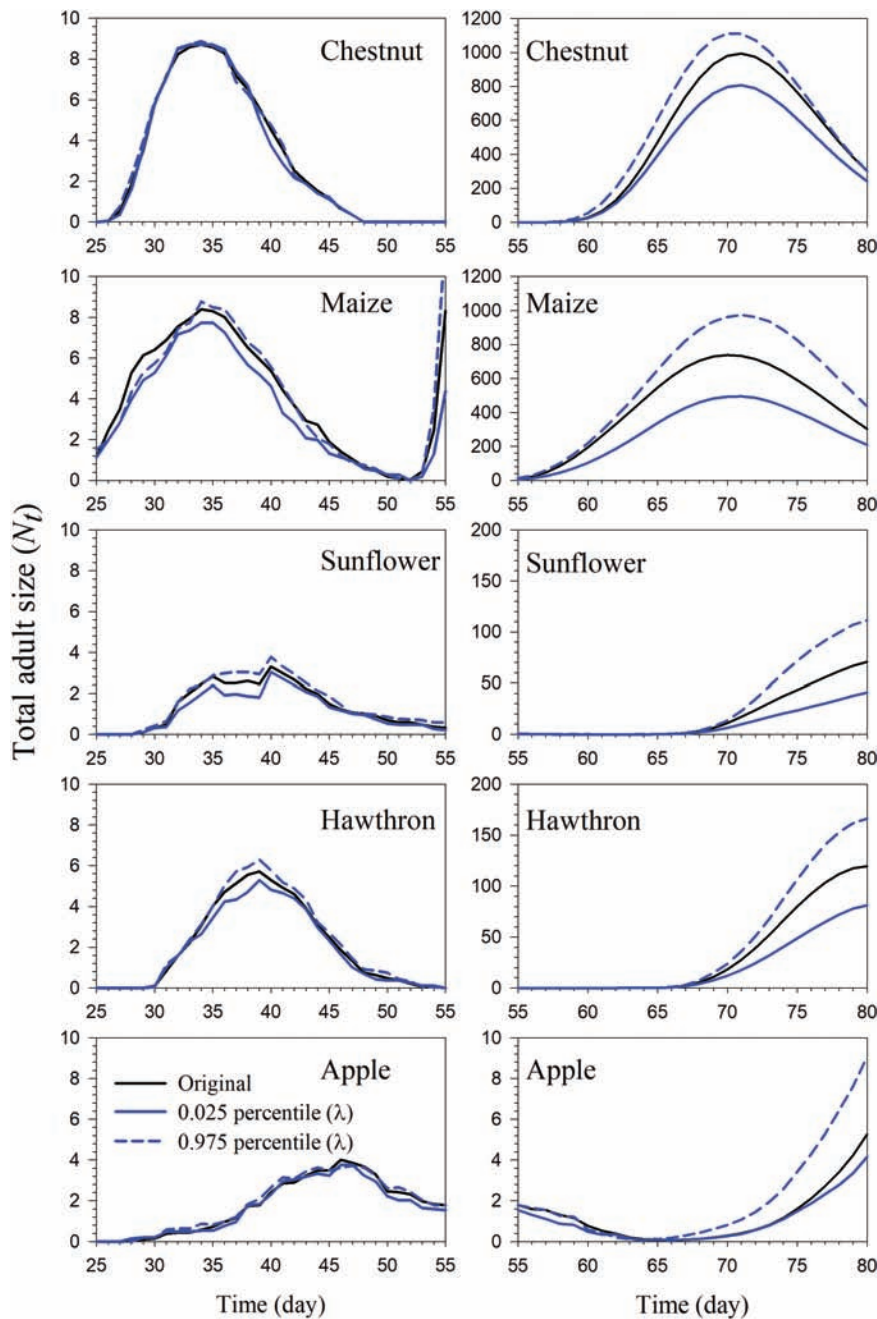
Fig. 6. Uncertainty of population projection of *C. punctiferalis* reared on different host plants.

$$R_0 = E_d \times O_d \times \frac{N_{fr}}{N} \tag{6}$$

All of the data contained in Tables 1 and 2 are consistent with the above equations. Because different researchers favor using different statistics in their reports, the above equations offer more options to examine their own data or to compare their data with other published studies.

If an insect species lays its eggs in masses or oothecae, the O_d will be much shorter when compared with adult longevity or oviposition period and can be related to the periodic reproduction due to maturity of oocytes or oothecae formation (Tsai and Chi 2007). The O_d and E_d parameters offer more

information and are more precise statistical measurements than "oviposition period" and "mean daily eggs during an oviposition period."

Our results provide a comprehensive description of life history data of *C. punctiferalis* on five host plants, including durations of different development stages, adult longevity, fecundities, sex ratios, and their combined effects on various demographic parameters. This study demonstrates that life tables are ideal tools for providing a complete description and comparison of the fitness of insect populations on different rearing media. We also demonstrated the variability of population growth by using computer projections. This information can be used in practical applications in managing this economically important pest.

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