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Fitness of the papaya mealybug, *Paracoccus marginatus* (Hemiptera: Pseudococcidae), after transferring from *Solanum tuberosum* to *Carica papaya*, *Ipomoea batatas* and *Alternanthera philoxeroides*

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Abstract: The papaya mealybug, *Paracoccus marginatus* Williams and Granara de Willink (Hemiptera: Pseudococcidae) is a polyphagous invasive pest in China. The effect that shifting of host plant has on the fitness of a polyphagous pest is critical to its prevalence and potential pest control. In order to assess the fitness change of *P. marginatus* after transferal from potato [*Solanum tuberosum* (Tubiflorae: Solanaceae)] to papaya [*Carica papaya* (Parietales: Caricaceae)], sweet potato [*Ipomoea batatas* (Tubiflorae: Convolvulaceae)], and alligatorweed [*Alternanthera philoxeroides* (Centrospermae: Amaranthaceae)], the life table data of three consecutive generations were collected and analyzed by the age-stage, two-sex life table method. The results showed that when *P. marginatus* transferred from *S. tuberosum* to papaya, higher values of intrinsic rate of increase (r) and finite rate of increase (λ) were observed. *Paracoccus marginatus* transferal to *I. batatas* had the significantly lower population parameters than those on *C. papaya*; however, the fitness recovered on *I. batatas* after two generations. *Paracoccus marginatus* were unable to complete development on *A. philoxeroides*. Our results conclusively demonstrated that *P. marginatus* can readily adapt to *C. papaya* and *I. batatas* even after host plant shifting and are capable of causing severe damage to these hosts.

Keywords: *Paracoccus marginatus*; host plant shifting; two-sex life table; fitness

1. Introduction

The papaya mealybug, *Paracoccus marginatus* Williams and Granara de Willink (Hemiptera: Pseudococcidae) is a globally invasive pest, which attacks host plants by sucking sap from the leaves, stems and **so on** (Wu et al. 2014). Since the 1990s, *P. marginatus* had spread rapidly through the Americas, Africa, and most provinces of southern China (Miller et al. 1999, Finch et al. 2021). *Paracoccus marginatus* is a polyphagous pest of many economic crops and weeds included in more than 64 families, such as Euphorbiaceae, Rubiaceae, and Caricaceae (Krishnan et al. 2016). In our preliminary field investigation, *P. marginatus* has been found on important field crops including potato [*Solanum tuberosum* (Tubiflorae: Solanaceae)], papaya [*Carica papaya*

(Parietales: Caricaceae)], and sweet potato [*Ipomoea batatas* (Tubiflorae: Convolvulaceae)]. It has also been observed on ~~a worst weed~~, alligatorweed [*Alternanthera philoxeroides* (Centrospermae: Amaranthaceae)]. Most of insects were observed on the leaves of the above plants. *Solanum tuberosum* has been used for a number of years as a host for mass-rearing of *P. marginatus* in the laboratory.

Polyphagous insects, which characteristically have a wide range of host plants in nature, are often associated with host shifting. Huang et al. (2014) demonstrated that the rapid host shifting of *Phenacoccus solenopsis* (Tinsley) (Hemiptera: Pseudococcidae) was due to its efficient host plant fitness. The fitness of insects on a new host plant can be evaluated from the population growth rate on the new host plant **versus old host plant** (Lu et al. 2016, Ning et al. 2017). Therefore, it is important to understand how invasive pests adapt on the new host plant using demographic characteristics.

Many studies have shown that significant effects may occur in an insect species after host plant shifting, such as changes in their development and fecundity. For example, Milanović et al. (2016) reported that when *Lymantria dispar* L. (Lepidoptera: Lymantriidae) transferred from Hungarian oak to Turkey oak, the developmental time shortened while the efficiency of food utilization increased. Mody et al. (2007) demonstrated that host plant shifting had a strong effect on *Chrysopsyche imparilis* (Lepidoptera: Lasiocampidae), especially in adult fecundity and the mean body mass of second-instar larvae. Furthermore, when assessing the effects of host plant shifting based on the life table and population dynamics of *Aphis gossypii* (Glover) (Hemiptera: Aphididae), Fan et al. (2018) showed that the fecundity (F), intrinsic rate of increase (r), finite rate of increase (λ), and net reproductive rate (R_0) significantly increased when transferred from wheat to cotton. Amarasekare et al. (2008) reported the survival rate of *P. marginatus* on different host plants. Nisha and Kennedy (2017), using the female age-specific life table, reported life table results of *P. marginatus* on different host plants. But the results were limited by ignoring the males in the population (Huang and Chi 2012).

Thus, in this study, we assessed the fitness changes that occurred after *P. marginatus* was transferred from *S. tuberosum* to *C. papaya*, *I. batatas* and *A. philoxeroides* through the age-stage, two-sex life table method. The objectives of this study were to 1) measure the development, fecundity, and population parameters in *P. marginatus* over a span of three consecutive generations after host plant shifting, and 2) project the population growth of *P. marginatus* on *C. papaya*, *I. batatas*, and *S. tuberosum*.

2. Materials and Methods

2.1. Cultivation of Host Plants

Carica papaya (Parietales: Caricaceae), *I. batatas* (Tubiflorae: Convolvulaceae), *S. tuberosum* (Tubiflorae: Solanaceae), and *A. philoxeroides* (Centrospermae: Amaranthaceae) were obtained from the Institute of Plant Protection, Fujian Academy of Agricultural Sciences. Host plants were cultivated (40.0 cm in length, 30.0 cm in width, and 15.0 cm in height) with nutrient soil (Cuijun, Fuzhou, China) and kept in growth chambers (PRX-450D, Haishu Safe Apparatus, Ningbo, China) at $28 \pm 1^\circ\text{C}$, $70 \pm 5\%$ RH, and a photoperiod of 14: 10 (L: D) h. Young leaves (< 30-d old) were used for the study.

2.2. *Paracoccus marginatus*

The eggs of *P. marginatus* were originally obtained from a papaya orchard in Fuzhou city (Fujian Province, China, $25^\circ15'\sim26^\circ39'\text{N}$, $118^\circ08'\sim120^\circ31'\text{E}$), and reared on the leaves of *S. tuberosum* in a growth

chamber for 20 generations to allow *P. marginatus* to adapt to *S. tuberosum* as a host. The female life cycle (which differs from that of the male) consists of the egg, three larval instars, and the adult stage, while the males' include the egg, three larval instars, a pupal stage, and the adult stage.

2.3. Life Table Study of *P. marginatus*

Egg masses laid within a 24 h period on potato leaves were randomly selected for the life table study. In order to accurately observed the lifespan of each insect, eggs were placed on leaves of *C. papaya*, *I. batatas*, *S. tuberosum*, or *A. philoxeroides* in plastic dishes (3.5 cm in diameter and 2.0 cm in height) containing agar (3%). After hatching, each 1st instar was transferred into a fresh dish containing leaves of the same plant and reared individually. Following the advice of Mou et al. (2015), only hatched eggs were used in the life table studies to accurately estimated the life table parameters. Newly emerged adult males and females were paired. The daily fecundity and survival were recorded until the death of all individuals. The life table data of three consecutive generations (F_0 , F_1 and F_2) were recorded. Because *P. marginatus* reared on *A. philoxeroides* only survived for a single generation (F_0), only one life table could be constructed for insects on this host.

2.4. Life Table Data Analysis

The raw life history data of all individual *P. marginatus*, including developmental duration, longevity, and female fecundity, were analyzed according to the age-stage, two-sex life table procedure (Chi and Liu 1985, Chi 1988) using the program TWOSEX-MSChart (Chi 2022a). The variances and standard errors of parameters were estimated by using the bootstrap technique (Efron and Tibshirani 1993, Chi et al. 2020). Differences between treatments were assessed using paired bootstrap tests (Wei et al. 2020). The age-stage-specific survival rate (s_{xj}), is the probability that each hatched egg will survive to age x and stage j . The age-specific survival rate (l_x) was calculated as:

$$l_x = \sum_{j=1}^k s_{xj} \quad (121)$$

where k is the number of stages. The age-specific fecundity (m_x) was calculated as:

$$m_x = \frac{\sum_{j=1}^k s_{xj} f_{xj}}{\sum_{j=1}^k s_{xj}} \quad (123)$$

The intrinsic rate of increase (r) was estimated using the Euler-Lotka equation (Euler 1760, Lotka 1907) with age indexed from 0 (Goodman 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (126)$$

The finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T) were calculated as follows:

$$\lambda = e^r \quad (129)$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (130)$$

$$T = \frac{\ln R_0}{r} \quad (131)$$

The age-stage specific life expectancy (e_{xj}), i.e., 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):

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^a s'_{iy}$$

where s'_{iy} is the probability that an individual of age x and stage j can survive to age i and stage y by assuming that $s'_{iy} = 1$. The age-stage reproductive value (v_{xj}) which represents the contribution each individual in age x and stage j makes to the future population (Fisher 1930, Tuan et al. 2014), was calculated as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(x+1)} \sum_{y=j}^{\beta} s'_{iy} f_{iy}$$

2.5. Population Projection

The population growth of *P. marginatus* was simulated according to Chi (1990) by using the computer program TIMING-MSChart (Chi 2022b). An initial population of 10 newly laid eggs was used for the simulation. The stage growth rate of stage j was calculated according to Huang et al. (2018).

$$\phi_{j,t} = \log \left(\frac{n_{j,t+1} + 1}{n_{j,t} + 1} \right)$$

$$r_{j,t} = \log \left(\frac{n_{j,t+1} + 1}{n_{j,t} + 1} \right)$$

As the population approaches a stable age-stage distribution, the number of individuals of each stage ($n_{j,t}$) and the total population size ($n_{total,t}$) will increase at the finite rate of increase (λ) and the intrinsic rate of increase (r). These can be expressed as:

$$\phi_{j,t} = \log \left(\frac{n_{j,t+1} + 1}{n_{j,t} + 1} \right) \approx \log \left(\frac{\lambda n_{j,t}}{n_{j,t}} \right) = \log \left(\frac{\lambda n_{total,t}}{n_{total,t}} \right) = \log \lambda$$

$$r_{j,t} = \log \left(\frac{n_{j,t+1} + 1}{n_{j,t} + 1} \right) = \ln(n_{j,t+1} + 1) - \ln(n_{j,t} + 1)$$

3. Results

3.1. Development and Fecundity of *P. marginatus* after Host Plant Shifting

The development and fecundity of *P. marginatus* in the F₀, F₁ and F₂ generations following host plant shifting are shown in Table 1. There were no significant differences in the egg duration among the four host plants in the F₀ generation. However, the developmental times of female and male larvae fed on *C. papaya* were significantly shorter than those on the three other hosts. Extremely long developmental times occurred in both female and male larvae when fed on *A. philoxeroides*. Detailed development durations for each instar are contained in Supplementary Table S1. Female adults reared on *C. papaya* lived significantly longer than those fed on the other three plants, although there was no significant difference between those fed on *C. papaya* and *S. tuberosum*. The egg duration was, however, significantly longer in the F₁ and F₂ generations when reared on *I. batatas* and *S. tuberosum*. The durations of male larvae on *I. batatas* and *S. tuberosum* were shortened in the F₁ and F₂. The

larvae durations of females were unchanged when reared on the three host 170
plants. The female adult longevities were unchanged on *C. papaya* and *I. bata-* 171
tas, but were shortened on *S. tuberosum*. The adult longevities of the males 172
were shortened on *I. batatas* and *S. tuberosum*, but unchanged on *C. papaya*. 173

Table 1. Developmental time of *Paracoccus marginatus* reared on four different host plants (F₀ - F₂).

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Stage (d)	Generation	<i>Carica papaya</i>		<i>Ipomoea batatas</i>		<i>Solanum tuberosum</i>		<i>Alternanthera philoxeroides</i>	
		<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE
Egg	F ₀	95	5.18 ± 0.04aA	100	5.21 ± 0.04aC	100	5.20 ± 0.08aB	100	5.23 ± 0.05a
	F ₁	92	5.16 ± 0.06bA	98	6.22 ± 0.05aB	88	6.26 ± 0.06aA	-	-
	F ₂	100	5.24 ± 0.06cA	90	6.91 ± 0.04aA	84	6.13 ± 0.09bA	-	-
Female larvae	F ₀	47	12.36 ± 0.16cA	17	14.29 ± 0.41bA	45	14.04 ± 0.30bA	2	18.50 ± 0.50a
	F ₁	45	11.98 ± 0.18bA	30	14.00 ± 0.31aA	40	15.07 ± 0.47aA	-	-
	F ₂	49	12.24 ± 0.16bA	33	13.70 ± 0.34aA	40	14.32 ± 0.35aA	-	-
Male larvae	F ₀	39	13.92 ± 0.21dA	65	17.18 ± 0.30bA	44	15.43 ± 0.20cA	9	20.22 ± 1.05a
	F ₁	40	13.50 ± 0.26bA	53	15.53 ± 0.24aB	44	15.20 ± 0.19aAB	-	-
	F ₂	44	13.64 ± 0.21cA	51	15.55 ± 0.15aB	38	14.61 ± 0.24bB	-	-
Female adult	F ₀	47	20.09 ± 0.55aA	17	15.65 ± 1.23bA	45	19.87 ± 0.94abA	2	8.00 ± 1.00c
	F ₁	45	19.18 ± 0.56aA	30	18.53 ± 1.63aA	40	13.97 ± 1.27bB	-	-
	F ₂	49	19.67 ± 0.56aA	33	17.12 ± 1.22aA	40	14.28 ± 1.44bB	-	-
Male adult	F ₀	39	3.28 ± 0.18aA	65	3.48 ± 0.14aA	44	3.41 ± 0.20aA	9	3.67 ± 0.62a
	F ₁	40	3.48 ± 0.17aA	53	3.21 ± 0.14aAB	44	3.11 ± 0.15aAB	-	-
	F ₂	44	3.50 ± 0.16aA	51	3.00 ± 0.13bB	38	2.87 ± 0.13bB	-	-

The data (Mean ± SE) followed by the same letters were not significantly different by paired bootstrap test ($P < 0.05$). Lowercase letters indicated comparison among different host plants, and capital letters indicated comparison among different generations. 1st instar, 2nd instar, 3rd instar, and pupa were combined to larvae in data statistics.

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The age-stage-specific survival rates (s_{xj}) of *P. marginatus* reared on the four host plants (F_0) are plotted in Figure 1. Because the age-stage life table is capable of describing the stage differentiation, obvious stage overlapping can be observed in Figure 1. When *P. marginatus* were reared on *A. philoxeroides*, the probability of an egg surviving to the 2nd instar was extremely low (i.e., 0.150, 11 individuals), and significantly lower than on other host plants. Only two eggs successfully developed into female adults. In contrast, the survival rates to the 2nd instar larvae when reared on *C. papaya* were as high as 0.924 and 0.930 in F_1 and F_2 , respectively; higher survival rates to female adult (0.489 and 0.490) were also observed in the F_1 and F_2 . Similar high survival rates occurred in the male adults (0.435 in F_1 and 0.440 in F_2). Lower survival rates were observed when reared on *I. batatas* and *S. tuberosum*, (Figure 2). The narrow distribution of male adult survival curves (s_{xj}) showed that all male adults had shorter lifespans than the females.

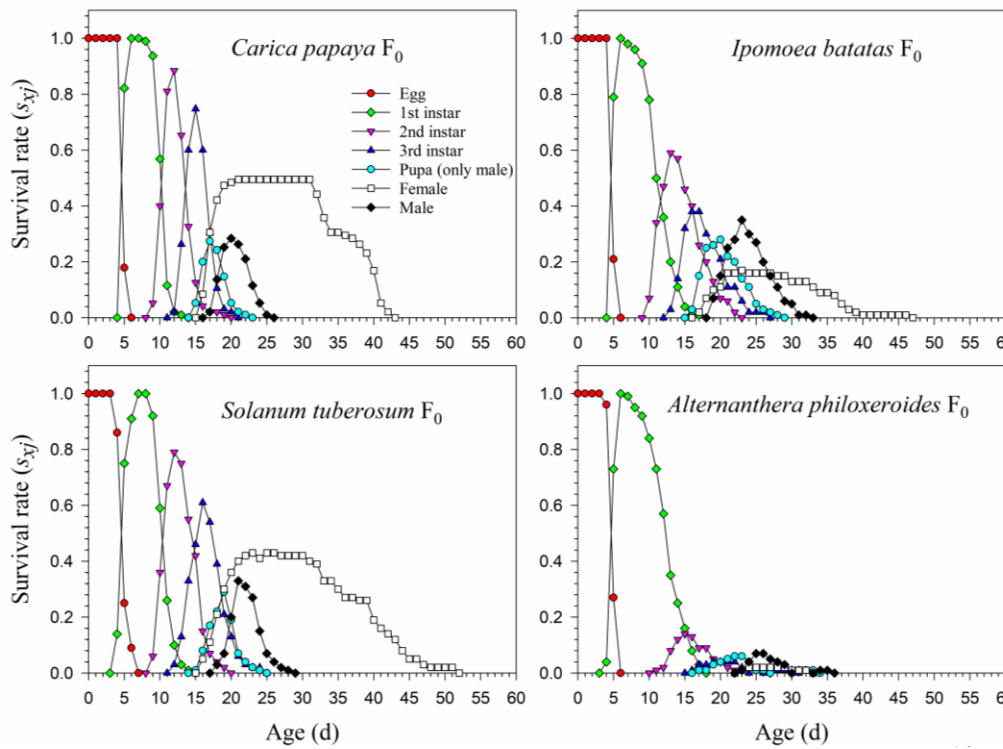


Figure 1. Age-stage-specific survival rate (s_{xj}) of *Paracoccus marginatus* reared on four different host plants (F_0).

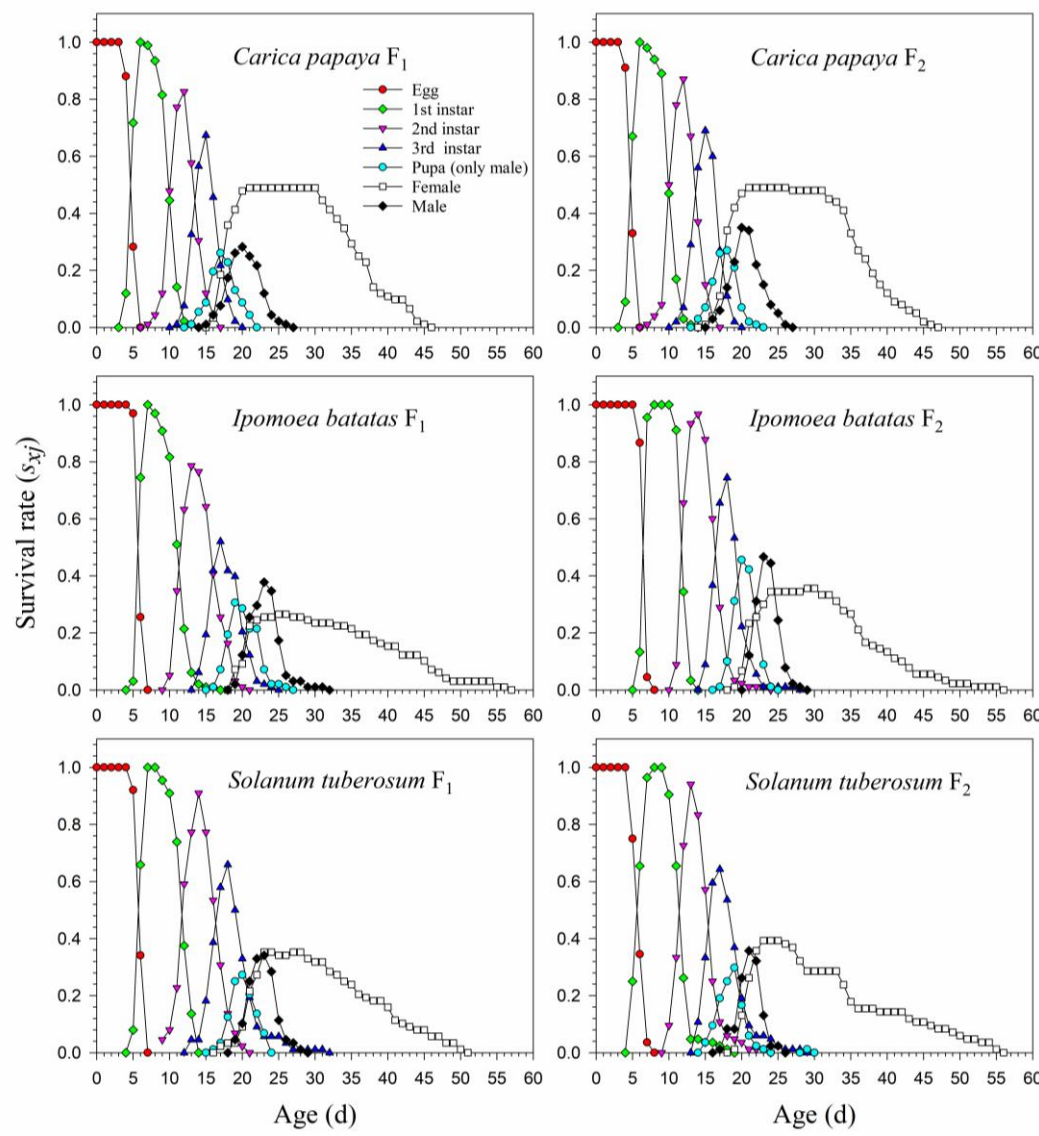


Figure 2. Age-stage-specific survival rate (s_{xj}) of *Paracoccus marginatus* reared on three different host plants (F1- F2).

The preadult survival rate of *P. marginatus* reared on *A. philoxeroides* in F_0 was extremely low ($s_a = 0.110$), while no significant differences occurred among *C. papaya*, *I. batatas* and *S. tuberosum*. The preadult survival rate of *P. marginatus* reared on *I. batatas* increased to 0.933 in F_2 . A higher proportion of female adults of *P. marginatus* were observed in F_0 on *C. papaya* ($N_f/N = 0.495$) and *S. tuberosum* ($N_f/N = 0.450$). The N_f/N value on *I. batatas* was 0.170. An extremely low N_f/N value (0.023) was observed on *A. philoxeroides*. In the F_2 the N_f/N values remained constant on *C. papaya* and *S. tuberosum*; but increased to 0.367 on *I. batatas*. In F_0 , a significantly highest proportion of male adults (N_m/N) of *P. marginatus* was observed on *I. batatas* (0.650). The N_m/N values on *C. papaya* and *S. tuberosum* were 0.411 and 0.440, respectively. An extremely low N_m/N ratio (0.090) was observed on *A. philoxeroides*. The N_m/N ratio did not change from F_1 to F_2 (Table 2).

In the F_0 generation, the highest fecundity (F) of *P. marginatus* occurred on *C. papaya* (202.70 hatched eggs/female), which was significantly higher than in the other three plants. *Paracoccus marginatus* produced, on average,

6.50 eggs/female when reared on *A. philoxeroides*. Because none of the eggs 216
produced on this host were viable, the mean fecundity was zero (Table 2). 217
Lower fecundities were observed on *I. batatas* and *S. tuberosum* as 98.83 218
hatched eggs/female and 127.46 hatched eggs/female, respectively. On *I. bata-* 219
tas, the fecundity increased in F₁ (229.50 hatched eggs/female) and F₂ (203.76 220
hatched eggs/female) (Table 2). 221

Table 2. Preadult survival rate (s_a), proportion of female adults (N_f/N), proportion of male adults (N_m/N), and fecundity (F) of *Paracoccus marginatus* reared on four different host plants (F₀ - F₂).

Population parameter	Generation	<i>Carica papaya</i>	<i>Ipomoea batatas</i>	<i>Solanum tuberosum</i>	<i>Alternanthera philoxeroides</i>
Preadult survival rate (s_a)	F ₀	0.905 ± 0.030aA	0.820 ± 0.038aB	0.890 ± 0.031aA	0.110 ± 0.031b
	F ₁	0.924 ± 0.028abA	0.847 ± 0.036bB	0.955 ± 0.022aA	-
	F ₂	0.930 ± 0.026aA	0.933 ± 0.026aA	0.929 ± 0.028aA	-
Proportion of female adults (N_f/N)	F ₀	0.495 ± 0.051aA	0.170 ± 0.038bB	0.450 ± 0.050aA	0.023 ± 0.012c
	F ₁	0.489 ± 0.052aA	0.306 ± 0.047bA	0.455 ± 0.053aA	-
	F ₂	0.490 ± 0.050aA	0.367 ± 0.051aA	0.476 ± 0.055aA	-
Proportion of male adults (N_m/N)	F ₀	0.411 ± 0.050bA	0.650 ± 0.048aA	0.440 ± 0.049bA	0.090 ± 0.050c
	F ₁	0.435 ± 0.052aA	0.541 ± 0.050aA	0.500 ± 0.053aA	-
	F ₂	0.440 ± 0.049aA	0.567 ± 0.052aA	0.452 ± 0.054aA	-
Fecundity (F) (hatch eggs/female)	F ₀	202.70 ± 17.68aA	98.93 ± 23.04bB	127.46 ± 18.79bA	0
	F ₁	202.46 ± 24.08aA	229.50 ± 41.84aA	127.38 ± 25.40bA	-
	F ₂	215.27 ± 20.32aA	203.76 ± 35.72abA	121.51 ± 25.35bA	-

The data (Mean ± SE) followed by the same letters were not significantly different by paired bootstrap test ($P < 0.05$). Lowercase letters indicated comparison among different host plants, and capital letters indicated comparison among different generations.

The age-specific survival rate (l_x) of *P. marginatus* in F_0 is shown in Figure 3. Because the l_x curve is the simplified version of s_{xj} , the stage differentiation is not observable. The 50% survival rate of *P. marginatus* occurred at age 26, 25, 26, and 13 d on *C. papaya*, *I. batatas*, *S. tuberosum*, and *A. philoxeroides*, respectively. In F_2 , the 50% survival rate of *P. marginatus* on *I. batatas* and *S. tuberosum*, changed at age 26 and 24, respectively. Higher curves of the age-specific fecundity (m_x) and net maternity ($l_x m_x$) were observed on *C. papaya*. Although there was a relatively high peak of 27 eggs at 40 d on *I. batatas*, the low survival rate (l_x) caused the net maternities ($l_x m_x$) to be very low. When reared on *S. tuberosum*, the high peak of m_x (18.4 eggs) occurred at age 26 d, the remaining m_x values were, for the most part, greater than 5 eggs. The m_x and $l_x m_x$ values on *C. papaya* and *S. tuberosum* did not change significantly; they did, however, increase on *I. batatas* during the F_1 and F_2 generations (Figure 4).

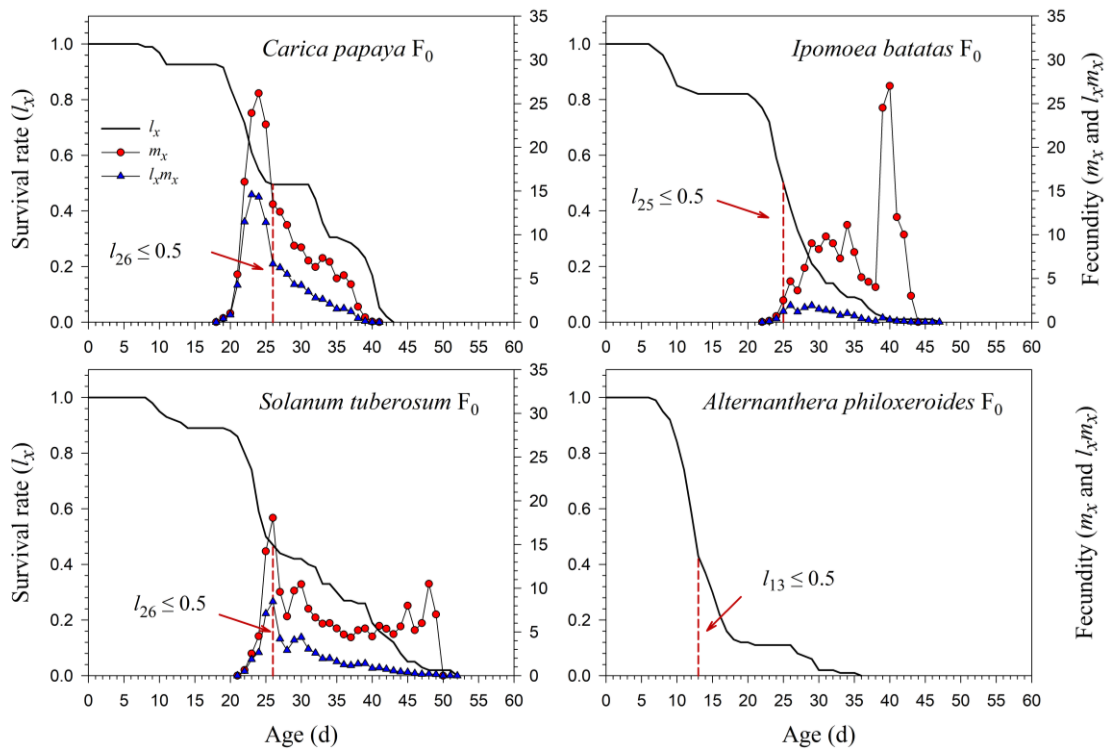


Figure 3. Age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of *Paracoccus marginatus* reared on four different host plants (F_0). The red vertical dashed line in the Figures denotes the age at which the survival rate $l_x \leq 0.5$.

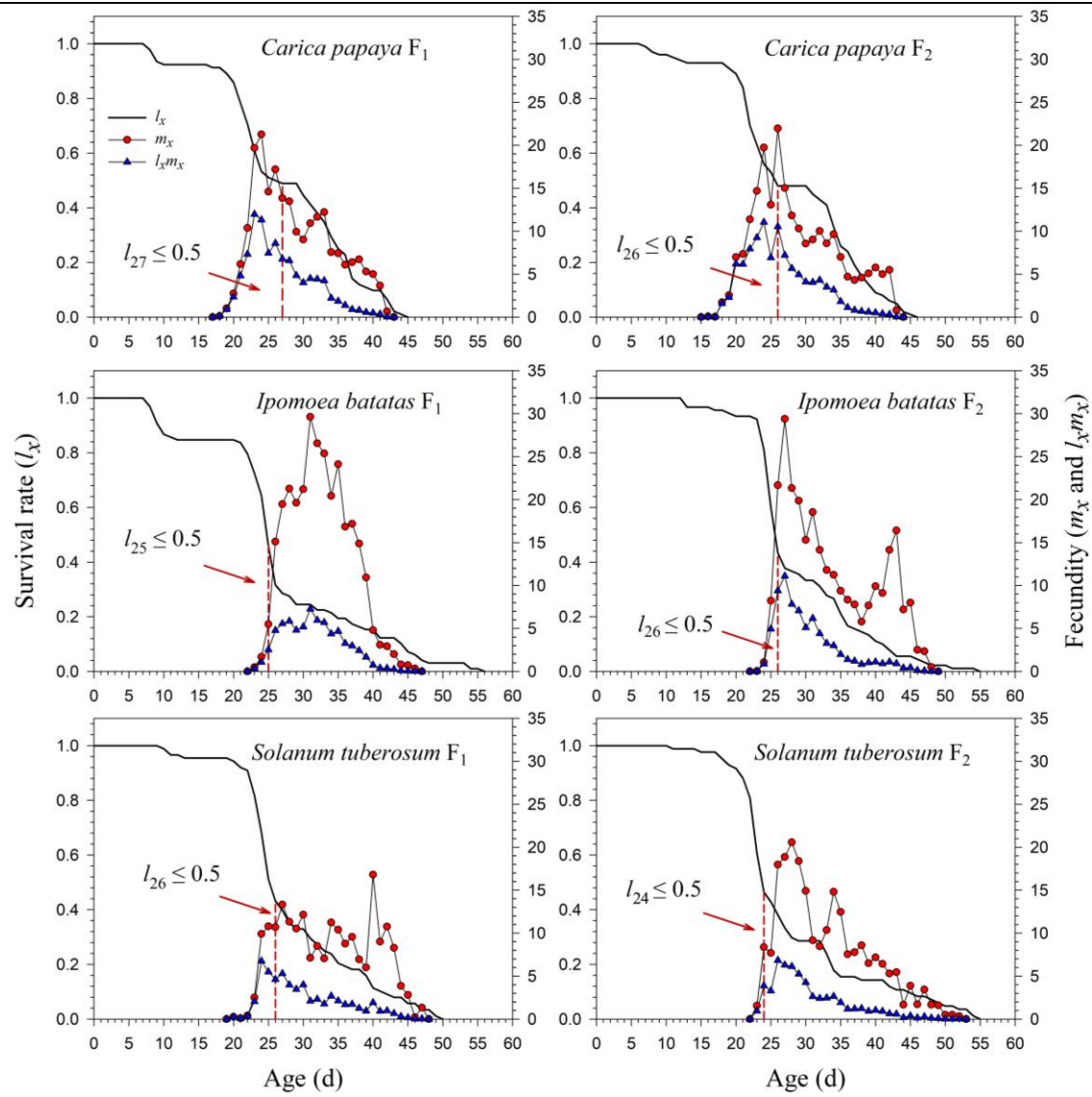


Figure 4. Age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of *Paracoccus marginatus* reared on three different host plants (F1–F2). The red vertical dashed line in the Figures denotes the age at which the survival rate $l_x \leq 0.5$.

The age-stage-specific life expectancy (e_{xj}) values for the F_0 generation of *P. marginatus* on the four host plants are shown in Figure 5. The life expectancy of a newly laid egg of *P. marginatus* was 29.0, 24.5, 29.3, and 14.9 d in the F_0 . Because the survival rate from the 1st instar to the 2nd instar on *A. philoxeroides* was extremely low (0.15), and individuals surviving to the 2nd instar could, for the most part, complete their development to adults, the e_{xj} curve of the 2nd instar was significantly higher than in the 1st instar. The detailed e_{xj} curves on *C. papaya*, *I. batatas* and *S. tuberosum* during F_1 and F_2 are shown in Supplementary Figure S1.

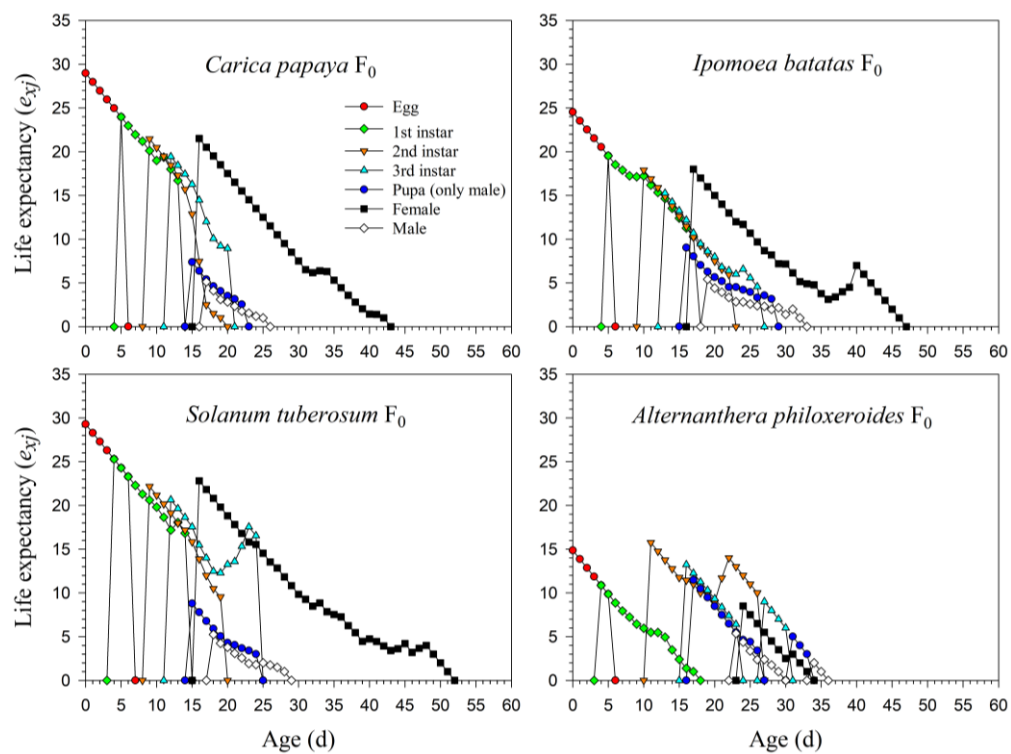


Figure 5. Age-stage-specific life expectancy (e_{xj}) of *Paracoccus marginatus* reared on four different host plants (F_0). 259 260

The age-stage specific reproductive value (v_{xj}) of *P. marginatus* in F_0 is 261 shown in Figure 6. The v_{xj} at age zero is exactly equal to the finite rate of in- 262 crease (λ), i.e., 1.1945, 1.0970 and 1.1475. The v_{xj} increased with age. When 263 reared on *I. batatas*, the v_{xj} curve significantly increased when female adults 264 emerged. Similar increases in the v_{xj} curves were observed on *C. papaya* and *S.* 265 *tuberosum*; due to the high percentage of female adults, however, this increase 266 is not obvious. The peak dates of v_{xj} were close to the total pre-oviposition 267 period (TPOP). Detailed v_{xj} curves on *C. papaya*, *I. batatas* and *S. tuberosum* for 268 F_1 and F_2 are shown in Supplementary Figure S2. 269

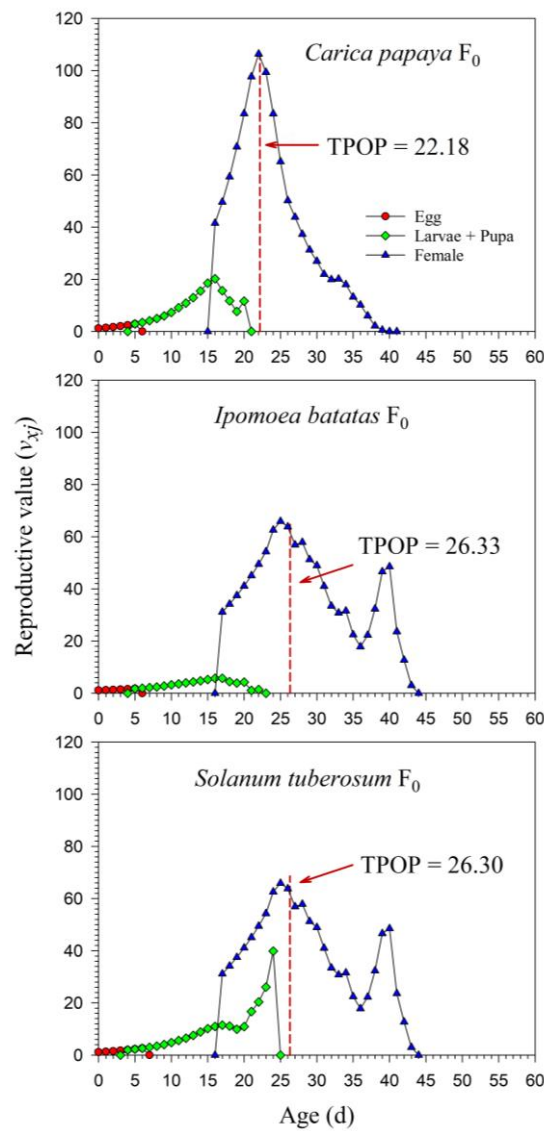


Figure 6. Age-stage-specific reproductive value (v_{xj}) of *Paracoccus marginatus* reared on three different host plants (F_0). The red vertical dashed line in each figure denotes the total preoviposition period (TPOP).

3.2. Population Parameters of *P. marginatus* after Host Plant Shifting

There were significant differences in the population parameters in the F_0 generation of *P. marginatus* after host plant shifting (Table 3). The highest values of the net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ) for *P. marginatus* occurred on *C. papaya* (i.e., 100.26 offspring, 0.1778 d^{-1} and 1.1945 d^{-1}). Significantly lower R_0 , r and λ values were observed when reared on *I. batatas* and *S. tuberosum*. Because only inviable eggs were produced on *A. philoxeroides*, population parameters could not be estimated on this host. The mean generation time (T) of *P. marginatus* reared on *C. papaya* was significantly shorter than on *I. batatas* and *S. tuberosum*. Although the R_0 , r and λ values were not significantly changed in the F_1 and F_2 individuals when reared on *C. papaya* and *S. tuberosum*, higher values did occur in the F_1 and F_2 when reared on *I. batatas*.

Table 3. Population parameters of *Paracoccus marginatus* reared on three different host plants (F₀ - F₂).

288

Population parameter	Generation	<i>Carica papaya</i>	<i>Ipomoea batatas</i>	<i>Solanum tuberosum</i>
Net reproductive rate (R_0) (offspring)	F ₀	100.26 ± 13.56aA	16.82 ± 5.31cB	57.36 ± 10.53bA
	F ₁	98.97 ± 15.76aA	70.32 ± 16.63abA	57.98 ± 13.31bA
	F ₂	105.51 ± 4.98aA	74.64 ± 5.09abA	57.88 ± 13.74bA
Intrinsic rate of increase (r) (d ⁻¹)	F ₀	0.1778 ± 0.0053aA	0.0926 ± 0.0109cB	0.1376 ± 0.0069bA
	F ₁	0.1747 ± 0.0064aA	0.1357 ± 0.0080bA	0.1389 ± 0.0084bA
	F ₂	0.1824 ± 0.0064aA	0.1435 ± 0.0075bA	0.1361 ± 0.0085bA
Finite rate of increase (λ) (d ⁻¹)	F ₀	1.1945 ± 0.0064aA	1.0970 ± 0.0119cB	1.1475 ± 0.0079bA
	F ₁	1.1909 ± 0.0076aA	1.1454 ± 0.0091bA	1.1490 ± 0.0097bA
	F ₂	1.2000 ± 0.0076aA	1.1543 ± 0.0086bA	1.1459 ± 0.0097bA
Mean generation time (T) (d)	F ₀	25.92 ± 0.30bA	30.48 ± 1.08aAB	29.43 ± 0.61aA
	F ₁	26.30 ± 0.46cA	31.34 ± 0.42aA	29.23 ± 0.58bA
	F ₂	25.56 ± 0.40bA	30.05 ± 0.39aB	29.81 ± 0.61aA

The data (Mean ± SE) followed by the same letters were not significantly different by paired bootstrap test (P < 0.05). Lowercase letters indicated comparison among different host plants, and capital letters indicated comparison among different generations.

289

290

291

3.3. Population Projection of *P. marginatus*

The population growth and stage structures of *P. marginatus* reared on *C. papaya*, *I. batatas* and *S. tuberosum* (F₂) are shown in Figure 7. Starting with an initial population of 10 newly eclosed 1st instar larvae, *P. marginatus* could develop to the third generation on *C. papaya* within 60 d, with a population size reaching as many as 89,552 individuals. However, only two intact generations were observed on *I. batatas* and *S. tuberosum*, where the population sizes at 60 d were 12,067 and 15,555 individuals, respectively. When the life tables of the 2.5th and 97.5th percentiles of the net reproductive rate (R_0) were used to project the variability of population growth, the population size on *C. papaya* ranged from 49,033 to 144,038. However, when the life tables of the 2.5th and 97.5th percentiles of the finite rate of increase (λ) were used to project the variability of population growth, the population size of *P. marginatus* ranged from 47,452 to 131,289. The stage growth rates ($r_{j,t}$) of *P. marginatus* reared on *C. papaya*, *I. batatas* and *S. tuberosum* in F₂ are shown in Figure 8. The growth rate curves of all stages fluctuated around the intrinsic rate of increase (r).

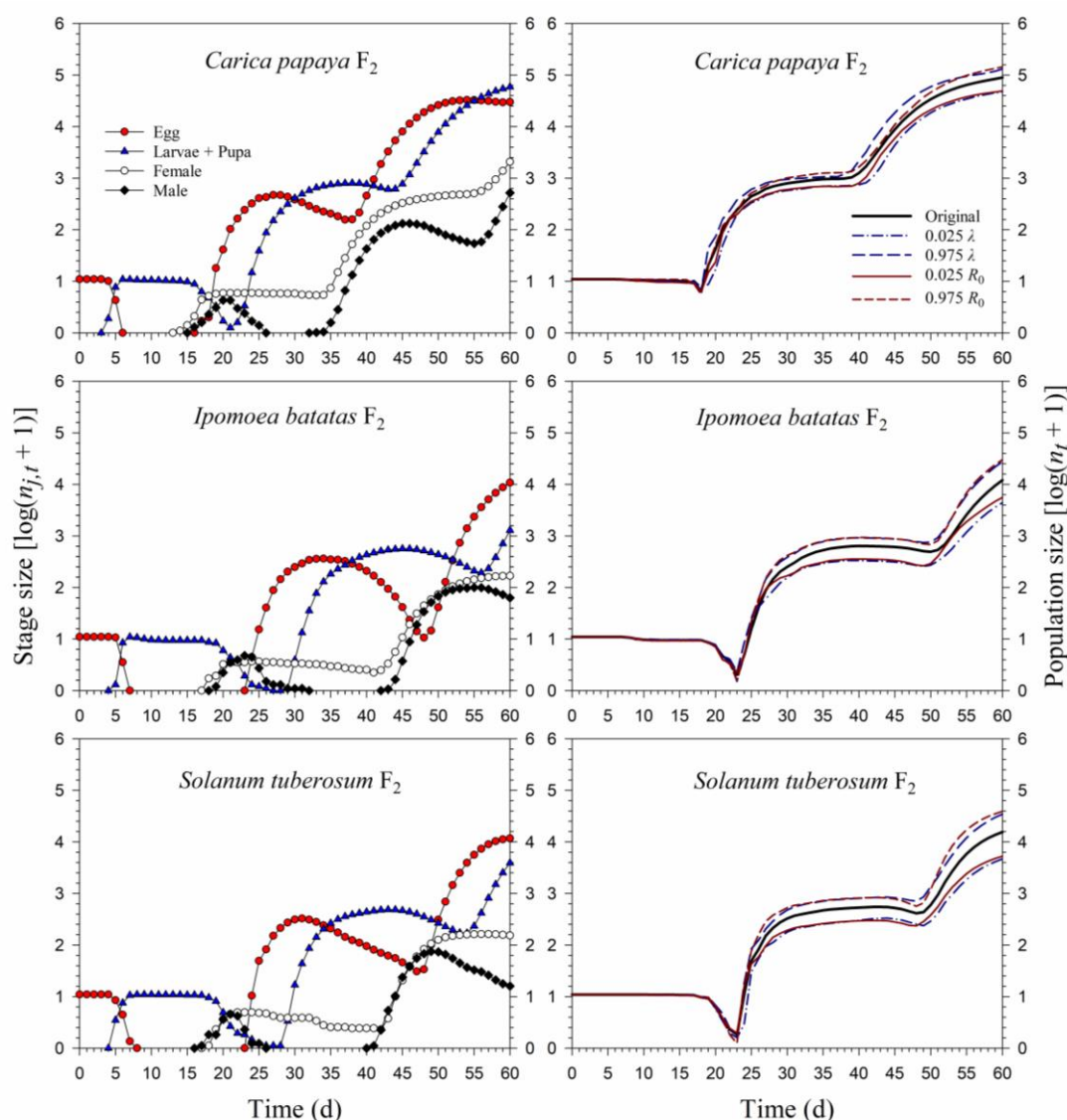


Figure 7. Stage size $[\log(n_{j,t} + 1)]$ and population size $[\log(n_t + 1)]$ of *Paracoccus marginatus* reared on three different host plants (F₂).

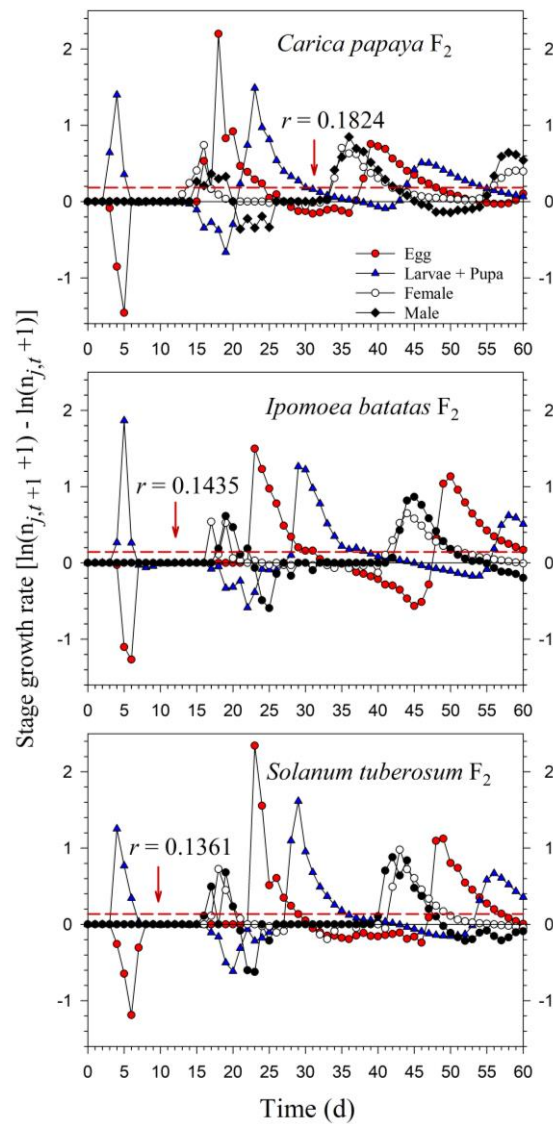


Figure 8. Fluctuation of growth rate of each life stage of *Paracoccus marginatus* reared on three different host plants (F₂). The red vertical dashed line in each figure denotes the intrinsic rate of increase (*r*).

4. Discussion

Multiple factors such as population growth and total egg production should be adequately considered when evaluating the fitness of insect population. The construction and comparison of life tables is the most comprehensive method for describing population growth, development, survival, and reproduction of species. Because insects of different sexes and stages will usually demonstrate different responses when exposed to variations in their host plants, numbers and composition of their biological enemies, extreme climate condition, pesticides, etc., it is necessary to take all of these into consideration prior to formulating an effective pest management strategy (Fu et al. 2016, Chen et al. 2018, Mastoi et al. 2018, Shi et al. 2019). In order to accomplish this, life tables are fundamental to achieving a comprehensive assessment of a population's fitness on a given host plant. Thus, it is important to use the age-

stage, two-sex life table method to assessed the fitness changes that occurred after host plant shifting in *P. marginatus*.

The age-stage, two-sex life table not only includes the male component of a population, but is also capable of describing the overlapping and differentiation of each stage (Huang et al. 2018). Although the males and females of *P. marginatus* have a different number of developmental stages, the stage differentiation can still be precisely described as shown in Figures 1, 2, 5 and Supplementary Figure S1.

Because the hatch rate of eggs varies with the age of the female adults, using only hatched eggs will enable a more accurate estimate of the population parameters being studied (Jha et al. 2012, Mou et al. 2015). The highest fecundity of *P. marginatus* was observed on *C. papaya* ($F = 215.27$ hatched eggs/female). Seni et al. (2015) reported the fecundity of *P. marginatus* on *C. papaya* as 291 total eggs/female (greater than 215.27 hatched eggs/female), however, the hatch rate was omitted in their study.

By using the age-stage, two-sex life table, He et al. (2021) reported a longer developmental duration and lower intrinsic rate of increase for *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) when reared on soybean, while a shorter developmental duration and higher intrinsic rate occurred on sunflower. Karimi-Pormehr et al. (2018) reported a shorter developmental time, higher survival rate and fecundity in *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) on a more suitable cultivar ('19A1') of barley, while noting a longer developmental time and lower fecundity when reared on a less suitable cultivar ('Fajr30'). In this study, when *P. marginatus* was reared on *C. papaya*, the developmental durations of the 1st, 2nd and 3rd instar (female) was significantly reduced (Supplementary Table 1), however, the reverse occurred when reared on *I. batatas* and *S. tuberosum*. While the fecundity of *P. marginatus* was significantly higher on *C. papaya* overall in this study, it was significantly lower on *I. batatas* (F_0). The insects have trade-offs between development and reproduction. When the basic 'development' need of insects were met by suitable host plants, insects tend to allocate more energy to reproduction.

Our results showed that *P. marginatus* reared on *C. papaya* had a significantly higher proportion of female adults (N_f/N), while a lower N_f/N occurred on *I. batatas* in the F_0 generation. Lewontin (1965) demonstrated the first age of reproduction plays an important role on the values of r and λ . When *P. marginatus* was reared on *C. papaya*, reproduction in the F_0 generation started at 18 d, but advanced to 15 d in F_2 . The three days change resulted in the value of r increasing from 0.1778 d^{-1} (F_0) to 0.1824 d^{-1} (F_2), while λ increased from 1.1945 d^{-1} (F_0) to 1.2000 d^{-1} (F_2) (Fig 4-5). Consequently, this change resulted in *P. marginatus* reared on *C. papaya* having higher values for their population parameters (r and λ) due to their higher survival and fecundity on this host. The opposite was true when reared on *I. batatas* and *S. tuberosum*.

By using the age-stage, two-sex life table, the stage structure and fluctuation of growth rate of different stages can be observed using population projection. In addition, the life tables constructed based on the 2.5th and 97.5th percentiles of R_0 and λ can be used to disclose the variabilities that occur during population growth (Huang et al. 2018).

When host plant shifting happens, the fitness of the insect population to the new host plant may recover after a few generations. Quezada et al. (2015) showed that *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) consecutively reared on less nutritional host plants three generations would show an "adaptive response". Meihls et al. (2008) demonstrated that after three generations of being reared on Bt corn, the survival rate of *Diabrotica v. virgifera* (LeConte) (Coleoptera: Chrysomelidae) was comparable to beetles

reared on normal corn. In this study, when *P. marginatus* transferred from *S. tuberosum* to *C. papaya*, all population parameters were significantly higher than that on other plants during three generations. It demonstrated that, even though *P. marginatus* initially **survival** on *S. tuberosum* for multiple generations, the insects transferred to *C. papaya* still had a higher fitness. However, after transferal to *I. batatas*, the fitness of *P. marginatus* initially decreased in F_0 and then rebounded in F_1 and F_2 . *Paracoccus marginatus* showed a higher ability to recover fitness on *I. batatas*. Based on the observation that females were unable to produce viable eggs on *A. philoxeroides*, we concluded that this host was unsuitable for *P. marginatus*. This difference in the fitness of *P. marginatus* to host plants may be due to the volatiles, nutrients of host plants, and so on (unpublished data of authors).

The age-stage, two-sex life table has been used in a number of studies involving adaptation of insects on different host plants. Guo et al. (2021) reported that, compared with reared on potato and tobacco, *Spodoptera frugiperda* reared on maize exhibited a shorter developmental time in the larval period, more female individuals, and higher reproductive rate. Nemati-Kalkhoran et al. (2018) reported life table characteristics of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) on different barley cultivars, demonstrating a higher net reproductive rate and intrinsic rate of increase occurred on the cultivar 'Mahoor'. Jaleel et al. (2018) reported that *Bactrocera dorsalis* (Diptera: Tephritidae) females produced more eggs on guava than banana.

Cipollini and Peterson (2018) pointed out potential effects of host shifting including the importance of phytophagous insects being able to find and utilize their ancestral hosts, potentially leading to host range expansions. The present study **reported** the fitness of *P. marginatus* after transferal from *S. tuberosum* to *C. papaya*, *I. batatas* and *A. philoxeroides*. Because *I. batatas* and *S. tuberosum* are important food crops and *C. papaya* is an important fruit (Tan et al. 2015, Singh et al. 2021, Tian et al. 2021). Our results demonstrate the potential damage of *P. marginatus* to *I. batatas* and *S. tuberosum*, and again verify the severe damage of *P. marginatus* to *C. papaya*, even if insects transfer from suboptimal host plants. These results indicate that outbreaks of *P. marginatus* are possible in the future and, should they occur, may result in serious economic damage.

Supplementary Materials: The following supporting information are available at *Insects* online, Table S1: Developmental time of *Paracoccus marginatus* reared on four different host plants ($F_0 - F_2$); Figure S1: Age-stage-specific life expectancy (e_{xj}) of *Paracoccus marginatus* reared on three different host plants (F_1-F_2); Figure S2: Age-stage-specific reproductive value (v_{xj}) of *Paracoccus marginatus* reared on three different host plants (F_1-F_2).

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