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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. To improve our understanding of the expansion and prevalence of *P. marginatus* individuals on host plants, it is important to explore the fitness changes of insects after host plant shifting. In this study, we measured the development, fecundity, and population parameters in *P. marginatus* individuals over a span of three consecutive generations after being transferred from potato (*Solanum tuberosum*) to papaya (*Carica papaya*), sweet potato (*Ipomoea batatas*), and alligator weed (*Alternanthera philoxeroides*). Further, the population growth rates of insects on *C. papaya*, *I. batatas*, and *S. tuberosum* in the F2 generation were projected. We found that *P. marginatus* individuals transferred to *C. papaya* had higher fitness. When transferred to *I. batatas*, the fitness of *P. marginatus* initially decreased in F0 and then rebounded in F1 and F2. *Paracoccus marginatus* individuals could rapidly expand their populations on the above host plants. However, *P. marginatus* individuals were unable to complete their development on *A. philoxeroides*. Our findings provide new insights into the host plant fitness, prevalence, and potential pest control of *P. marginatus*.

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 suck-
We also predicted that with nutrient soil (Cuijun, Fuzhou, China) and kept in growth chambers (PRX-450D, Haishu P.Amarasekare et al. (2008) reported the survival rates of (L: D) h. Young leaves (<30-d old) were used for the study. (166x323) The host plants were cultivated (40.0 cm in length, 30.0 cm in width, and 15.0 cm in height) (Paracoccus marginatus) projected the population growth of the insects on (C. marginatus) used for a number of years as a host for the mass-rearing of P. marginatus in the laboratory.

The eggs of P. marginatus were originally obtained from a papaya orchard in Fuzhou city (Fujian Province, China, 25°15′–26°39′ N, 118°08′–120°31′ E), and reared on the leaves of S. tuberosum in a growth chamber for 20 generations to allow P. marginatus to adapt to ing sap from the leaves, stems, and other plant parts [1]. Since the 1990s, P. marginatus had spread rapidly through the Americas, Africa, and most provinces of southern China [2,3]. Paracoccus marginatus is a polyphagous pest of many economic crops and weeds included in more than 64 families, such as Euphorbiaceae, Rubiaceae, and Caricaceae [4]. In our preliminary field investigation, P. marginatus was 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 alligator weed (Alternanthera philoxeroides (Centrospermae: Amaranthaceae)). Most of the insects were observed on the leaves of the above plants. Solanum tuberosum has been used for a number of years as a host for the 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 Phenococcus solenopsis (Tinsley) (Hemiptera: Pseudococcidae) was due to its efficient host plant fitness [5]. The fitness of insects on a new host plant can be evaluated from the population growth rate on the new host plant versus their old host plant [6,7]. 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 [8]. Mody et al. (2007) demonstrated that host plant shifting had a strong effect on Chrysopsycha imparilis (Lepidoptera: Lasiocampidae), especially in adult fecundity and the mean body mass of second-instar larvae [9]. 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 (R0) significantly increased when transferred from wheat to cotton [10]. Amarasekare et al. (2008) reported the survival rates of P. marginatus on different host plants [11]. Nisha and Kennedy (2017), using the female age-specific life table, reported the life table results for P. marginatus on different host plants [12]. However, the results were limited by ignoring the males in the population [13].

We hypothesized that the fitness of P. marginatus would change after host plant shifting. We also predicted that P. marginatus can readily adapt to some new host plants within a few generations. To test these hypotheses, we measured the development, fecundity, and population parameters in P. marginatus over a span of three consecutive generations after being transferred from S. tuberosum to C. papaya, I. batatas, and A. philoxeroides. Further, we projected the population growth of the insects on C. papaya, I. batatas, and S. tuberosum in the F2 generation.

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. The 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 ± 1 °C, 70 ± 5% RH, with 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°15′–26°39′ N, 118°08′–120°31′ E), and reared on the leaves of S. tuberosum in a growth chamber for 20 generations to allow P. marginatus to adapt to

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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 male life cycle includes 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 observe the lifespan of each insect, the 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 estimate the life table parameters [14]. 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 for three consecutive generations (F₀, F₁, and F₂) were recorded. Paracoccus marginatus reared on A. philoxeroides only survived for a single generation (F₀); therefore, 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 individuals of P. marginatus, including the developmental duration, longevity, and female fecundity, were analyzed according to the age-stage, two-sex life table procedure [15,16] using the program TWOSEX-MSChart [17]. The variances and standard errors of parameters were estimated using the bootstrap technique [18,19]. The differences between treatments were assessed using paired bootstrap tests [20]. The age-stage-specific survival rate (sₓj) is the probability that each hatched egg will survive to age x and stage j. The age-specific survival rate (lₓ) was calculated as:

\[ l_x = \sum_{j=1}^{k} s_{xj} \]

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

\[ m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \]

The intrinsic rate of increase (\( r \)) was estimated using the Euler–Lotka equation [21,22] with the age indexed from 0 [23]:

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

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

\[ \lambda = e^r \]
\[ R_0 = \sum_{x=0}^{\infty} l_x m_x \]
\[ T = \frac{\ln R_0}{r} \]

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) [24]:

\[ e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{a} s'_{iy} \]
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 of each individual in age \( x \) and stage \( j \) makes to the future population \([25,26]\), was calculated as:

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

2.5. Population Projection

The population growth of \( P.\ marginatus \) was simulated according to Chi (1990) \([27]\) by using the computer program TIMING-MSChart \([28]\). 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) \([29]\).

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

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

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

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

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

3. Results

3.1. Development and Fecundity of \( P.\ marginatus \) after Host Plant Shifting

There were no significant differences in egg duration among the four host plants in the \( F_0 \) generation. However, the developmental times of female and male nymphs fed on \( C.\ papaya \) were significantly shorter than those on the other three hosts. Extremely long developmental times occurred in both female and male nymphs when fed on \( A.\ philoxeroides \). The detailed development durations for each instar are contained in Supplementary Table S1. The female adults reared on \( C.\ papaya \) lived significantly longer than those fed on the other three plants. The egg duration was, however, significantly longer in the \( F_1 \) and \( F_2 \) generations when reared on \( I.\ batatas \) and \( S.\ tuberosum \). The durations of male nymphs on \( I.\ batatas \) and \( S.\ tuberosum \) were shortened in the \( F_1 \) and \( F_2 \) generations. The durations of the female nymphs were unchanged when reared on the three host plants. The female adult longevities were unchanged on \( C.\ papaya \) and \( I.\ batatas \), but were shortened on \( S.\ tuberosum \). The adult longevities of the males were shortened on \( I.\ batatas \) and \( S.\ tuberosum \), but unchanged on \( C.\ papaya \) (Table 1).
The age-stage life table is capable of describing the stage differentiation; therefore, obvious stage overlapping can be observed. When *P. marginatus* individuals were reared on *A. philoxeroides* in F₀, 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 (Figure 1). In contrast, the survival rates increased to 0.367 on *C. papaya* (F₀) and 0.933 in F₂. Lower survival rates were observed on *I. batatas* (0.170). An extremely low *N₁/N₀* value (0.023) was observed on *A. philoxeroides*. In the F₂ generation, the *N₁/N₀* values remained constant on *C. papaya* and *S. tuberosum*, but increased to 0.367 on *I. batatas*. In F₀, a significantly high proportion of male adults (N₃ₐ/N₀) of *P. marginatus* was observed on *I. batatas* (0.650). The N₃ₐ/N₀ values on *C. papaya* and *S. tuberosum* were 0.411 and 0.440, respectively. An extremely low N₃ₐ/N₀ ratio (0.090) was observed on *A. philoxeroides*. The N₃ₐ/N₀ ratio did not change from F₁ to F₂ (Table 2).

In the F₀ 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*. None of the eggs produced on this host were viable, so the mean fecundity was zero (Table 2). Lower fecundity rates were observed on *I. batatas* and *S. tuberosum*, with 98.83 hatched eggs/female and 127.46 hatched eggs/female, respectively. On *I. batatas*, the fecundity increased in F₁ (229.50 hatched eggs/female) and F₂ (203.76 hatched eggs/female) (Table 2).

### Table 1. The developmental times of *Paracoccus marginatus* individuals reared on four different host plants (F₀-F₂).

| Stage (d)       | Generation | Carica papaya | Ipomoea batatas | Solanum tuberosum | Alternanthera philoxeroides |
|-----------------|------------|---------------|-----------------|-------------------|----------------------------|
|                 | n          | Mean ± SE     | n               | Mean ± SE         | n                          | Mean ± SE                  |
| Egg             | F₀         | 95            | 5.18 ± 0.04 aA  | 100               | 5.21 ± 0.04 aC           | 100                        | 5.20 ± 0.08 aB             |
|                 | F₁         | 92            | 5.16 ± 0.06 bA  | 98                | 6.22 ± 0.05 aB           | 88                         | 6.26 ± 0.06 aA             |
|                 | F₂         | 100           | 5.24 ± 0.06 cA  | 90                | 6.91 ± 0.04 aA           | 84                         | 6.13 ± 0.09 bA             |
| Female nymph    | F₀         | 47            | 12.36 ± 0.16 aC | 17                | 14.29 ± 0.41 bA          | 45                         | 14.04 ± 0.30 bA            |
|                 | F₁         | 45            | 11.98 ± 0.18 bA | 30                | 14.00 ± 0.31 aA          | 40                         | 15.07 ± 0.47 aA            |
|                 | F₂         | 49            | 12.24 ± 0.16 bA | 33                | 13.70 ± 0.34 aA          | 40                         | 14.32 ± 0.35 aA            |
| Male nymph      | F₀         | 39            | 13.92 ± 0.21 aA | 65                | 17.18 ± 0.30 bA          | 44                         | 15.43 ± 0.20 cA            |
|                 | F₁         | 40            | 13.50 ± 0.26 bA | 53                | 15.53 ± 0.24 aB          | 44                         | 15.20 ± 0.19 aAB           |
|                 | F₂         | 44            | 13.64 ± 0.21 cA | 51                | 15.55 ± 0.15 aB          | 38                         | 14.61 ± 0.24 bB            |
| Female adult    | F₀         | 47            | 20.09 ± 0.55 aA | 17                | 15.65 ± 1.23 bA          | 45                         | 19.87 ± 0.94 bA            |
|                 | F₁         | 45            | 19.18 ± 0.56 aA | 30                | 18.53 ± 1.63 aA          | 40                         | 13.97 ± 1.27 bB            |
|                 | F₂         | 49            | 19.67 ± 0.56 aA | 33                | 17.12 ± 1.22 aA          | 40                         | 14.28 ± 1.44 bB            |
| Male adult      | F₀         | 39            | 3.28 ± 0.18 aA  | 65                | 3.48 ± 0.14 aA           | 44                         | 3.41 ± 0.20 aA             |
|                 | F₁         | 40            | 3.48 ± 0.17 aA  | 53                | 3.21 ± 0.14 aAB          | 44                         | 3.11 ± 0.15 aAB            |
|                 | F₂         | 44            | 3.50 ± 0.16 aA  | 51                | 3.00 ± 0.13 bB           | 38                         | 2.87 ± 0.13 bB             |

The data (means ± SE) followed by the same letters were not significantly different as assessed by paired bootstrap test (p < 0.05). The lowercase letters in the same row indicated comparisons among different host plants in the same generations, and the capital letters in the same column indicated comparisons among different generations on the same host plants. The 1st instar, 2nd instar, 3rd instar, and pupae samples were combined into nymph samples for the data statistics.
Proportion of female adults

Population Parameter | Generation | Carica papaya | Ipomoea batatas | Solanum tuberosum | Alternanthera philoxeroides
--- | --- | --- | --- | --- | ---
Preadult survival rate ($s_{xj}$) | F$_0$ | 0.905 ± 0.030 aA | 0.820 ± 0.038 aB | 0.890 ± 0.031 aA | 0.110 ± 0.031 b 
F$_1$ | 0.924 ± 0.028 abA | 0.847 ± 0.036 bb | 0.955 ± 0.022 aA | - 
F$_2$ | 0.930 ± 0.026 aA | 0.933 ± 0.026 aA | 0.929 ± 0.028 aA | - 

Proportion of female adults ($N_{f}/N$) | F$_0$ | 0.495 ± 0.051 aA | 0.170 ± 0.038 bB | 0.450 ± 0.050 aA | 0.023 ± 0.012 c 
F$_1$ | 0.489 ± 0.052 aA | 0.306 ± 0.047 bA | 0.455 ± 0.053 aA | - 
F$_2$ | 0.490 ± 0.050 aA | 0.367 ± 0.051 aA | 0.476 ± 0.055 aA | - 

Proportion of male adults ($N_{m}/N$) | F$_0$ | 0.411 ± 0.050 bA | 0.650 ± 0.048 aA | 0.440 ± 0.049 bA | 0.090 ± 0.050 c 
F$_1$ | 0.435 ± 0.052 aA | 0.541 ± 0.050 aA | 0.500 ± 0.053 aA | - 
F$_2$ | 0.440 ± 0.049 aA | 0.567 ± 0.052 aA | 0.452 ± 0.054 aA | - 

Fecundity ($F$) (hatch eggs/female) | F$_0$ | 202.70 ± 17.68 aA | 98.93 ± 23.04 bB | 127.46 ± 18.79 bA | 0 
F$_1$ | 202.46 ± 24.08 aA | 229.50 ± 41.84 aA | 127.38 ± 25.40 bA | - 
F$_2$ | 215.27 ± 20.32 aA | 203.76 ± 35.72 abA | 121.51 ± 25.35 bA | - 

The data (means ± SE) followed by the same letters were not significantly different as assessed by paired bootstrap test ($p < 0.05$). The lowercase letters in the same row indicated comparisons among different host plants in the same generations, and the capital letters in the same column indicated comparisons among different generations on the same host plants.

Figure 1. Age-stage-specific survival rates ($s_{xj}$) of Paracoccus marginatus individuals reared on four different host plants (F$_0$).

Table 2. Preadult survival rates ($s_{x}$), proportions of female adults ($N_{f}/N$), proportions of male adults ($N_{m}/N$), and fecundity rates ($F$) of Paracoccus marginatus individuals reared on four different host plants (F$_0$–F$_2$).
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Fecundity (F) (hatch eggs/female) F0 202.70 ± 17.68 aA 98.93 ± 23.04 bB 127.46 ± 18.79 bA 0 F 1 202.46 ± 24.08 aA 229.50 ± 41.84 aA 127.38 ± 25.40 bA - F 2 215.27 ± 20.32 aA 203.76 ± 35.72 abA 121.51 ± 25.35 bA -

The data (means ± SE) followed by the same letters were not significantly different as assessed by paired bootstrap test (p < 0.05). The lowercase letters in the same row indicated comparisons among different host plants in the same generations, and the capital letters in the same column indicated comparisons among different generations on the same host plants.

Figure 2. Age-stage-specific survival rates (sxj) of Paracoccus marginatus individuals reared on three different host plants (F1–F2).

The age-specific survival rate (lx) curve is the simplified version of sxj; thus, the stage differentiation is not observable. The 50% survival rates of P. marginatus in F0 occurred at 26, 25, 26, and 13 d on C. papaya, I. batatas, S. tuberosum, and A. philoxeroides, respectively (Figure 3). In F2, the 50% survival rates of P. marginatus on I. batatas and S. tuberosum changed at 26 and 24 d, respectively (Figure 4). Higher curves of the age-specific fecundity (mx) and net maternity (lxmx) were observed on C. papaya in F0. Although there was a relatively high peak of 27 eggs at 40 d on I. batatas, the low survival rate (lx) caused the net maternity rates (lxmx) to be very low. When reared on S. tuberosum, the high peak of mx (18.4 eggs) occurred at 26 d, and the remaining mx values were, for the most part, greater than 5 eggs (Figure 3). The mx and lxmx values on C. papaya and S. tuberosum did not change significantly; they did, however, increase on I. batatas during the F1 and F2 generations (Figure 4).
Figure 3. Age-specific survival \((l_x)\), fecundity \((m_x)\), and net maternity \((l_xm_x)\) rates of Paracoccus marginatus individuals reared on four different host plants \((F_0)\). The red vertical dashed lines in the figure denote the age at which the survival rate \(l_x \leq 0.5\).

The life expectancy rates of newly laid eggs of \(P.\ marginatus\) were 29.0, 24.5, 29.3, and 14.9 d in \(F_0\). 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; hence, the \(c_{ij}\) curve of the 2nd instar was significantly higher than in the 1st instar (Figure 5). The detailed \(c_{ij}\) curves on \(C.\ papaya, I.\ batatas,\) and \(S.\ tuberosum\) during \(F_1\) and \(F_2\) are shown in Supplementary Figure S1.

The age-stage-specific reproductive values \((v_{ij})\) at age zero were exactly equal to the finite rates of increase \((\lambda)\), i.e., 1.1945, 1.0970, and 1.1475. The \(v_{ij}\) increased with age. When reared on \(I.\ batatas\) in \(F_0\), the \(v_{ij}\) curve significantly increased when female adults emerged. Similar increases in the \(v_{ij}\) curves were observed on \(C.\ papaya\) and \(S.\ tuberosum\); due to the high percentage of female adults, however, this increase was not obvious. The peak dates of \(v_{ij}\) were close to the total preoviposition period \((TPOP)\) (Figure 6). The detailed \(v_{ij}\) curves on \(C.\ papaya, I.\ batatas,\) and \(S.\ tuberosum\) for \(F_1\) and \(F_2\) are shown in Supplementary Figure S2.

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. The highest values of the net reproductive rate \((R_0)\), intrinsic rate of increase \((r)\), and finite rate of increase \((\lambda)\) 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 \(\lambda\) values were observed when reared on \(I.\ batatas\) and \(S.\ tuberosum\). Only inviable eggs were produced on \(A.\ philoxeroides\); thus, the 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 \(\lambda\) 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 \(F_2\) generations when reared on \(I.\ batatas\) (Table 3).
Figure 4. Age-specific survival ($l_x$), fecundity ($m_x$), and net maternity ($l_xm_x$) rates of *Paracoccus marginatus* individuals reared on three different host plants (F1–F2). The red vertical dashed lines in the figure denote the age at which the survival rate $l_x \leq 0.5$.

Figure 5. Age-stage-specific life expectancy ($e_{xj}$) rates of *Paracoccus marginatus* individuals reared on four different host plants (F0).
Figure 5. Age-stage-specific life expectancy (exj) rates of *Paracoccus marginatus* individuals reared on four different host plants (F0).

Figure 6. Age-stage-specific reproductive value (vxj) rates of *Paracoccus marginatus* individuals reared on three different host plants (F0). The red vertical dashed line in each figure denotes the total preoviposition period (TPOP).

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

| Population Parameter         | Generation | *Carica papaya* | *Ipomoea batatas* | *Solanum tuberosum* |
|------------------------------|------------|------------------|-------------------|---------------------|
| Net reproductive rate (R0) (offspring) | F0         | 100.26 ± 13.56 aA | 16.82 ± 5.31 cB   | 57.36 ± 10.53 bA    |
|                              | F1         | 98.97 ± 15.76 aA | 70.32 ± 16.63 abA | 57.98 ± 13.31 bA    |
|                              | F2         | 105.51 ± 4.98 aA | 74.64 ± 5.09 abA  | 57.88 ± 13.74 bA    |
| Intrinsic rate of increase (r) (d⁻¹) | F0         | 0.1778 ± 0.0053 aA | 0.0926 ± 0.0109 cB | 0.1376 ± 0.0069 bA  |
|                              | F1         | 0.1747 ± 0.0064 aA | 0.1357 ± 0.0080 bA | 0.1389 ± 0.0084 bA  |
|                              | F2         | 0.1824 ± 0.0064 aA | 0.1435 ± 0.0075 bA | 0.1361 ± 0.0085 bA  |
| Finite rate of increase (λ) (d⁻¹) | F0         | 1.1945 ± 0.0064 aA | 1.0970 ± 0.0119 cB | 1.1475 ± 0.0079 bA  |
|                              | F1         | 1.1909 ± 0.0076 aA | 1.1454 ± 0.0091 bA | 1.1490 ± 0.0097 bA  |
|                              | F2         | 1.2000 ± 0.0076 aA | 1.1543 ± 0.0086 bA | 1.1459 ± 0.0097 bA  |
| Mean generation time (T) (d)  | F0         | 25.92 ± 0.30 bA   | 30.48 ± 1.08 aAB  | 29.43 ± 0.61 aA     |
|                              | F1         | 26.30 ± 0.46 cA   | 31.34 ± 0.42 aA   | 29.23 ± 0.58 bA     |
|                              | F2         | 25.56 ± 0.40 bA   | 30.05 ± 0.39 aB   | 29.81 ± 0.61 aA     |

The data (means ± SE) followed by the same letters were not significantly different as assessed by paired bootstrap test (p < 0.05). The lowercase letters in the same row indicated comparisons among different host plants in the same generations, and the capital letters in the same column indicated comparisons among different generations on the same hosts.
3.3. Population Projection of *P. marginatus*

Starting with an initial population of 10 newly enclosed 1st-instar nymphs, *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 (*R₀*) were used to project the variability of the population growth, the population sizes 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 sizes of *P. marginatus* ranged from 47,452 to 131,289 (Figure 7). The growth rate curves of all stages fluctuated around the intrinsic rate of increase (*r*) (Figure 8).

![Figure 7. Stage size (log (*n*_j,t + 1)) and population size (log (*n*_t + 1)) rates of *Paracoccus marginatus* individuals reared on three different host plants (F2).](image-url)
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Figure 8. Fluctuations in the growth rates of each life stage of Paracoccus marginatus individuals reared on three different host plants (F2). The red vertical dashed lines in each figure denote the intrinsic rate of increase (r).

4. Discussion

With the intention to improve our understanding in the fitness changes of P. marginatus after host plant shifting, we investigated the development, fecundity, and population parameters in P. marginatus within three consecutive generations after being transferred from S. tuberosum to C. papaya, I. batatas, and A. philoxeroides. In addition, the population growth rates of the insects on C. papaya, I. batatas, and S. tuberosum were projected. The study showed that P. marginatus transferred to C. papaya had a higher fitness level. When transferred to I. batatas, the fitness decreased initially and then recovered after two generations. Paracoccus marginatus individuals could rapidly expand their populations on the above host plants. Alternanthera philoxeroides was not suitable for the development of P. marginatus.

Multiple factors such as the population growth and total egg production should be adequately considered when evaluating the fitness of an insect population. The construction and comparison of life tables is the most comprehensive method for describing the population growth, development, survival, and reproduction of a species. Insects of different sexes and stages will usually demonstrate different responses when exposed to variations.
in their host plants, the numbers and composition of their biological enemies, extreme climate conditions, and pesticides, and consequently it is necessary to take all of these into consideration prior to formulating an effective pest management strategy [30–33]. 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 was 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 [29]. Although the males and females of P. marginatus have different numbers of developmental stages, the stage differentiation can still be precisely described.

The hatch rates of eggs vary with the age of the female adults; hence, using only hatched eggs will enable a more accurate estimate of the population parameters being studied [14,34]. 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) [35]; 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 [36]. Karimi-Fornehr et al. (2018) reported a shorter developmental time, higher survival rate, and greater fecundity in Sitotherea cerealella (Olivier) (Lepidoptera: Gelechiidae) on a more suitable cultivar (‘19A,’) of barley, while noting a longer developmental time and lower fecundity when reared on a less suitable cultivar (‘Fajr30’) [37]. In this study, when P. marginatus was reared on C. papaya, the developmental durations of the 1st, 2nd, and 3rd instar (female) individuals were significantly reduced (Supplementary Table S1); 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 (F0). The insects have trade-offs between development and reproduction. When the basic ‘development’ need of insects are 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 (Nf/N), while a lower Nf/N occurred on I. batatas in the F0 generation. Lewontin (1965) demonstrated that the first age of reproduction plays an important role in the values of r and λ [38]. When P. marginatus was reared on C. papaya, reproduction in the F0 generation started at 18 d, but advanced to 15 d in F2. The three-day change resulted in the value of r increasing from 0.1778 d⁻¹ (F0) to 0.1824 d⁻¹ (F2), while λ increased from 1.1945 d⁻¹ (F0) to 1.2000 d⁻¹ (F2) (Figures 4 and 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 rates 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 fluctuations in growth rate in different stages can be observed using population projection. In addition, the life tables constructed based on the 2.5th and 97.5th percentiles of R0 and λ can be used to disclose the variabilities that occur during population growth [29].

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 for three generations would show an adaptive response [39]. 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 [40]. In this study, when P. marginatus transferred from S. tuberosum to C. papaya, all population parameters were significantly higher than on other plants during three generations. This demonstrated that even though P. marginatus initially survived on...
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S. tuberosum for multiple generations, the insects transferred to C. papaya still had a higher fitness level. However, after transferal to I. batatas, the fitness of P. marginatus initially decreased in F₀ and then rebounded in F₁ and F₂. Paracoccus marginatus showed a higher ability to recover fitness on I. batata. 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 differences in the fitness of P. marginatus to host plants may be due to the volatiles, nutrients of host plants, and so on (unpublished data from the authors).

The age-stage, two-sex life table has been used in a number of studies involving the adaptation of insects on different host plants. Guo et al. (2021) reported that compared with being reared on potato and tobacco, Spodoptera frugiperda reared on maize exhibited a shorter developmental time in the larval period, more female individuals, and a higher reproductive rate [41]. Nemati-Kalkhoran et al. (2018) reported the life table characteristics of Rhizopertha dominica (Coleoptera: Bostrichidae) on different barley cultivars, demonstrating that a higher net reproductive rate and intrinsic rate of increase occurred on the cultivar ‘Mahoor’ [42]. Jaleel et al. (2018) reported that Bactrocera dorsalis (Diptera: Tephritidae) females produced more eggs on guava than banana [43].

Cipollini and Peterson (2018) pointed out the 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 [44]. The present study reports the fitness of P. marginatus after transferal from S. tuberosum to C. papaya, I. batatas, and A. philoxeroides. Ipomoea batatas and S. tuberosum are important food crops and C. papaya is an important fruit [45–47]. 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 the 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. This study provides new insights into the host plant fitness, prevalence, and potential pest control of P. marginatus.

Supplementary Materials: The following supporting information are available at: https://www.mdpi.com/article/10.3390/insects13090804/s1. Table S1: Developmental times of Paracoccus marginatus individuals reared on four different host plants (F₀–F₂). Figure S1: Age-stage-specific life expectancy (eₓ) rates of Paracoccus marginatus individuals reared on three different host plants (F₁–F₂). Figure S2: Age-stage-specific reproductive value (eₓj) rates of Paracoccus marginatus individuals reared on three different host plants (F₁–F₂).

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References

1. Wu, F.Z.; Liu, Z.H.; Shen, H.; Yu, F.; Ma, J.; Hu, X.N.; Zeng, L. Morphological and molecular identification of *Paracoccus marginatus* (Hemiptera: Pseudococcidae) in Yunnan, China. *Fla. Entomol.* 2014, 97, 1469-1473. [CrossRef]

2. Miller, D.R.; Williams, D.J. Notes on a new mealybug (Hemiptera: Cocccoidae: Pseudococcidae) pest in Florida and the Caribbean: The papaya mealybug, *Paracoccus marginatus* Williams and Granara de Willink. *Insecta Mundi*. 1999, 13, 179–181.

3. Finch, E.A.; Beale, T.; Chellappan, M.; Goergen, G.; Gadratagi, B.G.; Khan, M.A.; Rehman, M.A.; Rwomushana, I.; Sarma, A.K.; Wyckhuys, K.A.; et al. The potential global distribution of the papaya mealybug, *Paracoccus marginatus*, a polyphagous pest. *Pest Manag. Sci.* 2021, 77, 1361–1370. [CrossRef]

4. Krishnan, J.U.; George, M.; Ajesh, G.; Jithine, J.R.; Lekshmi, N.R.; Deepasree, M.I. A review on *Paracoccus marginatus* Williams, papaya mealybug (Hemiptera: Pseudococcidae). *J. Entomol. Zool. Stud.* 2016, 4, 528–533.

5. Huang, F.; Zhang, Z.J.; Li, W.D.; Lin, W.C.; Zhang, P.J.; Zhang, J.M.; Bei, Y.W.; He, Y.P.; Lu, Y.B. Host plant probing analysis reveals quick settlement of the solenopsis mealybug during host shift. *J. Econ. Entomol.* 2014, 107, 1419–1425. [CrossRef]

6. Lu, H.; Yang, P.C.; Xu, Y.Y.; Luo, L.; Zhu, J.; Cui, N.; Kang, L.; Cui, F. Performances of survival, feeding behavior, and gene expression in aphids reveal their different fitness to host alteration. *Sci. Rep.* 2016, 6, 19344. [CrossRef]

7. Ning, S.Y.; Zhang, W.C.; Sun, Y.; Feng, J.N. Development of insect life tables: Comparison of two demographic methods of *Delia antiqua* (Diptera: Anthomyiidae) on different hosts. *Sci. Rep.* 2017, 7, 4821. [CrossRef]

8. Milanović, S.; Janković-Tomanić, M.; Kostić, I.; Kostić, M.; Morina, F.; Živanović, B.; Lazarević, J. Behavioural and physiological plasticity of gypsy moth larvae to host plant switching. *Entomol. Exp. Et Appl.* 2016, 158, 152–162. [CrossRef]

9. Mody, K.; Unsicker, S.B.; Linsenmair, K.E. Fitness related diet-mixing by intraspecific host-plant-switching of specialist insect herbivores. *Ecology* 2007, 88, 1012–1020. [CrossRef]

10. Amarasekare, K.G.; Mannion, C.M.; Osborne, L.S.; Epsky, N.D. Life history of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table. *Entomol. Gen. 2020,* 113, 2343–2353. [CrossRef]

11. Euler, L. De aptissima figura rotarum dentibus tribuenda. *Novi Comment. Acad. Sci. Petropolitanae* 1760, 17, 299–316.

12. Lack, D.A. Studies on the mode of growth of material aggregates. *Am. J. Sci.* 1907, 24, 199–216. [CrossRef]

13. Goodman, D. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.* 1982, 119, 803–823. [CrossRef]

14. Chi, H.; Su, H.Y. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ. Entomol.* 2006, 35, 10–21. [CrossRef]

15. Fisher, R.A. *The Genetical Theory of Natural Selection*; Clarendon Press: Oxford, UK, 1930.

16. Tuan, S.J.; Lee, C.C.; Chi, H. Population and damage projection of *Spodoptera littura* (L.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table. *Pest Manag. Sci.* 2014, 70, 805–813. [CrossRef] [PubMed]

17. Chi, H. Timing of control based on the stage structure of pest populations: A simulation approach. *J. Econ. Entomol.* 1990, 83, 1143–1150. [CrossRef]

18. Huang, H.W.; Chi, H.; Smith, C.L. Linking demography and consumption of *Henosepilachna vigintioctopunctata* (Coleoptera: Coccinellidae) fed on *Solanum photeinocarpum*: With a new method to project the uncertainty of population growth and consumption. *J. Econ. Entomol.* 2018, 111, 1–9. [CrossRef]
30. Fu, J.W.; Shi, M.Z.; Wang, T.; Li, J.Y.; Zheng, L.Z.; Wu, G. Demography and population projection of flea beetle, *Agasicles hygrophila* (Coleoptera: Chrysomelidae), fed on alligator weed under elevated CO$_2$. *J. Econ. Entomol.* 2016, 109, 1116–1124. [CrossRef]

31. Chen, G.M.; Chi, H.; Wang, R.C.; Wang, Y.P.; Xu, Y.Y.; Li, X.D.; Yin, P.; Zheng, F.Q. Demography and uncertainty of population growth of *Conogethes punctiferalis* (Lepidoptera: Crambidae) reared on five host plants with discussion on some life history statistics. *J. Econ. Entomol.* 2018, 111, 2143–2152. [CrossRef]

32. Mastoi, M.I.; Adam, N.A.; Muhamad, R.; Ghani, I.A.; Gilal, A.A.; Khan, J.; Bhatti, A.R.; Zia, A.; Sahito, J.G.M. Efficiency of *Acerophagus papayae* on different host stage combinations of papaya mealybug, *Paracoccus marginatus*. *Pak. J. Agric. Sci.* 2018, 55, 375–379.

33. Shi, M.Z.; Li, J.Y.; Ding, B.; Fu, J.W.; Zheng, L.Z.; Chi, H. Indirect effect of elevated CO$_2$ on population parameters and growth of *Agasicles hygrophila* (Coleoptera: Chrysomelidae), a biocontrol agent of alligatorweed (Amaranthaceae). *J. Econ. Entomol.* 2019, 112, 1120–1129. [CrossRef]

34. Jha, R.K.; Chi, H.; Tang, L.C. Effects of survival rate and fecundity on the intrinsic rate of increase of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Formos. Entomol.* 2012, 32, 223–235.

35. Seni, A.; Sahoo, A.K. Biology of *Paracoccus marginatus* Williams and Granara de Willink (Hemiptera: Pseudococcidae) on papaya, parthenium and brinjal plants. *Res. Crop.* 2015, 16, 722–727. [CrossRef]

36. He, L.M.; Wu, Q.L.; Gao, X.W.; Wu, K.M. Population life tables for the invasive fall armyworm, *Spodoptera frugiperda* fed on major oil crops planted in China. *J. Integr. Agric.* 2021, 20, 745–754. [CrossRef]

37. Karimi-Pormehr, M.S.; Borzoui, E.; Naseri, B.; Dastjerdi, H.R.; Mansouri, S.M. Two-sex life table analysis and digestive physiology of *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) on different barley cultivars. *J. Stored Prod. Res.* 2018, 75, 64–71. [CrossRef]

38. Lewontin, R.C. *Selection for Colonizing Ability*; Baker, H.G., Stebbins, G.L., Eds.; The Genetics of Colonizing Species; Academic Press: San Diego, CA, USA, 1965; pp. 77–94.

39. Quezada, G.R.; Seehausen, M.L.; Bauce, É. Adaptation of an outbreaking insect defoliator to chronic nutritional stress. *J. Evolution. Biol.* 2015, 28, 347–355. [CrossRef]

40. Meihls, L.N.; Higdon, M.L.; Siegfried, B.D.; Miller, N.J.; Sappington, T.W.; Ellersieck, M.R.; Spencerc, T.A.; Hibbard, B.E. Increased survival of western corn rootworm on transgenic corn within three generations of on-plant greenhouse selection. *Proc. Natl. Acad. Sci. USA* 2008, 105, 19177–19182. [CrossRef]

41. Guo, J.F.; Zhang, M.D.; Gao, Z.P.; Wang, D.J.; He, K.L.; Wang, Z.Y. Comparison of larval performance and oviposition preference of *Spodoptera frugiperda* among three host plants: Potential risks to potato and tobacco crops. *Insect Sci.* 2021, 28, 602–610. [CrossRef] [PubMed]

42. Nemati-Kalkhoran, M.; Razmjou, J.; Borzoui, E.; Naseri, B. Comparison of life table parameters and digestive physiology of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) fed on various barley cultivars. *J. Insect Sci.* 2018, 18, 31. [CrossRef]

43. Jaleel, W.; Tao, X.B.; Wang, D.S.; Lu, L.H.; He, Y.R. Using two-sex life table traits to assess the fruit preference and fitness of *Bactrocera dorsalis* (Diptera: Tephritidae). *J. Econ. Entomol.* 2018, 111, 2936–2945. [CrossRef]

44. Cipollini, D.; Peterson, D.L. The potential for host switching via ecological fitting in the emerald ash borer-host plant system. *Oecologia* 2018, 187, 507–519. [CrossRef]

45. Tan, S.L. Sweet potato-*Ipomoea batatas*-a great health food. *Agric. Sci.* 2015, 3, 15–28.

46. Singh, A.; Yemmireddy, V. Fate of *Salmonella* spp. in fresh-cut papaya (*Carica papaya* L.) at different storage temperature and relative humidity. *LWT Food Sci. Technol.* 2021, 148, 111810. [CrossRef]

47. Tian, W.J.; He, G.D.; Qin, L.J.; Li, D.D.; Meng, L.L.; Huang, Y.; He, T.B. Genome-wide analysis of the NRAMP gene family in potato (*Solanum tuberosum*): Identification, expression analysis and response to five heavy metals stress. *Ecotoxicol. Environ. Saf.* 2021, 208, 111661. [CrossRef] [PubMed]