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ORIGINAL RESEARCH PAPER

Effect of host alternation on fitness of *Diaphorina citri* (Hemiptera: Psyllidae), huanglongbing bacterium vector

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Abstract

The psyllid *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) is the vector of the bacterium that causes huanglongbing (HLB), the most serious disease of citrus plants. The range of host species available in the field provides ample food for nymph development and adults support, allowing the psyllids to persist and pose a risk to healthy groves. This study aimed to understand the effects of remaining on or changing between host-plant species on psyllid fitness, and the effects of the parental diet on the offspring. Psyllid populations were established on two host species, *Citrus sinensis* (commercial plant) and *Murraya paniculata* (ornamental plant). The insects were kept on the same host or alternated between *M. paniculata* to *C. sinensis*, and their biological parameters were recorded daily. The results indicated that move to another host during the adult phase did not cause changes in psyllids fitness or in the development of their offspring; however, this change can impact negatively the performance of the subsequent generation (i.e. the offspring of their offspring). The diet of immatures can be a key factor affecting the population dynamics of psyllids. This information will help to improve psyllid management techniques according to the heterogeneity of the landscape surrounding a grove.

Keywords Asian citrus psyllid · Parental diet · Intra- and intergenerational effects · Population persistence

Introduction

The Asian citrus psyllid *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) transmits the bacterium that causes greening or huanglongbing (HLB), the most economically damaging citrus disease (Aubert et al. 1985; Su and Huang 1990; Teixeira et al. 2008). This disease, which causes greening and stunting of fruits (da Graça et al. 2016), has caused enormous damage in different regions of the world, such as India (Fraser 1978), Philippines (Martinez and Wallace 1968), Thailand (Bhavakul et al. 1981), Saudi Arabia (Bové 1986), Florida, United States (Spreen et al. 2014), and Brazil (Bové 2006).

The main causes of HLB persistence in citrus are the rapid spread of the disease by insect dispersal (Palmieri et al. 2016) and the relatively wide range of available alternative hosts for psyllids, where they find food and sites for egg laying and offspring development (Aubert 1987). Alternative plants include varieties of *Citrus* and many plants of the family Rutaceae, such as the orange jessamine *Murraya paniculata* (L.) Jack, which is commonly used as a hedge or ornamental (Parra et al. 2010).

In the search for flushes, which are essential because *D. citri* lays eggs only on tender flushes (Yamamoto et al. 2001), psyllid adults move constantly between commercial areas and areas with alternative hosts (Boina et al. 2009; Gottwald 2010; Hall et al. 2012). In commercial areas, plants tend to synchronize flush production at certain times of the year (Garcia et al. 2019), and management techniques are based on this flush rhythm, to interfere with the insect's life cycle (Laranjeira et al. 2019). On the other hand, alternative hosts favor psyllid population growth by sprouting randomly throughout the year, and receive no phytosanitary treatments, allowing psyllids to persist even when commercial crops do not allow full insect development (Costa 2009). In this case, the presence of areas with alternative hosts may

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allow psyllids to reinfest commercial areas, thus expanding transmission and dissemination of HLB.

The temporal variation in flush availability means that psyllid populations use different hosts to feed and reproduce. Many studies have quantified the effects of different plant hosts on *D. citri* population fitness (Alves et al. 2014; Nava et al. 2007; Stockton et al. 2016; Tsai and Liu 2000); however, little is known about the consequences of host-plant exchange for insect populations over generations. Effects of the parental diet on offspring have been reported for other insects (Mousseau and Dingle 1991a, b), indicating that environmental variation and maternal feeding can affect the offspring phenotype and fitness, resulting in evolutionary responses and variations within a population (Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Riska et al. 1985). The availability of host plants at different times of the year may affect the population dynamics and rates of insect dispersal to healthy groves, becoming a source of infestation and contributing to disease persistence (Bergamin et al. 2016).

Despite the knowledge of the negative effects of abandoned groves on healthy groves and studies of *D. citri* biology (Alves et al. 2014; Nava et al. 2007; Tsai and Liu 2000); little is known about the effect of an insect's parental diet on its biotic potential. This study evaluated the effects on *D. citri* fitness of remaining on and exchanging between two host plants, *Citrus sinensis* Osbeck and *M. paniculata*, by experimentally simulating scenarios in which insects that develop on alternative host plants (*M. paniculata*) then disperse as adults to commercial groves of *C. sinensis*. We attempted to answer two questions: (i) Does the plant on which adults feed alter their fitness and the development of their offspring (intragenerational effect)? (ii) Does the plant on which immatures feed alter the fitness of *D. citri* and the development of their offspring (intergenerational effect)? The results are discussed based on the estimated potential for occurrence and persistence of HLB-vector psyllid populations in areas with commercial citrus groves.

Materials and methods

Insect colony and host plants

Adults of *D. citri* were obtained from the rearing colony maintained at the Insect Biology Laboratory of the University of São Paulo in Piracicaba, with insects from this region in *M. paniculata* plants since 2012. The rearing colony is kept in a glass greenhouse under natural light, with automatic ventilation that maintains the temperature between 25 and 28 °C.

The seedlings of *C. sinensis* and *M. paniculata* from a nursery in Rio Claro, São Paulo (22°22′26.5″ S, 47°39′04″ W), were kept in a greenhouse with automatic ventilation, and were irrigated and fertilized (Peters® 20:20:20) twice a week.

Establishment of experimental populations: effects of the two host plants on *Diaphorina citri*

To obtain the initial generation (G_0), the insects were reared according to the method of Parra et al. (2016) in two different hosts for three generations. The three generations were standardized based on the maximum flushing period in commercial areas available for the development of the psyllid (Cifuentes-Arenas et al. 2018; Garcia et al. 2019).

To ensure that all insects had already reached sexual maturity, since *D. citri* has a mean pre-oviposition period of 9 days (Nava et al. 2007) and lays eggs after 1 day of mating (Wenninger and Hall 2007), 5-day-old adult psyllids were used for the experiments. The insects were collected randomly from each of the two experimental populations. Couples of insects were formed, according to their host plant: 14 couples from *M. paniculata* and 10 couples from *C. sinensis*. Each couple was confined on a 1 cm flush (Diniz 2013) of the host plant, using small cages closed with a wire. Each host plant had three flushes. The insects were monitored daily, to quantify the pre-oviposition period, number of eggs laid, number of daily ovipositions over a female's lifespan (number of days in which female laid eggs, independently of the number of eggs), and male and female longevity. Daily, after each group of eggs was laid, the adult couple was transferred to a new host-plant flush, and these transfers continued until the adults died. For each couple, the first oviposition was maintained in flushing to evaluate the duration of the egg and nymph phases and their respective viability.

Experimental simulations

Scenario 1: Intragenerational effects of host alternation: does the plant on which adults feed alter the fitness of *Diaphorina citri* and the development of its offspring (effects on the first generation, G_1)?

To determine whether an exchange of plants during adulthood alters the fitness of adult *D. citri* and consequently the development of their offspring, the first experiment simulated a scenario where, in the field, the adult insects disperse from an alternative host (*M. paniculata*) to commercial groves (*C. sinensis*). Two groups of insects from the pre-established *M. paniculata* population (G_0) were separated into couples: one group of *M. paniculata* couples ($n = 17$) was transferred to feed on *C. sinensis* flushes, while another group ($n = 14$) continued to feed on *M. paniculata* flushes (control group) (Fig. 1). Couples were isolated and monitored daily, as described in the previous section, for evaluation of the pre-oviposition period, number of eggs laid, number of days in which was observed oviposition over a female's lifespan, and male and female longevity. For each couple, the eggs were maintained to evaluate the duration and viability of the egg and nymph phases.

Scenario 2: Intergenerational effects of host alternation—does the plant on which immatures feed alter the fitness of *Diaphorina citri* and the development of its offspring (effects on the second generation, G_2)?

In scenario 1 we quantified the direct effect of host exchange on *D. citri*, evaluating whether feeding adults on different hosts affects the biological parameters of their offspring (G_1). However, the effects of host-plant exchange may be due not only to the insects' feeding during the adult phase, but also due to the plant on which these insects fed in the immature phase.

Aiming to determine the effect of host-plant exchange by parents on the fitness and demographic parameters of successive generations of *D. citri*, a scenario was simulated in which individuals growing on *M. paniculata* disperse, as adults, to *C. sinensis* groves (due to insect density, environmental factors and plant nutritional status (Tomaseto et al. 2017), where they lay their eggs (G_1). The offspring of these individuals (G_1) remain on *C. sinensis*, where they grow and after maturing, lay eggs that give rise to a new generation (G_2) in *C. sinensis* groves, which then develop into adults (Fig. 2). The objective of this experiment was to quantify the effect of parental diet on such a psyllid population on *C. sinensis*, by comparing a population in which the parents developed on *M. paniculata* (G_1) with a population in which the parents developed on *C. sinensis* (G_2). Couples ($n = 17$) from the established *M. paniculata* population were transferred to *C. sinensis*. After eggs were laid and the nymphs hatched (G_1), the nymphs were observed daily until emergence, allowing quantification of biological parameters as described in previous items. After the emergence of G_1, couples were again separated ($n = 12$) and the offspring generated (G_2) were evaluated daily until emergence and death of the adults (Fig. 2). At the end, it was possible to evaluate the intergenerational effect of host alternation on psyllid fitness. The orange plants were replaced every insect new generation. All plants used had same size and number of flushes.

Data analysis

The effects of host plants on the number of egg clutches produced by females over their lifespan and on the total number of eggs produced were analyzed by fitting generalized linear models assuming a Poisson distribution, and using quasi-Poisson models when overdispersion was found. The effects of host plants on egg and nymph viability were analyzed by fitting generalized linear models with a binomial distribution, using quasi-binomial models when overdispersion was

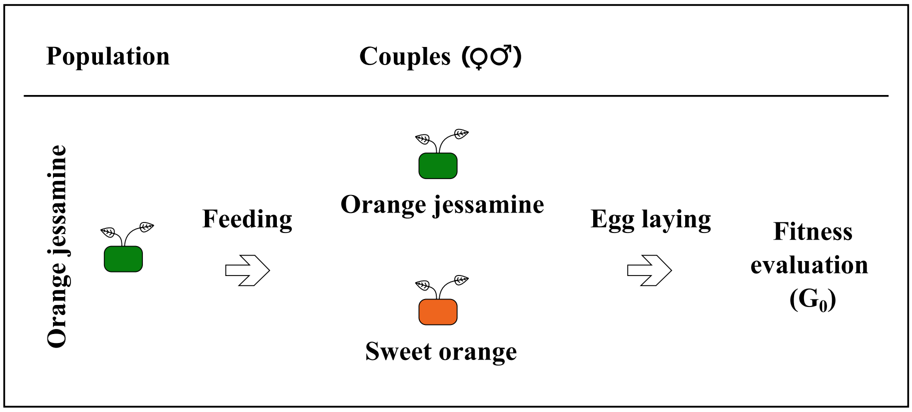

Fig. 1 Design of experimental simulation to evaluate the effects of alternating host plants on the fitness of *D. citri* adults: after emergence, adults from orange jessamine (*Murraya paniculata* [L.] Jack) are transferred to sweet orange (*Citrus sinensis* Osbeck) or remain on orange jessamine

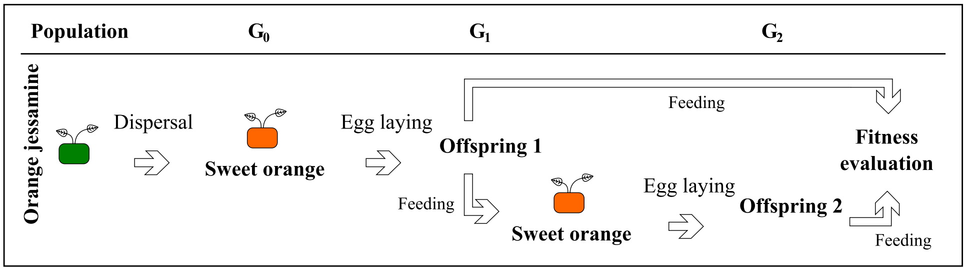

Fig. 2 Experimental design used to test the effects of parental diet on successive generations of *Diaphorina citri*

found. The effects of host plants on the biological variables of *D. citri* was assessed using F tests. Goodness-of-fit for all models was assessed using half-normal-plot (R-package HNP) graphs with simulation envelopes (Moral et al. 2016).

Embryonic development time, nymph phase, pre-oviposition period, and adult longevity were analyzed by survival curves, where the means and standard errors were estimated from the Kaplan–Meier estimators (R-package survival). The means of experimental populations were compared by log-rank test. The *p* values were corrected by the Bonferroni method. All statistical analyses were performed using R software version 3.6.1 (R Core Team 2019).

Results

Host plants had significant effects on the total number of eggs laid by females of *D. citri* throughout their lifespans (Table 1) in the initial experimental populations (G_0). The experimental population established on *C. sinensis* produced fewer eggs than the populations on *M. paniculata* (Table 3, supplementary material). The mean daily oviposition rate varied over time for the two host plants (Fig. 3); however, the host plant had no significant effect on the mean number of daily ovipositions over a female's lifespan (Table 1). The viability of eggs and nymphs was not affected by the host plants on which the insects developed (Table 1).

The analyses indicated that the different host plants had significant effect on the pre-oviposition period of *D. citri* (G_0). However, the host plant significantly affected the embryonic period: the embryo development time was significantly shorter for insects reared on *M. paniculata* than on *C. sinensis* (Table 2). The host plant had no effect on nymph development or adult longevity (Table 2).

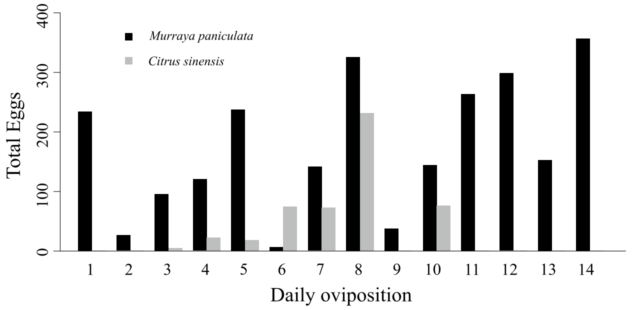

Fig. 3 *Diaphorina citri*, total number of eggs laid daily on the two species of host plants: *Murraya paniculata* (L.) Jack and *Citrus sinensis* Osbeck (G_0)

Scenario 1: Intragenerational effects of host alternation: does the plant on which adults feed alter the fitness of *Diaphorina citri* and the development of its offspring (effects on the first generation, G_1)?

In scenario 1 (intragenerational effects of host alternation), whether a population remained on *M. paniculata* or changed from *M. paniculata* to *C. sinensis* had variation over time on the daily oviposition rates (Fig. 4), total number of eggs, mean number of daily oviposition, egg viability or embryonic period (Table 1, 2). Host-plant exchange had no effect on the nymph development period, nymph viability and female longevity. However, the host-plant exchange influenced the pre-oviposition period and male longevity (Table 1, 2).

Table 1 Analysis of the number of eggs, daily oviposition/female, and viability of eggs and nymphs (*p* value) of *Diaphorina citri* populations that developed for different generations (G_0, G_1 and G_2) at 25 ± 2 °C, 70 ± 10% RH and 14 L: 10 D photoperiod

	Analysis			
Comparisons	Number of eggs (mean)	Daily oviposition/female	Viability of eggs	Viability of nymphs
A. Population established (*Murraya paniculata* × *Citrus sinensis*—G_0)	$F_{22,23}=9.63$, $p<0.005$*	$F_{19,20}=3.75$, $p=0.06$	$F_{19,20}=0.2$, $p=0.66$	$F_{16,17}=0.003$, $p=0.95$
B. Intragenerational effects (*Murraya paniculata*G_1 × *Citrus sinensis*—G_1)	$F_{29,30}=0.278$, $p=0.6$	$F_{27,28}=0.3483$, $p=0.56$	$F_{27,28}=1.48$, $p=0.234$	$F_{18,19}=3.19$, $p=0.09$
C.Intergenerational effects (*Citrus sinensis*—G_1 × *Citrus sinensis*—G_2)	$F_{22,23}=20.497$, $p<0.05$*	$\mathrm{Dev}_{22,23}=21.157$, $p<0.05$*	$F_{22,23}=0.50$, $p=0.48$	$\mathrm{Dev}_{11,12}=-1.09$, $p=0.29$

*Indicates significant difference ($p<0.05$) at $\alpha=5\%$ significance level

Table 2 Analysis of the pre-oviposition, immature development time, and adult longevity (p value) of *Diaphorina citri* populations that developed for different generations (G_0, G_1, and G_2) at 25 ± 2 °C, 70 ± 10% RH and 14 L: 10 D photoperiod

	Analysis				
		Development time (d)		Longevity	
Comparisons	Pre-oviposition period	Embryo	Nymph	Male	Female
A. Population established (G_0)	$\chi^2=8.9$, $df=1$, $p<0.05$*	$\chi^2=10.1$, $df=1$, $p<0.05$*	$\chi^2=3.0$, $df=1$, $p=0.08$	$\chi^2=2.7$, $df=1$, $p=0.1$	$\chi^2=1.1$, $df=1$, $p=0.3$
B. Intragenerational effects (G_1)	$\chi^2=4.9$, $df=1$, $p<0.05$*	$\chi^2=0.3$, $df=1$, $p=0.6$	$\chi^2=3.2$, $df=1$, $p=0.07$	$\chi^2=7.1$, $df=1$, $p<0.05$*	$\chi^2=0.3$, $df=1$, $p=0.6$
C. Intergenerational effects ($G_1 \times G_2$)	$\chi^2=0.5$, $df=1$, $p=0.5$	$\chi^2=2.4$, $df=1$, $p=0.1$	$\chi^2=16.4$, $df=1$, $p<0.005$*	$\chi^2=8.2$, $df=1$, $p<0.05$*	$\chi^2=8.6$, $df=1$, $p= <0.05$*

*Indicates significant difference ($p<0.05$) at $\alpha=5\%$ level

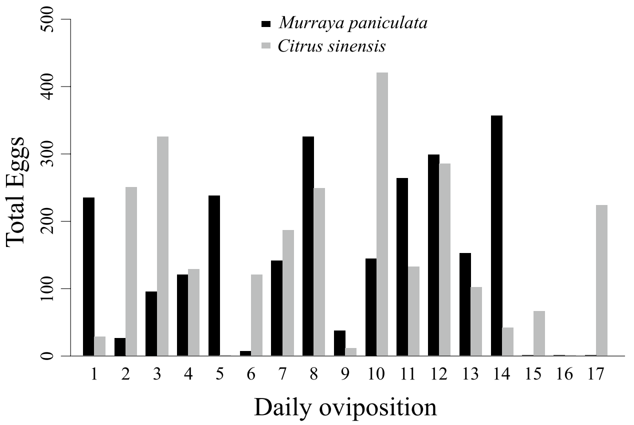

Fig. 4 *Diaphorina citri*, total number of eggs laid daily on *Murraya paniculata* (L.) Jack and *Citrus sinensis* Osbeck (G_1)

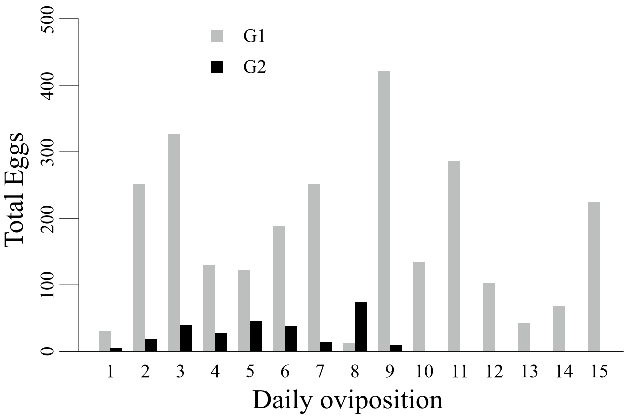

Fig. 5 Daily oviposition of *Diaphorina citri* populations reared on *Citrus sinensis* for one (G_1) and two (G_2) consecutive generations

Scenario 2: Intergenerational effects of host alternation—does the plant on which immatures feed alter the fitness of *Diaphorina citri* and the development of its offspring (effects on the second generation, G_2)?

In scenario 2 (intergenerational effects of host alternation), alternation of hosts in successive *D. citri* generations significantly affected the rate of daily oviposition, total number of eggs and mean number of egg clutches (Table 1). The daily oviposition of *D. citri* is shown in Fig. 5. The first generation (G_1), in which the parents grew on *M. paniculata*, produced more eggs in more clutches than the second generation (G_2), in which the parents grew on *C. sinensis* (Table 3, supplementary material). There was no significant intergenerational effect on egg viability or nymph viability (Table 1).

Host alternation of *D. citri* generations did not affect the embryonic period. However, the effects of host alternation on the development time of the nymphs and the longevity of the adults over the generations were significant (Table 2). In general, the G_1 population showed a longer nymph development time and adult longevity than the G_2 population (Table 4, supplementary material). The pre-oviposition periods of females from the G_1 and G_2 populations did not differ significantly (Table 2).

Discussion

The first experiment compared the biological parameters of populations that were standardized to the host plants (G_0). Egg production was higher in populations established on *M. paniculata* than on *C. sinensis*. In general, *M. paniculata* and *C. sinensis* allowed the psyllid populations to maintain themselves in the experimental simulations where these plants were the only hosts available.

The effects of host plants found here may be related to the plant physiology, which can affect the insect's development through the plant's nutritional value, and also to the plant morphology, particularly the characteristics of the cuticle, which may be difficult for the insect to penetrate (Liu et al. 2015; Zalucki et al. 2002). Unfortunately, studies of the effects of tissue-level morphological characteristics of citrus plants on *D. citri* fitness are scarce.

In addition to the plant effects, the morphology of *D. citri* eggs can affect the population viability. Eggs of *D. citri* have a pedicel at the lower end, which is inserted into the plant tissue when the egg is laid (Blowers and Moran 1967; Husain and Nath 1927). The pedicel attaches the egg to the plant and may also absorb water, ensuring sufficient moisture for egg development (Deshpande 1936; Poinar 1965). Several studies have found that psyllids do not lay eggs on plant tissue with a hard cuticle (Ammar et al. 2013, 2014; Moran et al. 1975), which may explain their preference for new flushes and the low mean number of eggs deposited by *D. citri* on *C. sinensis,* which may have the more rigid plant tissue. *Diaphorina citri* prefers *M. paniculata* as a host plant (Alves et al. 2014; Nava et al. 2007; Tsai and Liu 2000); this species provides new flushes throughout the year according to environmental conditions. No pest-control measures are used on *M. paniculata* (Belasque et al. 2010; Tsai et al. 2002), which allows successive generations of *D. citri* to benefit from the parental host plant to improve their performance and fitness (Fox et al. 1995; McLean et al. 2009; Spitzer 2007; Via 1991).

Several studies have assessed the effects of different host plants on the biology and life cycle of *D. citri* (Alves et al. 2014; Nava et al. 2007; Tsai and Liu 2000). However, these studies evaluated the insects for only one generation; that is, the insects were influenced by the same parental generation, derived from populations reared in the laboratory on *M. paniculata*. For *D. citri*, host alternation affected biological and morphological aspects of the psyllid in the same generation (Stockton et al. 2017); however, there are no studies evaluating such intergenerational effects of the insect. The present study is the first to evaluate the effect of parental diet on offspring of *D. citri* over consecutive generations. Studies with the polyphagous species *Tachyporus hypnorum* (Coleoptera: Staphylinidae) concluded that the food of females can have profound effects on the performance of their offspring for up to two generations, specifically on egg size, copulation time, development period and survival (Kyneb and Toft 2006). Similar effects have been found in other insect species (Gould 1988; Langley et al. 1978; Morris 1967). Therefore, the results of an experiment may vary depending on the insect generation observed. Because *D. citri* can use different plants to feed and produce offspring, and because *M. paniculata* is commonly present in the surroundings of citrus groves, the effect of all the available host plants on the biology and demographics of psyllid populations should be considered. Psyllids in and near commercial groves can have different life histories, since the agricultural landscapes are quite complex with regard to the available host-plant species and their periods of susceptibility to the psyllid (flushing periods). Therefore, the effects of host exchange must be considered to better understand psyllid population dynamics in the field and to plan more-effective control strategies. The present results reinforce the importance of management in areas where alternative hosts are present.

The availability of flushes is also important, since females of *D. citri* oviposit on new flushes of the host plant (Hall et al. 2012; Yamamoto et al. 2001). Considering that citrus-growing areas have controlled and managed peaks of flushes according to the production cycle, areas with alternative hosts, where flushing is not controlled and no treatments are used, are suitable for the psyllids to develop when trees in commercial groves are not producing flushes (Laranjeira et al. 2019). Because of this, since 2008 several regulations have been promulgated in attempts to eradicate *M. paniculata* (Fundecitrus 2016).

Experimental scenario 1 simulated the dispersal of psyllids from *M. paniculata* to *C. sinensis* groves; *i.e*., after emergence, some insects fed on a different host during the adult phase. The results indicated that the change of diet did not affect the adults' fitness or the development of their offspring, since this host exchange did not significantly affect the biological parameters in the first generation, G_1. However, although the differences were not significant, lower values were observed for the number of eggs, number of daily oviposition, and viability of eggs and nymphs on *C. sinensis* compared to populations adapted to each host in the first part of the experiment. The results indicated that the good performance of the G_1 population on *M. paniculata* and *C. sinensis* may be related to their parental host plant (*M. paniculata*). These results are similar to those found in the study by Stockton et al. (2017), which showed that *D. citri* females prefer to lay eggs on the same host species in which they developed. The provision of optimum conditions for psyllid development in *M. paniculata* has been described in other studies (Teck et al. 2011; Nava et al. 2007). In addition, it is widely known that the parental diet can have significant effects on the offspring, such as favoring the transmission of acquired nutritional and environmental conditions (Mousseau and Dingle 1991a).

In experimental scenario 2, after the simulated dispersal to *C. sinensis*, the insect population that remained on this host originated the second generation (G_2), which suffered significant effects of the host plant on the number of eggs, number of egg clutches laid, time of development of the nymph phase, and the egg-adult period. The G_2 population showed lower values of biological parameters than the G_1 population, indicating that the parental diet affected the descendants (Fox et al. 1995). Comparison of the results for the G_1 and G_2 populations with the result for the experimental population on *C. sinensis* suggests that the performance of G_1 was due to the parental diet on *M. paniculata*, the host on which the insect reproduces for successive generations, which improved its performance (Belasque 2010; Fox et al. 1995; McLean et al. 2009; Spitzer 2007; Via 1991). According to Liu et al. (2015) the development of *D. citri* in *M. paniculata* plants induces a greater expression of detoxifying enzymes, which allow the psyllid a fitness increase to better face the defenses of other host plants. The decrease in fitness observed in G_2 was an effect of the change to the other host, *C. sinensis*, on which the insect finds it difficult to maintain its population, probably due to the growers' treatments in the commercial groves (Costa 2009; Laranjeira et al. 2019). The results obtained for populations previously standardized to *C. sinensis* suggest that after the insects establish on the host plant, their numbers may again increase. Since G_2 had a parental *C. sinensis* diet, could transmit the ability to establish on this host to the offspring, this phenomenon was mentioned previously by before Newcombe et al. (2015).

Diaphorina citri is found more frequently in areas peripheral to commercial groves (Belasque et al. 2010), because these locations do not receive the same phytosanitary treatment as the groves themselves. Since the use of alternative hosts simultaneously or at different times contributes to the insect's population density, distribution and expansion in the landscape (Wardhaugh et al. 1980), it is believed that control efforts, especially control of *M. paniculata,* in these areas would be more effective; since, these areas (uncontrolled) provide 20 to 30 times more migrating psyllids than commercial orchard areas and of which about 70% are infected with HLB (Chinelato 2017; Pazolini et al. 2021). Plans have been made to eradicate *M. paniculata* (Fundecitrus 2016), as the results indicated that this is the most efficient host plant for insect development, in addition to contributing to the continued use of *Tamarixia radiata* as biological control in these areas (Diniz et al. 2020, 2021; Parra et al. 2016).

The present results support the conclusion that host alternation affects the fitness of *D. citri.* Alternate feeding by adults did not affect the biological parameters of their offspring, but the food of immature psyllids affected their reproductive performance. Of the two host species, parental feeding on *M. paniculata* most benefited the psyllids in terms of population increase.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13355-021-00758-2.

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