Revista Brasileira de Entomologia 68(1):e20230077, 2024

SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

Lower reproductive rates of Asian citrus psyllid (Hemiptera: Psyllidae) on ‘Tahiti’ acid lime than on ‘Valencia’ sweet orange

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ARTICLE INFO

Article history:
Received 05 September 2023
Accepted 11 March 2024
Available online 22 April 2024
Associate Editor: Ricardo Siqueira da Silva

Keywords:
Citrus
Host
Huanglongbing
Psyllid

ABSTRACT

The ‘Tahiti’ acid lime and orange trees are hosts of ‘*Candidatus* Liberibacter asiaticus’ (*C*Las), the pathogen associated with the severe Asian form of huanglongbing (HLB), the most devasting citrus disease. They are also hosts of the vector of *C*Las, the Asian citrus psyllid (ACP) *Diaphorina citri* Kuwayama. Relatively small numbers of lime trees occur in gardens and small orchards near large commercial ‘Valencia’ sweet orange orchards in Brazil. Applications of insecticides to suppress populations of ACP on the lime trees are usually nil or less frequent than in the orange orchards. Abundance of the psyllid on lime trees may therefore increase the risk of *C*Las spreading to the orchards. Because the abundance of the psyllid is influenced by the suitability of the trees as hosts, we compared reproductive potential of the insect on the two hosts in a controlled environment chamber (CEC) and in a greenhouse (GH). Daily temperature and relative humidity averaged 22ºC and 60% inside the CEC and 24°C and 70% inside the GH. Two pairs of adult male and female psyllids were caged for 3 days on new shoots and the fecundity and durations of development and survival of eggs and nymphs evaluated. Overall, acid ‘Tahiti’ was 3.5 times less suitable to ACP than ‘Valencia’. Fecundity and survival of nymphs were 27% and 59% lower, and the life cycle 34% longer on ‘Tahiti’ than on ‘Valencia’. Potential impacts of the results on *C*Las spread and HLB control are discussed.

Introduction

The Asian citrus psyllid (ACP) *Diaphornia citri* Kuwayama (Hemiptera: Sternorrhyncha: Psyllidae) is present in most citrus-growing regions in Asia and the Americas, and has recently become established in several countries in Africa (Shimwela et al. 2016; Rwomushana et al., 2017; Ajene et al., 2020; Oke et al., 2020; Aidoo et al., 2023; Sétamou et al., 2023). As a sap-sucking insect, high populations can cause curling of leaves and twisting and poor development of shoots (Tsai et al., 2002; Michaud, 2004). However, major impacts result from its ability to transmit the phloem-limited α-Proteobacteria ‘*Candidatus* Liberibacter asiaticus’ (*C*Las), the causal agent of the severe Asian form of huanglongbing (HLB), the most devastating disease of citrus. HLB has reduced yields and caused death of millions of citrus trees in Asia and the Americas, leading to huge economic losses (Halbert and Manjunath, 2004; Bové, 2006; Gottwald, 2010; Grafton-Cardwell et al., 2013; Kanga et al., 2016). There is no cure for the disease and, as part of successful HLB management programs incidence of ACP in orchards must be aggressively and regionally suppressed. This requires strategic and frequent applications of insecticides (Bassanezi et al., 2020).

Hosts of ACP include citrus species, hybrids and relatives (Halbert and Manjunath, 2004; Felisberto et al., 2019; Beattie, 2020). Reproduction and population size dynamics are dependent on the developmental stages of the young new flushes present on tree canopy (Cifuentes-Arenas et al., 2018). Both ACP and flushing occurrence and development also are strongly impacted by the environment (Tsai et al., 2002; Hall and Albrigo, 2007; Hall et al., 2008). On ‘Tahiti’ acid lime (*Citrus* × *latifolia* (Yu. Tanaka Tanaka) (Rutaceae: Aurantioideae: Aurantieae) flushing occurs more frequently than on sweet oranges (*C.* × *aurantium* L.), resulting to several fruit production cycles a year (Vieira, 1988). Frequent flushing provides conditions for ACP populations to remain high over time (Pluke et al., 2008; Tsagkarakis et al., 2012) which, in the presence of diseased trees facilitates spread of the pathogen within and between orchards. In Brazil, ‘Tahiti’ is common in home gardens and small orchards in close proximity to large commercial ‘Valencia’ sweet orange orchards, the main citrus cultivar grown for export of concentrated orange juice (FUNDECITRUS, 2021). This situation

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https://doi.org/10.1590/1806-9665-RBENT-2023-0077

has caused concerns that healthy and diseased trees of 'Tahiti' may support high populations of ACP and compromise suppression of HLB in commercial sweet orange orchards.

Citrus and citrus relatives vary in their suitability as hosts of ACP. Rates of oviposition and development and survival of eggs and nymphs are higher on sour orange (*Citrus* × *aurantium* L.) than on 'Cleopatra' mandarin (*Citrus reticulata* Blanco) (Tsagkarakis and Rogers, 2010). Oviposition rates also were higher on 'Ponkan' tangerine (*C. reticulata*) or 'Valencia' than on 'Hamlin' sweet orange (Alves et al., 2014), and on orange jasmine (*Murraya paniculata* (L.) Jack) (Aurantieae) or 'Cravo' Rangpur lime ('*Citrus limonia*' Osbeck) than on 'Sunki' mandarin (Nava et al., 2007). Also, ACP adults survived longer and with higher reproductive rates on sour orange, lemon (*Citrus* × *limon* (L.) Osbeck), curry leaf (*Bergera koenigii* L.) (Aurantioideae: Clauseneae) and orange jasmine than on *Aegle marmelos* (L.) Corrêa (Aurantieae), *Atalantia buxifolia* (Poir.) Oliv. (Aurantieae), *Citrus wintersii* Mabb. (syn. *Microcitrus papuana* H.F. Winters), *Citrus* ('*Microcitrus*') sp., and *Helietta apiculata* Benth. (Rutaceae: Amyridoideae) (Felisberto et al., 2019). Felisberto et al. (2019) found that only a few eggs were laid on *H. apiculata*, and nymphs did not survive. Given the variation in host suitability to reproduce ACP and the lack of such information for 'Tahiti', a comparative study was undertaken to assess parameters involved in ACP reproduction on this host and on 'Valencia' sweet orange.

Materials and Methods

Plant material

Two-year-old nursery trees of 'Valencia' sweet orange and 'Tahiti' acid lime cv. 'Quebra-Galho', both grafted on 'Cravo' Rangpur lime, were grown in 4.7 L plastic pots containing the commercial substrate Multiplant citrus® (Terra do Paraiso, Holambra, SP), composed of 80% *Pinus* sp. bark, 15% vermiculite and 5% charcoal. Pots were irrigated two to three times a week and fertigated fortnightly with 100 mL pot^{-1} of a nutritive solution containing, in one litter, 1.35 g calcium nitrate ($Ca(NO_3)_2$, 0.111 g MAP, 0.4 g of magnesium sulfate ($MgSO_4$), 0.015 g copper (Cu), 0.01 g zinc (Zn), 0.0075 g manganese (Mn-EDTA), 0.00045 g ammonium molybdate $(NH_4)_2MoO_4$, and 0.075 g iron (Fe-EDTA). To stimulate growth of new flushes, the plants were pruned 15 cm above the graft union, and remaining leaves removed 10 to 15 days before the start of the experiments. After the appearance of new flushes, a single new shoot per plant at phenological stage V2 was selected for determining the suitability of the hosts for oviposition, and a single new shoot per plant at phenological stage V3 was selected for determining survival of nymphs on the hosts (Fig. 1). These two phenological stages are the most suitable for ACP to reproduce and develop on sweet orange (Cifuentes-Arenas et al., 2018).

Insect cultures

Insects free of *C*Las were reared on *C*Las-negative orange jasmine plants inside a greenhouse, where the temperature averaged 24 ± 4 ºC, and relative humidity (RH) 60% ± 5. Rearing procedures were as described by Skelley and Hoy (2004) with adaptations. Briefly, 50 adult individuals were confined on the newly formed flushes for 5 days, inside sleeve cages, to lay eggs. The eggs were allowed to hatch and become first-instar nymphs (nymph survival experiment) or develop through five nymphal instars to become adults (oviposition suitability experiment). As soon as adults emerged and then every 24 h they were separated by sex and transferred to new orange jasmine plants. Since ACP adults start to copulate four days after eclosion from fifth instar nymphs (Zanardi et al., 2018), the 24 h interval for separating males and females ensured that the adults had not mated. The adults were maintained in sleeve cages for a further 15 days on the new plants.

Settling and oviposition experiment

Two pairs of unmated 15-day-old ACP adults were confined, inside a 20 × 30-cm sleeve cage, on a single V2 shoot per plant. The shoots were observed every 24 hours for 3 consecutive days for the presence of eggs. During this 72-hour interval observations were made to determine if adults settled on the new shoots or were present elsewhere within the cage. At the end of the confinement period, the adults were removed from the cages using an aspirator made of a mesh-covered plastic Pasteur pipette inserted into a plastic tube and then discarded.

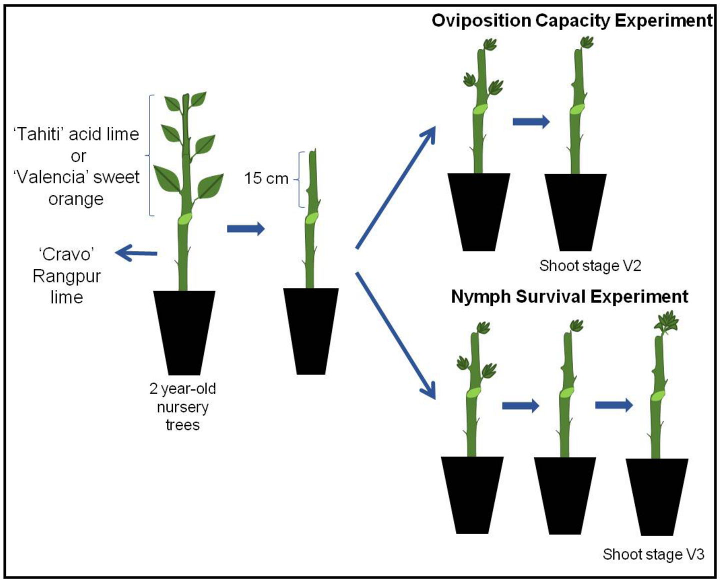

Figure 1 General schematic representation of set-up process of the different shoot stages of the 2-year-old potted plans of 'Valencia' sweet orange and 'Tahiti' acid lime cv. 'Quebra-Galho', both grafted on 'Cravo' Rangpur lime rootstock, for *Diaphorina citri* oviposition capacity and nymph survival experiments.

A 30× magnification hand lens was used to count eggs and nymphs on the shoots. The evaluated parameters were (i) pre-oviposition period (time from confinement to observation of the first eggs), (ii) numbers of eggs, (iii) egg incubation period (time from the end of pre-oviposition period to appearance of the first nymphs), (iv) egg viability (percentage of eggs that hatched), and (v) settling preference (SP) as given by the formulae $SP = \left[\frac{\sum_{i=1}^{n} ACPns_i}{NA_n}\right] * ACP_T$, where $ACPns_i$ is the number of psyllids found settled on the new shoot, NA_n the total number of assessments, and ACP_T the total number of psyllids confined per new shoot. The experiment was carried out twice in two different environments, namely, a controlled environment chamber (CEC), where the temperature averaged 24 ±5 °C, RH 70 ± 5%, and the photoperiod settled to 14 h light (60 µmol m^{-2} s^{-1}):10 h dark, and in a greenhouse (GH) where the temperature averaged 22 ± 13 ºC and RH 60% ±17.

Nymph survival experiment

Using a thin and delicate paintbrush and the 30× magnification lens, groups of 30 newly-emerged first-instar nymphs (younger than 24-hour-old) were individually transferred from the orange jasmine to a single V3 shoot per plant of 'Valencia' or 'Tahiti'. The insects were observed daily until they became adults. Competition for food and space between individuals was avoided or minimized. Emerging adults were collected daily, and their sex determined. Duration of development from egg-hatch to adult (nymphal period), nymph viability, and sex ratios of adults were evaluated. The experiment was carried out twice inside the GH, where the temperature averaged 26±10 ºC and RH 75% ±12 (first replication) and temperature 22±11 ºC and RH 80%±15 (second replication).

Statistical analysis

Prior to statistical analysis, data on egg and nymph viabilities were transformed in x'=arcsin(sqrt(x/100)), where x= original data and x'= transformed data (Zar, 2010). The transformed data was subjected to analysis of variance and the means compared by *t* test ($p \leq 0.05$). The percentage of emerged adults were analyzed by Chi-square test. Data on insect settling, pre-oviposition period, egg number, egg incubation period and nymphal period were compared by *t* test for independent samples, or by the *t* test of Welch (Welch, 1947) when uneven variances were detected. The logistic regression [$y = \left(e^{\beta_0+\beta_1 * day}\right) / \left(1+e^{\beta_0+\beta_1 * day}\right)$] was used to describe the dynamics of emergence of adults. Probability significance levels ≤ 0.05 were used for all tests.

Results

Settling and oviposition experiment

The plant host did not affect ACP settling preferences (CEC p=0.09; GH p=0.28). In both environments ACP most frequently settled on the new flushes than elsewhere inside the cages (Fig. 2).

Similarly, plant host did not influence the time for ACP females to start laying eggs (pre-oviposition period) (CEC p= 0.42, GH p= 0.12) (Figs. 3A and 3B) egg duration (incubation period) (CEC p= 0.74, GH p= 0.57) (Figs. 3G and 3H). However, host cultivar affected the progress of oviposition in both environments (CEC p= 0.04, GH p= 0.01) (Fig. 3C and 3D), and the viability of eggs in the CEC (p= 0.03) (Fig. 3E).

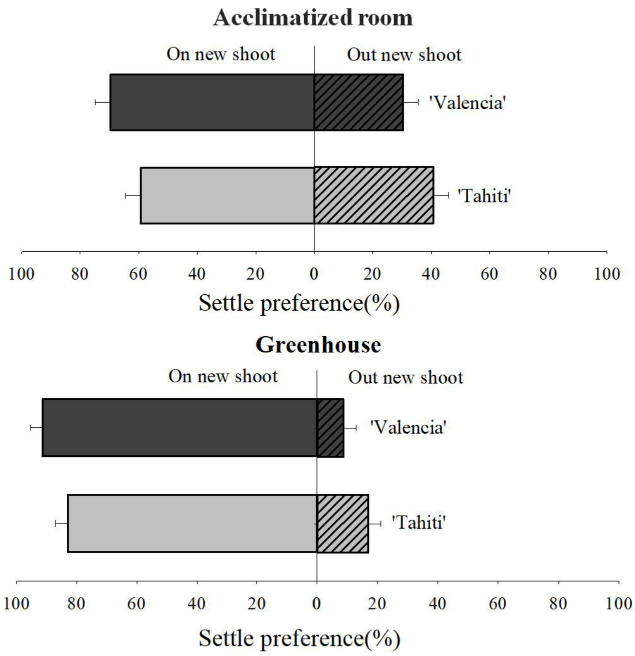

Figure 2 Frequency (%) of settling of adult *Diaphorina citri* on V2 shoots of 'Valencia' Sweet orange and 'Tahiti' acid lime plants inside a controlled environment chamber (or room?) (n=10; p= 0.092ns) and in a greenhouse (n=15; p= 0.28ns).

ACP laid higher number of eggs on 'Valencia' (115 and 210, inside the CEC and the GH, respectively) than on 'Tahiti' (69 and 167, respectively). Inside the GH, most eggs on both hosts were viable and hatched nymphs (Fig. 3F) while inside the CEC, egg viability reached 65% on 'Tahiti' and 85% on 'Valencia' (Fig. 3E). As indicated in Figs. 2 and 3, GH provided a more favorable environment for ACP than the CEC. Inside the GH the insects started to lay eggs in a shorter time and in higher numbers. Also, egg incubation period was shorter and the viability higher inside the GH than in the CEC (Fig. 3).

Nymph survival experiment

In this experiment we evaluated the influence of 'Tahiti' and 'Valencia' on the survival of nymphs. Both nymphal duration (p= 2.40x10^{-06} and p= 0.004, first and second replication, respectively) and viability (p= 6.21x10^{-8} and p= 4.03x10^{-7}) were affected by the host in both experiments. Inside the GH the duration was shorter (12.1 and 17.1 days) (Fig. 4AB) and survival higher (64.3 and 65%) (Figs. 4C and 4D) on 'Valencia' than 'Tahiti' (17.9 and 25.1 days, and 31.1 and 21.6%, respectively). Therefore, 'Tahiti' prolonged development of the five nymphal instars by 41% and reduced survival of nymphs by 48 and 33% as compared to 'Valencia'. However, the hosts did not influence sex ratios (Figs. 4E and 4F).

The plants host also impacted the rate of adult emergence in both experiments (Figs. 5A and 5B), with the logistic regression model providing a good description of the dynamics of ACP emergence over time (Table 1). Periods of 10 and 8 days were needed for half of the adults to emerge on 'Tahiti', in experiments 1 (Fig. 5A) and 2 (Fig. 5B), respectively, against 4 and 5 days on 'Valencia'.

Discussion

We compared reproduction of ACP on 'Tahiti' acid lime and 'Valencia' sweet orange. ACP settled mostly on new shoots of both plants, thus

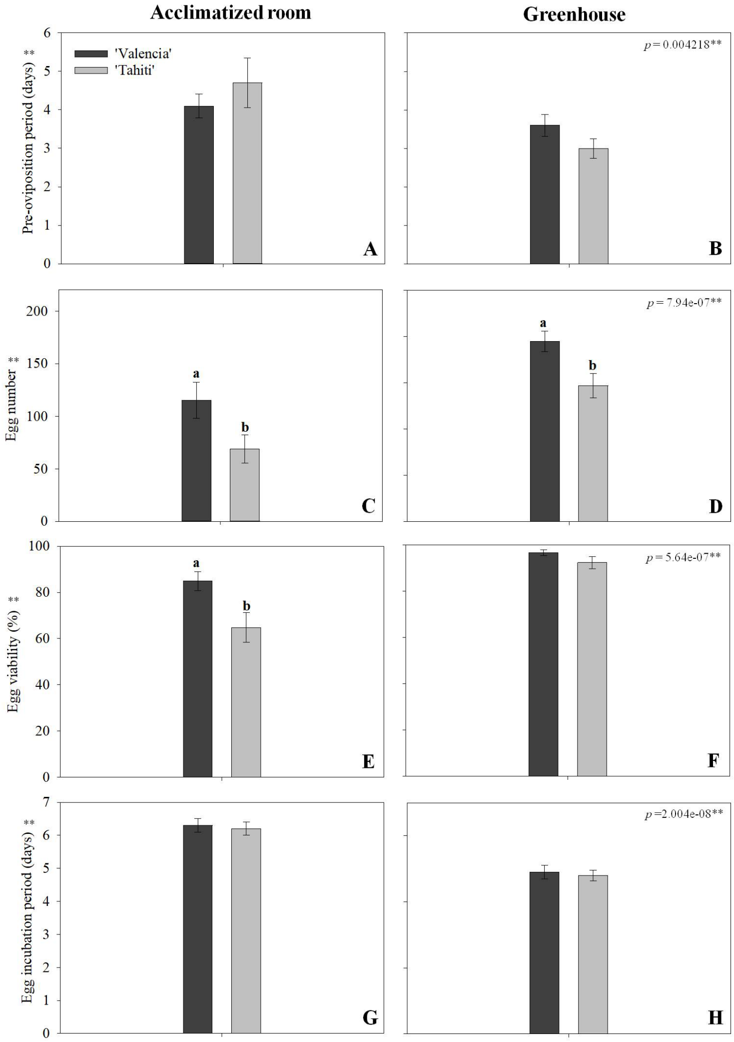

Figure 3 Oviposition by female *Diaphorina citri* on V2 shoots of 'Valencia' sweet orange and 'Tahiti' acid lime plants grown in a controlled environment chamber (n=10) or in a greenhouse (n=15) over 72 h. Mean (±SEM) pre-oviposition period from time of confinement on plants (A/B), numbers of eggs laid (C/D), egg viability (E/F) and egg incubation interval (G/H). Bars with different letters differ by *t* test, p< 0.05. **: differ between the environment by Anova test, p<0.001.

Table 1

Parameters of the logistic regression made on the daily frequency of emergence of adults of *Diaphorina citri* on V3 shoots of 'Valencia' sweet orange and 'Tahiti' acid lime under greenhouse conditions.

Host	Regression parameters							
	β_0	SE ^{x}	β_1	SE	Dev. (%) ^{y}	X^2	DF ^{z}	p
				Rep. 1 ^{1}				
'Valencia'	-2.86	0.10	0.79	0.02	97.38	4064.39	1	<0.0001
'Tahiti'	-2.64	0.10	0.32	0.01	89.21	1093.68	1	<0.0001
				Rep. 2 ^{1}				
'Valencia'	-2.75	0.11	0.52	0.02	98.55	3028.85	1	<0.0001
'Tahiti'	-2.11	0.13	0.20	0.01	85.66	589.29	1	<0.0001

^{x} *standard error of the parameter;* ^{y} *deviance percentage;* ^{z} *degree of freedom.*^{1} *Exp. 1: n=20, Exp. 2: n=15.*

confirming the attractiveness of young tissues to adults for feeding and oviposition (Sétamou et al., 2016; Cifuentes-Arenas et al., 2018). The interval between settling and oviposition was similar for both hosts, but other aspects of the insect life cycle differed. Females laid 1.5 times more eggs and nymphs developed more rapidly and survived 1.5 times longer on 'Valencia' than 'Tahiti'. This suggests that under field conditions potential spread of *C*Las related to 'Tahiti' might be lower than spread related to 'Valencia', on which higher populations of the psyllid could occur. However, because 'Tahiti' flushes more frequently than 'Valencia' (Spiegel-Roy and Goldschmidt, 1996), and most other sweet orange cultivars (Carvalho, 2020), potential spread of *C*Las from 'Tahiti' could be greater than indicated by oviposition and rates of development of nymphs in this study. Spread of *C*Las appears to be related also to *C*Las titers in new shoots (Lopes et al., 2017), that could influence acquisition of the pathogen by ACP. However, no significant differences in *C*Las titer and rates of pathogen acquisition by ACP from 'Tahiti' and 'Valencia' have been observed (Pulici, 2018).

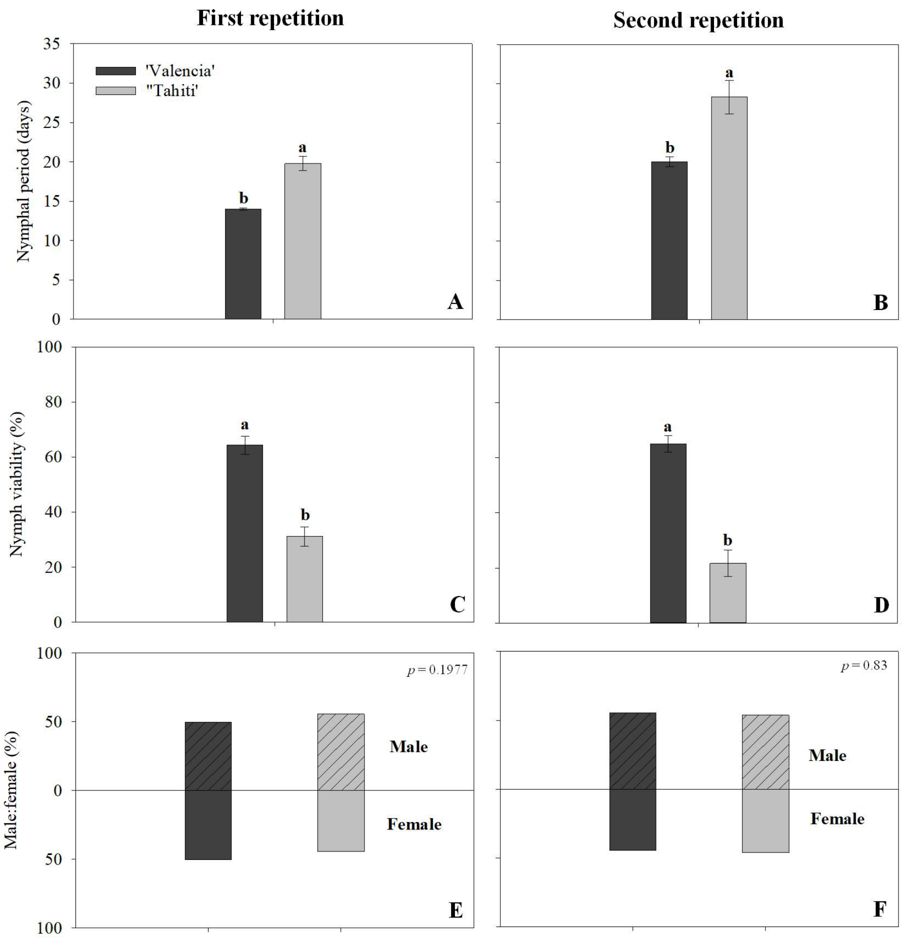

Figure 4 Mean (±SEM) nymphal duration (duration of development of nymphs from first nymphal stage to adults eclosion) (A/B), nymph viability (percentage of survival of nymphs to adult eclosion) (C/D) and male: female proportion (E/F) of *Diaphorina citri* rearing on V3 shoots of 'Valencia' sweet orange and 'Tahiti' acid lime plants under greenhouse conditions. Bars with different letters differ by *t* test, $p< 0.05$. First repetition n=20; Second repetition n=10.

Impact of the host plant on the population dynamics of insects other than ACP have been described. For example, on sycamore maple (*Acer pseudoplatanus* L. (Sapindales: Sapindaceae)), body size and fertility of the sycamore aphid (*Drepanosiphum platanoidis* (Schrank) (Hemiptera: Sternorrhyncha: Aphididae) were associated with variable levels of free amino acids (Awmack and Leather, 2002). Impacts of host plants on ACP had already been observed in other studies (Catling, 1970; Nava et al., 2007; Tsagkarakis and Rogers, 2010; Alves et al., 2014; Ramírez-Sánchez et al., 2016), but they did not include 'Tahiti' acid lime. In our study we recorded 5.6 and 7.0 eggs per female, respectively on 'Tahiti' and 'Valencia' in the GH and 3.4 and 5.8, respectively, in the CEC. These differences could be related to changes in the nutritional status of host plants (Leong et al., 2011) or presence in the phloem sap of compounds that are toxic to the insects (Vendramim and Guzzo, 2012). They could also be related to differences in the overall morphology and nutritional status of the new shoots where the insects fed and reproduced. The presence and thickness of fibrous rings influence stylet penetration and feeding by ACP (Ammar et al., 2014; George et al., 2017), and the N:C ratio and levels of total free and essential amino acids in young shoots influence the size of ACP populations (Sétamou et al., 2016).

In our study, environmental conditions also influenced ACP biology, as observed by others (Liu and Tsai, 2000; Nava et al., 2007; Milosavljević et al., 2020). Egg numbers and viability were higher, and the time required for the initiation of oviposition and egg hatching were lower on plants maintained inside the GH, in which ambient air

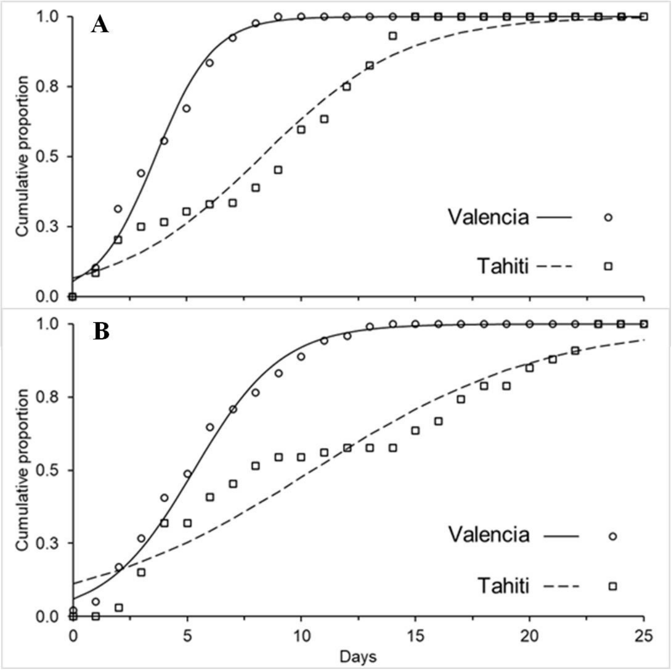

Figure 5 Cumulative frequency of adult eclosion of *Diaphorina citri* on V3 shoots of 'Valencia' sweet orange and 'Tahiti' acid lime under greenhouse conditions. (A) First repetition (n=20); (B) Second repetition (n=10).

temperatures varied from 9 to 35°C and RH from 43 to 77% than inside the CEC, in which the air temperatures ranged from 19 to 29°C and RH from 65 to 75%. Higher reproductive rates of insects in variable than in less variable controlled environments have been reported for other insects (Gullan and Cranston, 2010). However, Milosavljević et al (2020) reported faster development of ACP under constant temperatures than under variable temperatures. Such differences could be related to the intensity and quality of light, which vary in different environments, with a direct influence on the biology of the insect (Paris et al., 2015) and indirect influence in phloem sap flow and composition (Cohen et al., 1997; Ortuño et al., 2006; Hu et al., 2013; Dáder et al., 2014).

In this work significant differences on the reproductive potential of ACP on 'Tahiti' and 'Valencia' were observed. Fecundity and survival of nymphs were 27% and 59% lower on 'Tahiti' than 'Valencia'. This may indicate that in the field the abundance of ACP on 'Tahiti' might be lower than on 'Valencia' orchards. However, more frequent flushing on 'Tahiti' than on 'Valencia' might compensate for the lower suitability of 'Tahiti' as a host of ACP. As a result of a longer duration of nymphal development, the life cycle of ACP also was 34% longer on 'Tahiti' than that on 'Valencia'. As the vulnerability of nymphs to insecticides is related to the durations of their development (Hernández-Fuentes et al., 2012), the results of our study suggest that insecticides applied at the same doses and frequencies for minimizing ACP populations on the lime would be more effective than on the sweet orange. Both hypotheses warrant further investigation.

The lower reproductive potential and longer duration of nymphal development of ACP on 'Tahiti' acid lime suggest that this plant host would result in lower ACP populations that are more vulnerable to control with the regular chemicals sprays used in the field, and thus contribute to a lesser extent than sweet oranges to the spread of HLB. Both hypotheses require, however, further investigation.

Acknowledgments

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Fundecitrus for financial support to Jeane Dayse Pulici.

Conflicts of interest

The authors declare that they have no conflict of interest.

Author contribution statement

JDVSP, conceptualization and design, acquisition, analysis, and interpretation of data. Methodology, resources, and writing. JCCA, analysis of data, writing, and review. GACB, writing, review, and editing the manuscript critically for important intellectual content. SAL, conceptualization and interpretation of data. Methodology, resources, supervision, and writing. Review and editing the manuscript critically.

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