

Biology of the Huanglongbing Vector *Diaphorina citri* (Hemiptera: Liviidae) on Different Host Plants

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ABSTRACT Although many studies have been conducted on the development and reproductive potential of *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae) in different host species, few have evaluated these parameters on different varieties of the same host species. This study evaluated the influence of five commercial varieties of citrus (*Citrus* spp. L.)—Hamlin, Natal, Pêra, Ponkan, and Valencia—and orange jasmine [*Murraya exotica* (L.) Jack] on the development of *D. citri*. Survival rates for the egg stage were highest on orange jasmine (85.7%) and on Valencia (83.3%). The lowest viability of the nymphal stage was also observed on Hamlin, averaging 57.4%. Values for total viability ranged from 65.9 to 32.6%, and were highest on Valencia. The longest egg–adult development time was on Natal, with a mean of 18.4 d; the shortest total development time was on orange jasmine, with a mean of 17.3 d. Based on the fertility life table, the net reproductive rate (R_0) of *D. citri* was 2.5 times higher when reared on Valencia than on Hamlin. The other parameters (duration of each generation [T], finite rate of increase [λ], and innate capacity to increase in number [r_m]) also demonstrated that Valencia is best suited to this insect. The results obtained for the biological parameters and the fertility life table indicate that Valencia and orange jasmine were the most suitable hosts, whereas Hamlin was least suitable for the development of *D. citri*. These results provide information for the installation of new citrus groves, especially in the choice of varieties to be planted and the location of different varieties within the groves, with a view toward the management of Huanglongbing or HLB.

KEY WORDS Asian citrus psyllid, citrus variety, *Murraya exotica*, fertility life table, Huanglongbing

Brazil is the largest world producer of orange juice, which is highly important for the international balance of trade of the country (Neves 2010). The most important citrus disease is Huanglongbing or HLB (also known as citrus greening), which represents an enormous risk to the sustainability of citrus groves in Brazil and worldwide (Halbert and Manjunath 2004, Bové 2006, Hall et al. 2012, Grafton-Cardwell et al. 2013). According to Gottwald (2010), the disease is associated with three bacteria: *Candidatus Liberibacter asiaticus*, *Candidatus Liberibacter africanus*, and *Candidatus Liberibacter americanus*. These bacteria are spread by the psyllid *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae). In Brazil, HLB was first recorded in 2004 in the groves of central São Paulo state (Teixeira et al. 2005). In 2005, the disease was identified in south Florida (Gottwald 2010). Since then, groves in the two largest citrus-producing states in the world, São Paulo and Florida, have been devastated by the disease.

According to Belasque et al. (2010), groves in different regions of the world may become economically unviable within 10 years after symptomatic plants are first detected, if control measures are not taken. An

example was reported by Bové (2006) in China, where a grove with no control measures became 100% infected within five years.

After citrus greening was detected in Brazil, its psyllid vector *D. citri* has been considered a key pest in citrus (Parra et al. 2010). According to these authors, *D. citri* was first recorded attacking citrus groves by Costa Lima in 1942, but HLB was only identified 62 yr after this insect was recorded in the country. *D. citri* has a host range of ≈ 20 species in the family Rutaceae, including all species of *Citrus*, although the insect cannot develop fully on all its hosts (Aubert 1987). Some hosts are used only for feeding or oviposition by the adult. Orange jasmine [*Murraya exotica* (L.) Jack] has been reported to be the preferred host of *D. citri* (Halbert and Manjunath 2004, Teck et al. 2011); this ornamental plant is widespread in Brazil and worldwide, and is also used as a hedgerow plant in grove areas.

Some studies have found differences in the development of *D. citri* on different host species (Tsai and Liu 2000, Nehru et al. 2004, Nava et al. 2007, Tsagarakis and Rogers 2010, Westbrook et al. 2011); however, studies comparing the development of *D. citri* on different varieties of the same plant are still scarce. The current study evaluated the development of *D.*

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Table 1. Mean (\pm SD) duration of *D. citri* reared on different host plants

Hosts	n	Duration (d) ^a		
		Egg	Nymph	Egg to adult
Valencia	17	4.79 \pm 0.14AB	13.19 \pm 0.22A	17.98 \pm 0.20A
Natal	17	4.91 \pm 0.14A	13.46 \pm 0.18A	18.43 \pm 0.13A
Pêra	17	4.43 \pm 0.15AB	13.43 \pm 0.20A	17.88 \pm 0.19A
Ponkan	19	4.24 \pm 0.20B	13.65 \pm 0.18A	17.93 \pm 0.15A
Hamlin	15	4.33 \pm 0.16AB	13.35 \pm 0.25A	17.75 \pm 0.26A
Orange jasmine	18	4.57 \pm 0.14AB	12.93 \pm 0.22A	17.26 \pm 0.26A
F		2.69	0.85	1.55
df		5, 97	5, 88	5, 88
P		\leq 0.05	=0.51	=0.18

Temperature 25 \pm 2°C, 60 \pm 10% RH, and a photoperiod of 14:10 (L:D) h.

^a Mean values followed by the same letter in the column do not differ by Tukey test ($P \leq 0.05$).

citri on different commercial varieties of citrus and on orange jasmine, to provide useful information for the installation of new citrus groves, in particular the choice of varieties, with a view toward managing the incidence of HLB.

Materials and Methods

Insect Rearing and Plant Maintenance. The insects used in this study were obtained from the maintenance rearing laboratory of Insect Biology, Department of Entomology and Acarology, "Luiz de Queiroz" College of Agriculture, University of São Paulo. The insects were reared according to the methodology adapted by Gomez-Torres (2009).

We used plants of sweet orange [*Citrus sinensis* (L.) Osbeck], mandarin orange [*Citrus reticulata* (L.) Blanco], and orange jasmine (*M. exotica*). The varieties used in the experiments were the sweet orange varieties Hamlin, Natal, Pêra, and Valencia and the mandarin variety Ponkan. All the varieties were cultivated on rootstock of the Rangpur lime *Citrus limonia* Osbeck.

The plants were kept in a greenhouse and irrigated daily. The plants were fertilized every 2 wk with a solution of Peters foliar fertilizer (NPK 20-20-20). To standardize the availability of vegetation from the different varieties, some of the shoots were removed,

keeping only one, with a mean length of 8–12 mm, to be offered to the insects.

Biology on Different Host Plants. On each plant, a pair of 15-d-old *D. citri* was confined in a mesh sleeve cage for 24 h. After that time, the pair was removed and the eggs were counted with a stereoscopic microscope. The study was conducted in climate-controlled chambers at a temperature of 25 \pm 2°C, 60 \pm 10% relative humidity (RH), and a photoperiod of 14:10 (L:D) h. The experimental design was fully randomized, with a total of 12 repetitions (pairs) for each treatment (host).

The hatched nymphs and dead nymphs were counted daily until the emergence of adults. The development time, viability, and sex ratio were evaluated. For the fertility life table, the following biological parameters were also evaluated: preoviposition period, longevity of males and females, and the daily rhythm of oviposition. These data were used to calculate the parameters: R_0 = net reproductive rate, T = duration of each generation, r_m = innate capacity to increase in number, and λ = finite rate of increase (Southwood 1978).

For the parameters preoviposition period, longevity, and daily rhythm of laying, newly emerged pairs of *D. citri* from different hosts were used, although they did not come from the same plants as in the previous test. The pairs were placed in mesh sleeve cages on seedlings of the same host on which they were reared. The pairs were observed daily, and the preoviposition period was determined from the appearance of the first egg. The number of eggs laid each day was counted with the aid of a stereomicroscope. Pairs were kept in these conditions until they died, and this period was considered to be the longevity.

Statistical Analysis. Data were analyzed for normality, homoscedasticity, and the presence of outliers by optimal Box-Cox transformation; then, data were subjected to analysis of variance, and the means were compared by Tukey test ($P \leq 0.05$), with the aid of SAS version 9.1 (SAS Institute 2000). The viability data were arcsine root-transformed. The data for the fertility life table were analyzed by Jackknife, and the means were compared by *t*-test (Maia and Luiz 2006).

Table 2. Mean (\pm SD) of survival and sex ratio of *D. citri* reared on different host plants

Hosts	n	Viability (%) ^a			Sex ratio ^b
		Egg	Nymph	Egg to adult	
Valencia	17	83.3 \pm 6.10A	79.12 \pm 4.1A	65.90 \pm 6.9A	0.62 \pm 0.07
Natal	17	74.26 \pm 3.8AB	71.18 \pm 5.8A	52.85 \pm 5.3AB	0.67 \pm 0.05
Pêra	17	71.77 \pm 5.3AB	65.45 \pm 7.9A	46.97 \pm 7.6AB	0.77 \pm 0.08
Ponkan	19	75.22 \pm 4.4AB	76.39 \pm 7.6A	57.46 \pm 7.0AB	0.58 \pm 0.07
Hamlin	15	56.83 \pm 4.4B	57.44 \pm 9.6A	32.64 \pm 5.9B	0.77 \pm 0.11
Orange jasmine	18	85.74 \pm 4.2A	74.99 \pm 7.3A	64.29 \pm 7.1A	0.74 \pm 0.04
F		2.24	1.35	3.36	
df		5, 88	5, 97	5, 97	
P		\leq 0.05	0.25	\leq 0.05	

Temperature 25 \pm 2°C, 60 \pm 10% RH, and a photoperiod of 14:10 (L:D) h.

^a Mean values followed by the same letter in the column do not differ by Tukey test ($P \leq 0.05$).

^b nonsignificant by chi-square test.

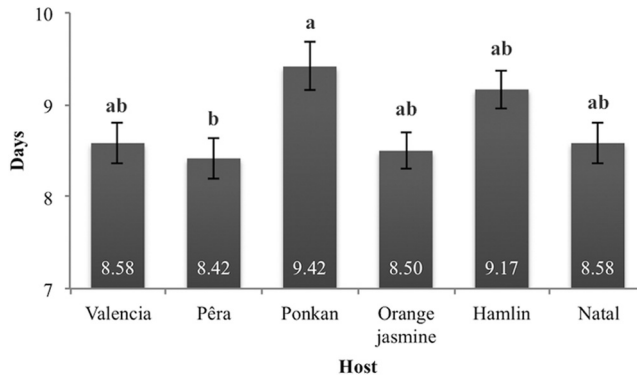


Fig. 1. Preoviposition period (d) of *D. citri* reared on different hosts. Temperature $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) h. Mean values followed by the same letter in the column do not differ significantly by Tukey test ($P \leq 0.05$).

The nonparametric chi-square test was used to evaluate the sex ratio.

Results and Discussion

The development time differed on each variety. The duration of the egg stage was significantly longest on Natal, with a mean of 4.91 d, and shortest on Ponkan (4.24 d). The total development cycle (egg to adult) ranged from 18.43 to 17.26 d on Natal and orange jasmine, respectively, although with no statistical differences (Table 1).

The development period of *D. citri* is also influenced by the host used, as observed by Teck et al. (2011), who obtained differences in egg-to-adult duration on three hosts tested, orange jasmine, curry leaf [*Murraya koenigii* (L.)], and mandarin orange (*C. reticulata*). The shortest development was obtained on orange jasmine (18.5 d) followed by mandarin orange (19 d), and the longest period was obtained on curry leaf (23 d).

The highest viability for the egg stage was observed on orange jasmine (85.7%) and Valencia (83.3%), and the smallest on Hamlin (56.8%). The viability of the

nymphal stage ranged from 57.4 to 79.1%, with no statistical differences among the different groups.

In this study, the hosts that provided the best development conditions for *D. citri* were Valencia and orange jasmine; on these, *D. citri* showed the highest total survival rates, 65.9 and 64.2%, respectively. However, these two hosts differed statistically only from Hamlin, which had the lowest total viability (32.6%) and is therefore the least favorable variety for the insect.

Differences in viability of *D. citri* were observed by Tsai and Liu (2000) on four different hosts. The authors obtained the best overall viability on grapefruit (*Citrus paradisi* Macfadyen; 84.5%) and the lowest viability on sour orange (*Citrus aurantium* L.), with a mean of 68.5%. Nava et al. (2007), using three hosts, orange jasmine, Rangpur lime, and Sunki mandarin orange (*Citrus sunki* [Hayata]), observed that viability was reduced on Sunki, with a nymphal survival of 44.6%.

Changes in the physiology of insects, which may manifest as differences in survival and development time, can be caused by ingestion of toxic compounds or even by the nutritional inadequacy of the host

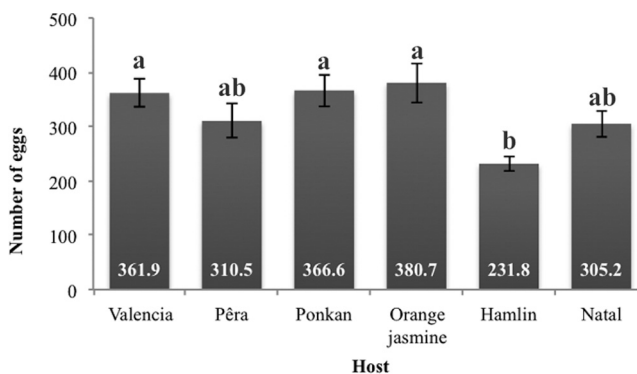


Fig. 2. Mean number of eggs of *D. citri* reared on different host plants. Temperature $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) h. Mean values followed by the same letter in the column do not differ significantly by Tukey test ($P \leq 0.05$).

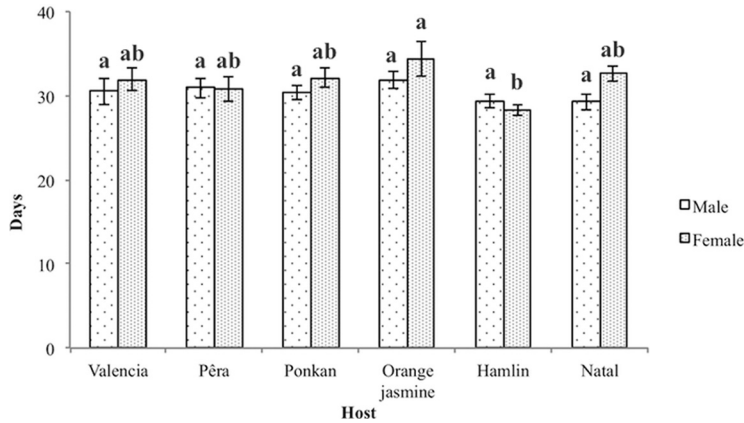


Fig. 3. Longevity (d) of males and females of *D. citri* reared on different host plants. Temperature $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) h. Mean values followed by the same letter in the column do not differ significantly by Tukey test ($P \leq 0.05$).

(Vendramim and Guzzo 2012). According to Teck et al. (2011), the development of *D. citri* is related to the nutritional status of the host plant, principally in the quality of the sap and the concentration of amino acids available. Thus, the results obtained in this study may indicate the existence of nutritional differences among the varieties tested, influencing the development of *D. citri*. This may be explained by the observations of Souza et al. (2012), who found differences of up to 20% in the nitrate content of sap from the Valencia and Hamlin varieties.

The different hosts had no influence on the psyllid sex ratio ($\chi^2 = 11.07$; $df = 5$; $P > 0.05$). Females predominated in all treatments (Table 2), demonstrating the high reproductive potential of the species.

The preoviposition period was, however, influenced by the host ($F = 3.31$; $df = 5, 66$; $P \leq 0.05$). The longest period was observed on Ponkan (9.42 d) and the shortest on Pêra (8.42 d). There were no significant differences in this parameter for the other hosts (Fig. 1).

Nava et al. (2007) obtained longer periods than those found in this study, i.e., ≈ 11 d for the preoviposition period on orange jasmine. The long preoviposition period is necessary for *D. citri* females, because in this species the ovaries do not mature after emergence (Dossi and Consoli 2010), i.e., it is a synovigenic insect.

The differences in the values of preoviposition obtained in this study and those obtained by Nava et al. (2007) may be owing to the characteristics of the shoots of the host used by these investigators. This phenomenon was noted by Uechi and Iwanami (2012), who found that 88% of females of *D. citri* had mature ovaries after 7 d feeding on young leaves, as opposed to those that fed on old leaves, which had only 33% mature ovaries on day 7.

The different hosts affected the fecundity of *D. citri* ($F = 4.48$; $df = 5, 66$; $P \leq 0.05$). The largest number of eggs was obtained on orange jasmine (380.7 eggs). These values differed significantly from those obtained for Hamlin (231.8 eggs; Fig. 2). Other studies have observed variations in the number of *D. citri* eggs depending on the host used. Nava et al. (2007) obtained, on orange jasmine, a mean of 348.4 eggs per plant. Tsai and Liu (2000) obtained a mean of 626 eggs on the same host, which is much higher than the number found in the current study. The differences among these values may be related to various factors such as the number of shoots available for laying, as the authors did not mention the number of shoots available for oviposition; population differences in strains of *D. citri* (León et al. 2011); or the nutritional quality of the host plant (Vendramim and Guzzo 2012).

The longevity of males of *D. citri* on all hosts was similar ($F = 0.87$; $df = 5, 66$; $P = 0.51$), ranging from

Table 3. Fertility life table of *D. citri* reared on different host plants

Hosts	Parameters from fertility life table ^a			
	R_0	r_m	T (d)	λ
Valencia	116.68 \pm 8.184A	0.1380 \pm 0.002A	34.504 \pm 0.338A	1.1480 \pm 0.002A
Pêra	84.53 \pm 8.529B	0.1339 \pm 0.002AB	33.172 \pm 0.676AC	1.1433 \pm 0.003AC
Ponkan	89.09 \pm 7.099B	0.1223 \pm 0.003C	36.722 \pm 0.295B	1.1301 \pm 0.003B
Orange jasmine	99.49 \pm 10.121AB	0.1315 \pm 0.002B	35.013 \pm 0.506C	1.1405 \pm 0.002C
Hamlin	45.27 \pm 2.796C	0.1145 \pm 0.001D	33.331 \pm 0.194D	1.1213 \pm 0.001D
Natal	83.005 \pm 6.536B	0.1289 \pm 0.002B	34.284 \pm 0.401C	1.1376 \pm 0.002C

Temperature $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) h.

^a Mean values followed by the same letter in the column do not differ by *t*-test ($P \leq 0.05$).

29.2 to 31.9 d on orange jasmine and Natal, respectively. The highest longevity of females was observed on orange jasmine (34.3 d), whereas the shortest was observed on Hamlin (28.3 d), values that differ significantly from the others ($F = 2.34$; $df = 5, 66$; $P \leq 0.05$; Fig. 3).

Using the fertility life table, we could determine the potential growth of *D. citri* on different hosts. The net reproductive rate (R_0) on Valencia was the highest (116.68); in other words, the insect population can increase 116 times in each generation. In contrast, on Hamlin this potential increase was 45.3 times. The generation time (T) of *D. citri* ranged from 36.7 to 33.1 d on Ponkan and Pêra, respectively. For the intrinsic rate of increase (r_m) and finite rate of increase (λ), the highest values were obtained on Valencia and the lowest on Hamlin (Table 3).

In a study conducted by Tsai and Liu (2000) with four different hosts, it was concluded that *C. paradisi* (grapefruit) was the most appropriate host, affording the highest net reproductive rate (R_0) and shortest development time (T). Nava et al. (2007) observed the highest net reproductive rate on orange jasmine (92.15) and the lowest rate on Sunki (13.70). Thus, the variation of biological parameters of *D. citri* on different varieties of *C. sinensis* (oranges), as observed in the current study, can also occur on different varieties of mandarins, and could explain the differences in reproductive rate recorded by Nava et al. (2007).

According to the results for the biological parameters and fertility life table, Valencia is the most suitable host for *D. citri*, and Hamlin is the least. These results are important in the epidemiology of HLB, because the largest increase of the population after each generation was obtained on Valencia compared with the other hosts. The Valencia orange comprises 28.5% of the trees grown in São Paulo state (Coordenadoria de Defesa Agropecuária [CDA] 2012). A study using a large sample size conducted in the state of São Paulo found that the Valencia variety had the highest incidence of HLB, with a mean of 41.3%, followed by Pêra (29.6%), Hamlin (14.9%), and Natal (14.2%) (Santos, personal communication). These results may explain why Valencia is the variety with the highest incidence of HLB.

According to Belasque et al. (2009), the largest populations of *D. citri* are concentrated on the edges of orchards. Therefore, when new orchards are being established, our findings indicate that it is important to avoid planting those varieties that better support the development of *D. citri* on the orchard edges, to aid in the management of HLB.

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