Biology of *Diaphorina citri* (Homoptera: Psyllidae) on Four Host Plants

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ABSTRACT The biology of the citrus psyllid *Diaphorina citri* Kuwayama was studied at 25°C on four commonly grown citrus and related plants [rough lemon, *Citrus jambhiri* Lush; sour orange, *C. aurantium* L.; grapefruit, *C. paradisi* Macfadyen; and orange jessamine, *Murraya paniculata* (L.) Jack] in the laboratory. The biological characteristics of each life stage are described. The average egg incubation periods on orange jessamine, grapefruit, rough lemon, and sour orange varied very little (4.1–4.2 d). The average nymphal developmental periods on these four host plants were essentially the same except the fifth stadium. Survival of immatures on orange jessamine, grapefruit, rough lemon, and sour orange was 75.4, 84.6, 78.3, and 68.6%, respectively. Female adults lived an average of 39.7, 39.7, 47.6, and 43.7 d on these respective host plants. The average number of eggs laid per female on grapefruit (858 eggs) was significantly more than those on other hosts ($P < 0.05$). The intrinsic rate of natural increase (r_m) for *D. citri* on grapefruit was highest. Jackknife estimates of r_m varied from 0.188 on grapefruit to 0.162 on orange jessamine and rough lemon. The mean population generation time on these hosts ranged from 31.6 to 34.1 d. The continuous flushes produced by orange jessamine could play an important role in maintaining high populations of this vector when the new flushes are not available in the commercial citrus groves.

KEY WORDS *Diaphorina citri*, bionomics, life table, host plant

Citrus is one of the most important economic crops in the United States, with ≈500,000 ha in citrus groves mostly in California, Florida, Texas, and Arizona. In Florida alone, citrus encompasses 342,105 planted hectares with a total of 107 million trees in the 33 citrus producing counties. The annual earning on citrus is estimated at $1.1 billion (Tsai and Wang 1999, Anonymous 2000). Citrus greening disease or "Huanglungbin" is the most serious disease of citrus in the world affecting most major citrus cultivars in Vietnam, Okinawa, China, Taiwan, Indonesia, The Philippines, India, Sri Lanka, Africa, and the Arabian Peninsula (Martinez and Wallace 1967, Moll and Van Vuuren 1977, Bove and Garnier 1984, Aubert 1987, Tsai et al. 1988, Su and Huang 1990, Aubert et al. 1996). Greening-affected citrus plants exhibit a variety of symptoms including initial leaf mottling and chlorosis followed by stunted growth, branch die back, and eventual death of trees. The citrus psyllid *Diaphorina citri* Kuwayama is the most efficient vector of citrus greening bacterium (*Liberobacter asiaticum*) throughout Asia and the Far East (Catling 1970, Pande 1971, Aubert 1987, Tsai et al. 1988). The combined presence of psyllid vector and greening agent has been the limiting factor in citrus production in these areas. On 3 June 1998, *D. citri* was first found in south Florida. The subsequent finding of *D. citri* widespread in Broward, Palm Beach, Martin, Dade, St. Lucie, Hendry, and Collier Counties in a 3-mo period has been reported (Halbert et al. 1998). Given high reproductive potential of this vector during the period of favorable weather conditions and food availability (Catling 1970, Mead 1977; J.H.T., unpublished data), this pest is expected to spread throughout citrus producing areas in Florida in 2–3 years. It poses a serious threat to other citrus producing states in the near future.

Diaphorina citri is of Far Eastern origin (Mead 1977). In the last three decades, research reports on this citrus psyllid have been mainly focused on the transmission of citrus greening agent by *D. citri* (Salibe and Cortez 1966, Martinez and Wallace 1967, Capoor et al. 1974, Su and Huang 1990). Currently, only information on field biology of this pest is available (Catling 1970, Pande 1971, Capoor et al. 1974, Yang 1989). Little is known of the biology of *D. citri*, especially about its life history and life table statistics in the Western Hemisphere. A thorough understanding of pest biology and population dynamics is essential for development of a reliable pest population prediction system and management strategies. Therefore, we initiated a study of the characteristics and to quantify *D. citri* development, reproduction, and longevity on four commonly grown citrus and related hosts to provide an experimental basis for controlling *D. citri.*

Materials and Methods

Psyllid and Host Sources. A stock culture of *D. citri* originated from orange jessamine [Murraya paniculata (L.) Jack] plants in Pompano Beach, Broward

Table 1. Mean ± SE developmental periods (days) of immature stages of *D. citri* on four host plants at 25°C

Hosts	*n*	Eggs	1st instar	2nd instar	3rd instar	4th instar	5th instar	Total nymphs	From egg to adult
Orange jessamine	34	4.15 ± 0.07a	2.00 ± 0.06a	1.58 ± 0.09a	1.68 ± 0.08a	2.35 ± 0.08a	5.21 ± 0.10ab	12.82 ± 0.10b	16.97 ± 0.18a
Grapefruit	26	4.31 ± 0.11a	2.23 ± 0.12a	1.65 ± 0.10a	1.58 ± 0.10a	2.46 ± 0.10a	4.65 ± 0.12c	12.58 ± 0.12b	16.88 ± 0.28a
Rough lemon	28	4.11 ± 0.09a	2.25 ± 0.08a	1.64 ± 0.09a	1.78 ± 0.08a	2.32 ± 0.09a	5.50 ± 0.12a	13.50 ± 0.12a	17.61 ± 0.17a
Sour orange	28	4.21 ± 0.11a	2.18 ± 0.10a	1.64 ± 0.11a	1.86 ± 0.07a	2.36 ± 0.09a	5.07 ± 0.15b	13.11 ± 0.15ab	17.32 ± 0.26a
F		0.81	1.77	0.11	2.11	0.42	7.43	3.72	2.19
df		3,112	3,112	3,112	3,112	3,112	3,112	3,112	3,112
P		0.492	0.156	0.956	0.102	0.742	<0.001	0.014	0.093

Within columns, means with the same letter are not significantly different at $P > 0.05$ (Duncan multiple range test).

County, FL. The culture was maintained on potted orange jessamine plants (40–50 cm tall) in a walk-in insect rearing room maintained at 28 ± 1°C, 75–80% RH, and a photoperiod of 13:11 (L:D) h. After a 4-mo rearing period, the ensuing colonies were used for the tests. The identity of *D. citri* was confirmed by S. E. Halbert at the Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL. Voucher specimens were deposited in the collection of the Division of Plant Industry. Seedlings of rough lemon (*Citrus jambhiri* Lush), sour orange (*C. aurantium* L.), grapefruit (*C. paradisi* Macfadyen), and orange jessamine at the two- to three-leaf stage, grown singly from seed, in plastic containers (6 by 6 by 8 cm), served as test plants.

Development and Survivorship of Immatures. For each experiment, ≈400–500 adults from the stock colonies were transferred to a group of 12–15 seedlings of each test species for a 6-h oviposition period. At the end of this period, the adults were removed and plants with eggs were checked and counted under a stereomicroscope. They were placed in growth chambers (Percival, Boone, IA) at 25°C, 75–80% RH, and a photoperiod of 13:11 (L:D) h for daily observation on incubation period. At least 26 first-instar nymphs collected within 4 h of egg hatch were transferred individually to a seedling of each test species using a camel's-hair brush and covered with a cylinder cage (8 by 4 cm diameter with a nylon cloth top). Covered plants were placed in the growth chambers at 25°C, 75–80% RH, and a photoperiod of 13:11 (L:D) h. Individual insects were checked daily for ecdysis and survivorship. The exuviae were used to determine molting.

Adult Longevity and Reproductive Capacity. One hundred to 200 matured nymphs reared from the each test species were collected and caged on potted plants. Adult females emerged within 6 h were singly aspirated into cylinder cages as described above. Two adult males were also introduced into each cage. At least 18 pairs were tested for each plant species. The caged adults were kept in growth chambers at 25°C, 75–80% RH, and a photoperiod of 13:11 (L:D) h. The paired adults were moved to new seedlings every 3 d and the eggs were counted under a stereomicroscope. Observations were made daily until the last female died.

Data Analysis. Life table parameters on four plant species were analyzed using general linear model procedures ($P < 0.05$; SAS Institute 1988), and means were separated by Duncan multiple range tests. The adults that died within 12 h of emergence or produced no eggs were excluded from the analysis.

Life table statistics were calculated from the populations on four host plants as described by Hulting et al. (1990). The sex ratio of 0.5224 based on 3,500 laboratory reared adults (J.H.T., unpublished data) was used to calculate the statistics. The differences in r_m values among populations were also analyzed using Newman–Keuls sequential tests (Sokal and Rohlf 1981) based on jackknife estimates of variance for r_ms (Meyer et al. 1986). For any difference between two r_ms from the sequence, in which the r_ms were arrayed in order of magnitude, to be significant at the α level, it must be equal to or greater than

$$LSR = Q_{a[K,V]}\sqrt{S_{av}^2}\ \sqrt{\frac{n_i+n_j}{2n_in_j}},$$

where K is the number of r_ms in the set whose range is tested. The degrees of freedom equal V. The n_i and n_j were sample sizes of the two r_ms; and $Q_{\alpha[K,V]}$ is a value from the table of the studentized range. S_{av}^2 is the weighted average variance of r_m and it is calculated as follows:

$$S_{av}^2 = \frac{\sum^{a} (n_i - 1)S_i^2}{\sum^{a} (n_i - 1)},$$

where a equals the number of r_ms to be tested, the sample size of the ith r_m is n_i. S_i^2 is the jackknife estimate of the variance for the ith r_m.

Results

Characteristics and Development of Egg. Gravid females of *D. citri* oviposited within 2-cm lengths of terminal tissue including leaf folds, petioles, axillary buds, upper and lower surfaces of young leaves, and tender stems. The egg was anchored on a slender stock-like process arising from the plant tissue. The egg was elongate with a broad basal end and tapering toward its distal and curved end. The average size of egg measured 0.31 mm long and 0.14 mm wide (n = 63). Freshly deposited eggs were light yellow, and turned bright orange with two distinct red eye spots at maturity.

Table 2. Survivorship (%) of immature stages of *D. citri* on four host plants at 25°C

Hosts	Eggs	1st instar	2nd instar	3rd instar	4th instar	5th instar	Total nymphs	From egg to adult
Orange	95.48a	87.19b	96.83ab	96.97a	99.42a	97.02a	78.97b	75.42b
Jessamine grapefruit	96.00a	91.78a	98.68a	99.12a	99.64a	98.57a	88.17a	84.58a
Rough lemon	95.99a	85.99b	98.76a	99.20a	97.97ab	98.95a	81.63b	78.34b
Sour orange	95.31a	86.41b	92.12b	98.29a	94.96b	96.85a	71.88c	68.55c
F	0.15	3.52	6.91	0.77	4.36	0.56	11.25	12.06
df	3, 12	3, 12	3, 12	3, 12	3, 12	3, 12	3, 12	3, 12
P	0.927	0.049	0.006	0.532	0.027	0.653	0.001	0.001

Within columns, means with the same letter are not significantly different at $P > 0.05$ (Duncan multiple range test).

The average incubation period and survivorship on orange jessamine, grapefruit, rough lemon, and sour orange were not significantly different ranging from 4.1 to 4.3 d and 95.3 to 96.0%, respectively (Tables 1 and 2; $P > 0.05$).

Characteristics, Development, and Survivorship of Nymph. All nymphs reared on four host plants underwent four molts. First- and second-instar nymphs mostly aggregated and fed on inside the folded leaves, the terminal stem and between the axillary bud and the stem of tender shoots. Young nymphs were quite docile and moved only when disturbed or overcrowded. The nymphs continuously secreted a copious amount of honeydew from the anus and thread-like waxy substance from the circumanal glands resulting in the growth of black sooty mold on the lower leaves. The average size of first-instar nymphs measured 0.30 mm in length and 0.17 mm in width ($n = 47$) with light pink body and a pair of red compound eyes. The measurement of second-instar nymphs averaged 0.45 mm long and 0.25 mm wide ($n = 52$). The rudimentary wing pads were visible on dorsum of thorax. The average size of third-instar nymphs was 0.74 mm long and 0.43 mm wide ($n = 62$). The wing pads were well developed and the segmentation of antenna was evident. The fourth-instar nymphs averaged 1.01 mm long and 0.70 mm wide ($n = 57$). The wing pads were well developed; the mesothoracic wing pads extended toward one-third of compound eyes and the metathoracic wing pads extended to third abdominal segment. The fifth-instar nymphs averaged 1.60 mm long and 1.02 mm wide ($n = 55$). The mesothoracic wing pads extended toward the front of compound eyes; the metathoracic wing pads extended to fourth abdominal segment. In some mature nymphs, the abdominal color turned bluish green instead of pale orange.

The average combined developmental periods for the five nymphal stages were 12.8, 12.6, 13.5, and 13.1 d on orange jessamine, grapefruit, rough lemon, and sour orange, respectively (Table 1).

Characteristics, Longevity, and Fecundity of Adults. Adults of *D. citri* were often found resting on the terminal portion of plant especially on the lower side of the leaves with their heads either pointing upward or downward to the leaf surface at a 30° angle. When disturbed they readily took flight to a short distance. The females only oviposited on the tender shoots. In the absence of suitable tissue, the oviposition ceased temporarily. The average size of adult females was 3.3 mm in length and 1.0 mm in width ($n = 32$); the mean size of adult males was 2.7 mm long and 0.8 mm wide ($n = 30$).

The average female longevity on rough lemon was significantly longer than those on grapefruit, orange jessamine, and sour orange (Table 3; Fig. 1; $P < 0.05$). The longest female longevity on grapefruit, orange jessamine, sour orange, and rough lemon was 54, 54, 60, and 66 d, respectively. The average number of eggs per female reared on grapefruit, orange jessamine, sour orange, and rough lemon were 858, 626, 613, and 572 eggs, respectively (Table 3; Fig. 1). The highest number of eggs per female reared on grapefruit, sour orange, orange jessamine, and rough lemon were 1,378, 994, 830, and 818 eggs, respectively.

Discussion

Diaphorina citri has a restricted host range including citrus species and related members of the Rutaceae (Mead 1977). No host comparison study has been reported. In this study, we found that host plants had some effects on the development, longevity, and reproduction of *D. citri* (Tables 1–4; Fig. 1). Eggs were placed where they were protected from the adverse environment and were supported by tube-like stocks, which prevented them from being washed off by rain or wind. The results showed that the mean incubation period on four host plants ranged from 4.1 to 4.3 d, which is shorter than the 4–20 d reported by Husain and Nath (1927) and Pruthi and Mani (1945) but longer than the 3 d reported by Catling (1970). These variations are expected because these observations

Table 3. Oviposition (eggs per female, mean ± SE) and longevity (in days ± SE) of female *D. citri* on four host plants at 25°C

Hosts	*n*	Mean longevity of female	Mean no. of eggs per female
Grapefruit	18	39.65 ± 1.88b	857.96 ± 45.82a
Orange jessamine	22	39.72 ± 1.39b	626.28 ± 22.33b
Rough lemon	25	47.55 ± 2.61a	572.10 ± 35.24b
Sour orange	21	43.69 ± 1.33ab	612.52 ± 31.69b
F		4.16	13.97
df		3, 87	3, 87
P		<0.01	<0.0001

Within columns, means followed by the same letters are not significantly different at $P < 0.05$ (Duncan multiple range test).

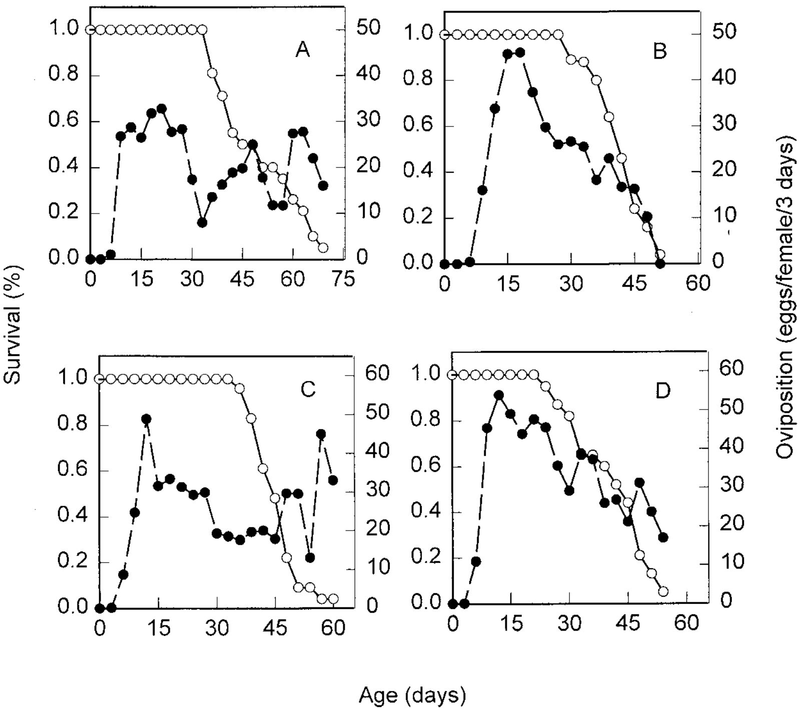

Fig. 1. Observed age-specific reproduction (solid dots and dashed line) and survivorship (circles and line) for *D. citri* females reared on (A) rough lemon, (B) orange jessamine, (C) sour orange, and (D) grapefruit.

were made at different temperatures and host species. The intrinsic rate of increase, mean generation time, and population doubling time are useful indices of population growth under a given set of growing conditions. It is generally believed that shorter developmental times and greater total reproduction on a host reflect the suitability of the plant tested (Van Lenteren and Noldus 1990). Therefore, *D. citri* reared on grapefruit showed a higher intrinsic rate of increase resulting from faster development, higher total nymphal survivorship, and higher reproductive rate (Tables 1–4; Fig. 1). This host plant is presumably more suitable host for *D. citri.* The reason for the high oviposition rate on grapefruit could be the result of physiological factors of the grapefruit plant or physical factors such as leaf hardness (Moran and Buchan 1975). We have noted that the surface of grapefruit tissue is more rippled and densely pubescent than that of other plants, resulting in more surface per unit area. In the current study, the total nymphal developmental period of *D. citri* on four host plants (12.6–13.5 d) was similar to the period (10–15 d) during February to September as reported by Pande (1971), and 11 to 25 d reported by Husain and Nath (1927), and 11 to 15 d reported by Catling (1970). The average adult female longevity on grapefruit and orange jessamine (39.7 d) was significantly shorter than that of rough lemon (Table 3; $P < 0.05$). The mean female longevity on four host plants (39.7–47.6 d) was similar to the report of 45 d by Pande (1971). However, Husain and Nath (1927) reported the adult longevity varied from 20 to 89 d, depending on the season.

The average reproductive rate of *D. citri* reared on grapefruit was significantly higher than those of other three hosts (Table 3; $P < 0.05$; Fig. 1). The mean number of eggs produced per female on these four

Table 4. Comparison of life-table parameters of *D. citri* on four host plants

Hosts	Parameters					
	n	r_m	95% *CI*	R_o	T	t
Orange jessamine	25	0.162b	0.159, 0.166	245.60 ± 8.41	33.91	4.27
Grapefruit	23	0.188a	0.183, 0.192	379.47 ± 20.32	31.63	3.69
Sour orange	23	0.168b	0.161, 0.176	236.64 ± 15.80	32.49	4.12
Rough lemon	20	0.162b	0.151, 0.173	247.12 ± 15.81	34.05	4.28

n, Number of females in analysis; r_m, jackknife estimate of the intrinsic rate of increase (per capita rate of population growth); *CI*, interval estimate for r_m; R_o, net reproductive rate (female offspring per adult female); *T*, mean generation time (in day); *t*, doubling time (in day) for population. Means within a column followed by different letters are significantly different ($P < 0.05$).

host plants (572–858 eggs) was higher than the 185–300 eggs reported by Pande (1971). The highest numbers of eggs produced by a *D. citri* female on grapefruit, sour orange, orange jessamine, and rough lemon were 1378, 994, 830 and 818 eggs, respectively. These numbers were lower than the 1,900 eggs reported by Husain and Nath (1927) and higher than the 520 eggs reported by Pande (1971). These variations in fecundity and longevity could be caused by different host plants, biotypes of *D. citri* or both factors.

Although the net reproductive rates for *D. citri* reared on orange jessamine, sour orange, and rough lemon were much lower, their populations doubling times were longer than the grapefruit (Table 4). These three plants play a very important role in the epidemiology of citrus greening agent and the spread of *D. citri*, especially orange jessamine, which is widely planted in urban areas as landscape hedges in southern Florida, and produces continuous young flushes throughout the seasons. It could serve as an alternate host for maintaining high *D. citri* populations during the periods when young citrus shoots are not available in the commercial groves (J.H.T., unpublished data).

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