Life Table Analysis of Diaphorina citri (Hemiptera: Psyllidae) Infesting Sweet Orange (Citrus sinensis) in São Paulo

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LIFE TABLE ANALYSIS OF *DIAPHORINA CITRI* (HEMIPTERA: PSYLLIDAE) INFESTING SWEET ORANGE (*CITRUS SINENSIS*) IN SÃO PAULO

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Abstract

An ecological life table for eggs and nymphs of *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) was constructed with data obtained from orange orchards (*Citrus sinensis* Osbeck) in 2 regions of the State of São Paulo, over 4 generations in the period from XI-2006 to V-2007, comprising spring, summer, and fall seasons. Young growing shoots with *D. citri* eggs present were identified, and live individuals were counted until adult emergence. No predatory arthropods were observed in association with *D. citri* eggs and nymphs during the study. The mean parasitism of fourth- and fifth-instar nymphs by *Tamarixia radiata* Waterston (Hymenoptera: Eulophidae) was 2.3%. The durations of the egg–adult period were similar among the 4 generations, ranging from 18.0 to 24.7 d (at mean temperatures ranging from 21.6 to 26.0 °C) and followed the temperature requirement models obtained in the laboratory for *D. citri*. However, survival from the egg to the adult stage for the same period varied considerably from 1.7 to 21.4%; the highest mortalities were observed in the egg and small nymphal (first- to thirdinstar) stages, which were considered to be key phases for population growth of the pest.

Key Words: abiotic mortality factor, citrus psyllid, ecology, HLB, temperature requirement model

Resumo

Uma tabela de vida ecológica foi construída para ovos e ninfas de *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) com dados obtidos em pomares de laranja (*Citrus sinensis* Osbeck) em 2 regiões do estado de São Paulo, com 4 gerações, no período de novembro de 2006 a maio de 2007, compreendendo as estações de primavera, verão e outono. Ramos jovens em crescimento com a presença de ovos de *D. citri* foram identificados e os indivíduos vivos foram contados até a emergência dos adultos. Nenhum predador foi observado associado a ovos e ninfas de *D. citri* durante o estudo. A taxa média de parasitismo de ninfas de quarto e quinto ínstares por *Tamarixia radiata* Waterson (Hymenoptera: Eulophidae) foi de 2,3%. A duração do período de ovo a adulto foi semelhante entre as quatro gerações, variando de 18,0 a 24,7 dias (com temperaturas médias de 21,6 a 26,0 °C) e seguiram os modelos de exigencias térmicas obtidas em laboratório para *D. citri*. Todavia, a sobrevivencia de ovo até o estágio adulto variou consideravelmente para o mesmo período, de 1,7 a 21,4%, sendo que as maiores mortalidades foram observadas nos estágios de ovos e ninfas pequenas (de primeiro a terceiro ínstares), as quais foram consideradas fases chaves para o crescimento populacional desta praga.

The Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), has a widespread geographical distribution, and is a cosmopolitan insect with worldwide economic importance as a crop pest. First reported in Brazil in the 1940s (Costa Lima 1942), it was considered of secondary importance until the occurrence of huanglongbing (HLB), or citrus greening, a disease transmitted by this insect, which was confirmed in São Paulo in 2004 (Coletta-Filho et al. 2004; Teixeira et al. 2005).

Although *D. citri* causes direct damage such as deformations of growing leaves , shoot drying, defoliation, and the presence of sooty mold (Hodkinson 1974; Aubert 1987; Michaud 2004), it is as a vector of the plant pathogens causing HLB that this psyllid has acquired major importance for citrus, becoming the main insect pest of this crop. In Brazil, 2 species of bacteria, "*Candidatus* Liberibacter americanus" and "*Candidatus* Liberibacter asiaticus", which inhabit the plant phloem, have been identified in association with plants showing HLB symptoms (Coletta-Filho et al. 2004; Teixeira et al. 2005). HLB is considered the most destructive and serious disease of citrus worldwide (Da Graça 1991; Halbert & Manjunath 2004; Bové 2006), and no effective control method is known, notably for the Asian HLB caused by "*Ca.* L. asiaticus".

Ecological studies of *D. citri*, particularly based on life tables, are scarce but may lead to improved management strategies by providing a better un-

derstanding of psyllid population biology. Ecological life tables are useful for studying insect population dynamics, as they provide an understanding of changes in the populations of a species over time in its natural environment, under natural weather conditions and in the midst of other local organisms (Harcourt 1969). Biotic mortality factors such as pathogens, predators, and parasitoids have been reported in the regulation of *D. citri* populations (Halbert & Manjunath 2004). Coccinelids have been noted as important predators of this pest and play an important role in its biological control (Michaud 2004). The parasitoid, *Tamarixia radiata* Waterston (Hymenoptera: Eulophidae), is also acknowledged as an important natural enemy of *D. citri* worldwide (Étienne et al. 2001), and was recently found in Brazil (Gómez Torres et al. 2006). We studied the changes in population densities and the main factors causing natural mortality of *D. citri* in orange orchards (*Citrus sinensis* Osbeck), based on an ecological life table that we developed in the regions of Araras and Piracicaba over 4 generations, in order to provide information for the control of this insect.

MATERIAL AND METHODS

Ecological Life Table

The first experiment was conducted in an orchard of 'Valencia' orange grafted onto Rangpur lime (*Citrus limonia* Osbeck), planted in II-2002, with trees without HLB symptoms, around 2.5 m tall on non irrigated land in the municipality of Araras, State of São Paulo. Field evaluations were performed from XI-XII-2006, spanning one generation of the insect. Daily weather data were obtained with a thermohygrometer and a pluviometer installed located 10 meters from the experimental site in the experiment area, which provided daily readings of temperature, relative humidity, and rainfall. The second experiment was conducted in an orchard of 'Valencia' orange grafted onto 'Swingle' citrumelo (*Citrus paradisi* Macfad × *Poncirus trifoliata* L. Raf.) planted in III-2005 with trees 2.0 m tall on non irrigated land without HLB symptoms in Piracicaba, São Paulo. This assay was conducted from II-2007 through V-2007 during 3 generations of the insect. Climatic data from the University of São Paulo-Piracicaba weather station around 15 kilometers from the experimental site were used with the exception of rainfall, which was measured with a pluviometer installed at the experiment site.

We selected trees with freshly sprouted flush shoots (new buds or shoots just beginning to grow) on which *D. citri* eggs were present. Each shoot was tagged with fine white sewing thread and a label numbered with a pencil. The eggs were then counted with a magnifying glass (10X). In the Araras experiment, 80 shoots were iden-

tified, while in Piracicaba 77, 58, and 60 shoots were identified in the first, second, and third generations, respectively.

At 2- to 4-d intervals, we counted the immature stages of the insect and determined the number of live individuals in each stage on each shoot. The nymphal stage was categorized as either "small nymphs" for the initial instars (first, second, and third) or "large nymphs" for the later instars (fourth and fifth). Preliminary observations were made to test the hypothesis that nymphs moved between shoots, but for all shoots investigated (*n* = 45), the nymphs remained on the shoots where they had hatched.

When nymphs on a flush shoot reached the large size category, the shoot and nymphs were caged to allow enumeration of nymphs reaching the adult stage. We fabricated each cage were from a 30 × 50 cm piece of fine-mesh fabric. Emerged adults were collected with a mouth-operated aspirator, and their gender was determined with a hand lens (10X), based on the presence of the ovipositor in females. Upon adult emergence, the shoots were measured with a ruler.

The age-specific (ecological) life tables in the field were constructed using the models proposed by Harcourt (1969), Silveira Neto et al. (1976) and Southwood (1978). The number of dead insects (dx) in each stage was obtained by the difference between the number of live insects in that stage (lx) and the number of live insects that entered the following stage (lx_1) (Kobayashi 1968). Mortality rate was obtained from the relationship between dead and live insects in the same stage (dx/lx); survival rate was obtained by the difference, Sx = 1 - dx/lx. Parasitism rates were obtained from the relationship between parasitized nymphs and large nymphs (live + parasitized). Sex ratio was obtained from the relationship between females and the total number of emerged adults (females + males).

Diaphorina citri Egg Survival in the Laboratory

Survival of *D. citri* eggs collected in the Piracicaba orchard was evaluated in an incubator in the laboratory. Eighteen shoots containing egg masses were collected in IV-2007. The eggs (*n* = 146) on each flushing shoot were counted under a stereoscopic microscope, and the shoots were arranged individually in plastic Petri dishes lined with filter paper. Temperature was maintained under 14:10 h L:D at 30 ± 1 °C; RH ranged from 35 to 45%. Hatched nymphs were counted under a stereoscopic microscope 24 and 72 h after the beginning of the experiment.

Statistical Analysis

Analyses of variance were performed for the linear regressions of final shoot length (independent

variable) and *D. citri* egg-adult survival (dependent variable), as well as for small-nymph density and survivorship (dependent variable). The egg-adult survival data were converted into percentages, then transformed to arcsin (x/100)1/2 and finally submitted to analysis of variance by the *F* test. The statistical analyses were conducted on SAS (2000), at a 0.05 significance level.

The field-observed values for duration from egg to adult in the 4 generations studied were compared with expected values obtained from the temperature requirements of mathematical models proposed by Liu & Tsai (2000), Nakata (2006), and Nava et al. (2007) using the chi-square test (0.05). The values expected in each model were estimated using the mean temperature for the same period in the field.

RESULTS AND DISCUSSION

Considering the data from all shoots in all 4 experiments, the overall means (± standard error of the mean) were as follows: 8.3 (±0.43) eggs, 3.5 (±0.33) small nymphs and 1.1 (±0.22) adults per flush shoot. In the Araras experiment, the highest mortalities were observed for both the small and large nymphal stages. As a consequence,

egg-adult survivorship was very low. From the 406 eggs observed at the beginning of the experiment, only 7 adults were obtained (Table 1). Of the 91 large, live nymphs, 6 were parasitized by *T. radiata*. Thus the estimated parasitism rate was 6.6%. In addition to parasitizing *D. citri* nymphs, *T. radiata* females may kill this host by their feeding activity (Skelley & Hoy 2004). However, no killed nymphs other than those that were parasitized (mummified) could be identified in this experiment.

In the 3 generations of the Piracicaba population, the egg stage showed the lowest survival (Table 1), with rates of 38.8, 30.2, and 35.7% in the first, second, and third generations, respectively. In Araras also, only a small number of adults emerged due to high mortality of small nymphs. A large population of eggs and nymphs were observed but the mortality rates of these stages were very high, and thus survivorship of eggs to adults was minimal. Increased control of eggs and small nymphs would have reduced survivorship even more.

No predator was observed in association with *D. citri* eggs or nymphs at either site. In other citrus groves in São Paulo, *Cycloneda sanguinea* (L.), *Harmonia axyridis* (Pallas), and *Scymnus*

TABLE 1. LIFE TABLE FOR IMMATURES OF THE PSYLLID *DIAPHORINA CITRI* ON *CITRUS SINENSIS*, FROM XI-2006 TO V-2007 IN 2 REGIONS OF THE STATE OF SÃO PAULO.

stage x	individuals lx	dead dx	mortality dx/lx	survival Sx	factor dxF
Araras region					
eggs	406	118	0.291	0.709	weather and infertility
small nymphs	288	197	0.684	0.316	weather and host
large nymphs	91	6	0.066	0.934	parasitism
large nymphs	85	78	0.917	0.083	weather and host
adults	7				
females	3				
Piracicaba region, 1st generation					
eggs	739	452	0.612	0.388	weather and infertility
small nymphs	287	114	0.397	0.603	weather and host
large nymphs	173	0	0.000	1.000	parasitism
large nymphs	173	42	0.243	0.757	weather and host
adults	131				
females	66				
Piracicaba region, 2nd generation					
eggs	516	360	0.698	0.302	weather and infertility
small nymphs	156	110	0.705	0.295	weather and host
large nymphs	46	1	0.022	0.978	parasitism
large nymphs	45	14	0.311	0.688	weather and host
adults	31				
females	19				
Piracicaba region, 3rd generation					
eggs	617	397	0.643	0.357	weather and infertility
small nymphs	220	45	0.205	0.795	weather and host
large nymphs	175	4	0.023	0.977	parasitism
large nymphs	171	39	0.228	0.772	weather and host
adults	132				
females	74				

sp., all coccinellids, have been found on shoots with *D. citri*, but they were often observed preying aphids. Only a larva of the green lacewing, *Chrysoperla externa* (Hagen), was observed preying nymphs and adults of *D. citri*. However, there could be additional mortality as a result of nocturnal predation.

The observed mortalities for large nymphs in Piracicaba were quite similar among generations, with 24.3, 33.3, and 25.1% in the first, second, and third generations, respectively. The ectoparasitoid, *T. radiata*, apparently made only a small contribution toward high nymphal mortality in the Piracicaba experiments, with 0.0, 2.2, and 2.3% parasitism in the first, second, and third generations, respectively. Additional mortality may have occurred due to parasitoid feeding, but insects killed by this action could not be identified, nor could the contribution of feeding be quantified.

Although egg survival was low in the field, less than 40% in the 3 generations of the Piracicaba population, the laboratory experiment showed egg survival above 70%. Egg survival of the same population was 75.3% at 30 °C and RH below 50%, conditions that are similar to those observed in the field in the period from 12:00 to 17:00 h.

The hypothesis was tested that shoots infested with numerous small nymphs would result in reduced survival from egg to adult because of a competition effect. However, the opposite was observed, since there was a positive relationship between initial small nymphal density and survivorship up to the adult stage ($F = 26.9$, df = 1,189, $P < 0.0001$, $r^2 = 0.12$), i.e., survivorship for that stage on shoots with a higher initial number of nymphs was higher. As a result, apparently there was no competition among the nymphs. It is likely that a no competition effect occurs at densities such as those observed in the Piracicaba populations, i.e., 7.9 ± 0.56 nymphs per shoot (considering only infested shoots). Hodkinson (1974) suggested that, in general, higher nymphal densities of psyllids would result in higher mortalities, whereas lower densities would be conducive to survival. It would be interesting to determine at what nymphal density per shoot such competition would occur in *D. citri* populations.

The sex ratios of emerged adults were similar in the 3 generations of the Piracicaba population, being 0.504, 0.613, and 0.561 for the first, second, and third generations, respectively. This indicates that field populations have ratios of not less than nearly 1 female to each male, as observed in the study of Nava et al. (2007).

Since *T. radiata* preferentially parasitizes third-, fourth- and fifth-instar nymphs (Étienne et al. 2001), the use of cages to obtain emerged *D. citri* adults may have limited the effect of the parasitoid in these experiments. In order to quantify parasitism in the area without cage interference, a parasitism estimate was obtained on 17-IV-2007 with insects collected from the same orchard, but outside the experiment area. Of 126 fourth- and fifth-instar nymphs inspected for parasitoid presence, only 2 were parasitized (1.6%), supporting the small contribution of parasitism toward *D. citri* nymphal mortality.

Larger nymphs, especially fifth instars, were found on the petioles of larger leaves. This behavior could be for feeding or to prevent parasitism, since no parasitized nymphs were observed at that site; on the other hand, this position on leaf petioles could prevent defoliation. This should be investigated in future studies.

Despite the higher incidence of defoliation, 74 females were obtained in the third Piracicaba generation, the largest population among the 4 generations studied. Defoliation reduced the plant surface that could be exploited by young insects with a possible effect on the amount of food. In addition to defoliation itself, the effect of defoliation on the nutritional quality of leaves for *D. citri* could be studied in the future. Nevertheless, defoliation is not a controllable factor, since in practice it cannot be increased and leaves are essential for citrus tree development and for the production of fruits.

In addition to weather factors, *D. citri* nymphal survival seemed to be influenced by the host tree and shoots where the insects develop. Nutritional aspects of the shoots may be important for insect development, since grafted trees are "unnatural" host plants for the insect. Two combined citrus species or compatible genera, such as *C. sinensis* orange grafted onto Rangpur lime *C. limonia*, or the 'Swingle' citrumelo, a hybrid between *C. paradisi* and *P. trifoliata*, present as an "unknown" host for the insect during its evolution. The evolution of *D. citri* occurred on seed-propagated hosts represented by species of *Citrus* and other members of Rutaceae. To our knowledge no information on this "unknown" host factor is available.

Egg-adult survival varied greatly between shoots; in Piracicaba population 70% of the shoots showed zero egg-adult survival and only 5% of the shoots had more than 80% survival. No relationship was observed between final shoot length and egg-adult survival in the first and third Piracicaba generations (first - $F = 0.002$, df = 1, 69, $P = 0.9635$, third - $F = 0.25$, df = 1, 57, $P = 0.6167$). The mean value for final shoot length (± sem) in the first and third generations were 25.0 ± 0.95 and 17.0 ± 1.11 cm, respectively. However, there was a significant and positive correlation between final shoot length, 21.2 ± 0.95 cm, and survivorship of the immature stages of *D. citri* in the second generation studied ($F = 5.64$, df = 1, 55, $P = 0.0210$, $r^2 = 0.09$). Considering the data from the 3 Piracicaba generations, survival from egg to adult did not depend on the final length (21.3 ± 0.66 cm) of the orange tree shoots where the insects developed ($F = 0.94$, df = 1, 185, $P = 0.3318$).

The hypothesis was tested that freshly sprouted buds or shoots beginning to grow, which produced larger shoots, would harbor more eggs. No

relationship was found between number of eggs and final shoot length ($F = 0.34$, df = 1, 185, $P = 0.5583$). The manner by which *D. citri* females select a host for oviposition is still unknown. However, oviposition is performed on freshly sprouted buds, which may have distinct physical and nutritional characteristics; this would explain the variation in the number of eggs laid on each shoot.

Duration of the psyllid egg-to-adult period was estimated from the interval between the beginning of the experiment (egg masses) and adult emergence. Survivorship for this period was obtained from the relationship between the number of emerged adults and the number of eggs in the beginning of the experiment (Table 2).

The estimated survival from egg to adult differed among the 4 *D. citri* generations studied ($F = 6.34$, df = 3, 241, $P = 0.0004$). The lowest survival rates were observed in Araras and in the second Piracicaba generation, at 1.7 and 6.0%, respectively. The highest survivals occurred in the first and third generations of the Piracicaba population, at 17.6 and 21.4%.

Laboratory studies have found shorter durations for the egg-adult period, from 17 to 18 d at 25 °C (Tsai & Liu 2000) and 17 d at the same temperature (Nava et al. 2007) in relation to those obtained in the present work. Survival values of *D. citri* immatures observed under controlled conditions, in the same studies, were significantly higher, i.e., 70% (Tsai & Liu 2000) and 70 to 80% (Nava et al. 2007) than survival estimates obtained by us in the field. Survival rates were lower than 10% in Araras and in the second generation in Piracicaba, and lower than 25% in the first and third generations in Piracicaba.

The times of adult emergence peaks were similar between the Araras populations (19 d) and the first and second generations from Piracicaba (19 and 20 d) (Fig. 1). In the third Piracicaba generation, the greatest emergence of adults occurred 25 d after the beginning of the experiment, due to lower temperatures. The emergence of adults over several d could be an evolutionary survival strategy in this insect species, since the development of growing citrus shoots, an essential resource for *D. citri* feeding and reproduction, also takes place over time. The emergence of adults over several d may make insect control more difficult.

The expected values obtained from the mathematical model proposed by Nava et al. (2007) with a Brazilian *D. citri* population did not differ from the estimated values for duration from egg to adult obtained in this study (Table 3). Similarly, the models proposed by Nakata (2006) with a population in Japan, and Liu & Tsai (2000) with a *D. citri* population in Florida, USA, also showed egg-adult durations similar to those observed in Brazilian orchards (Table 3). This information indicates that the São Paulo (Brazil) populations, both, those studied by Nava et al. (2007) and those

TABLE 2. MEAN DAILY MAXIMUM AND MINIMUM TEMPERATURES (±STANDARD ERROR OF MEAN), CUMULATIVE RAIN (MM), PRECIPITATION DAYS DURING THE EXPERIMENTS, AND BIOLOGICAL DATA FOR *DIAPHORINA CITRI* ON *CITRUS SINENSIS* BETWEEN XI-2006 AND V-2007, IN 2 REGIONS OF SÃO PAULO.

Site and generation	Period	Rain (mm) (days)	Maximum temp. (°C) (±SEM)	Minimun temp.(°C) (±SEM)	Egg-adult duration (days)	Egg-adult survival (%)
Araras region	18-XI-7-XII	92 (5)	31.5 (0.63)	20.4 (0.38)	18.0	1.7
Piracicaba region, 1st generation	17-II-17-III	111 (7)	32.6 (0.31)	19.6 (0.16)	21.7	17.6
Piracicaba region, 2nd generation	17-III-16IV	106 (7)	31.6 (0.53)	18.2 (0.23)	21.9	6.0
Piracicaba region, 3rd generation	16-IV-19-V	30 (2)	28.1 (0.64)	15.2 (0.47)	24.7	21.4

TABLE 3. DURATION OF *DIAPHORINA CITRI* FROM EGG TO ADULT, IN DAYS, IN 4 GENERATIONS STUDIED, AND VALUES ESTIMATED ACCORDING TO MATHEMATICAL MODELS FOR THE TEMPERATURE REQUIREMENTS OF DIFFERENT POPULATIONS.

| Site and generation	Mean temperatures (°C)	egg-adult duration (days)			
		Observed (field)	Liu & Tsai (2000) 1/D = 0.0040 * T-0.0418	Nakata (2006) 1/D = 0.0043 * T-0.0523	Nava et al. (2007) 1/D = 0.0047 * T-0.0641
Araras	26.0	18.0	16.1	16.8	16.9
Piracicab 1st generation	26.1	21.7	16.0	16.7	16.8
Piracicaba 2nd generation	24.9	21.9	17.3	18.3	18.5
Piracicaba 3rd generation	21.6	24.7	22.4	24.6	26.1
χ^2, 3 df			3.74	2.32	2.20
p			0.2914	0.5091	0.5321
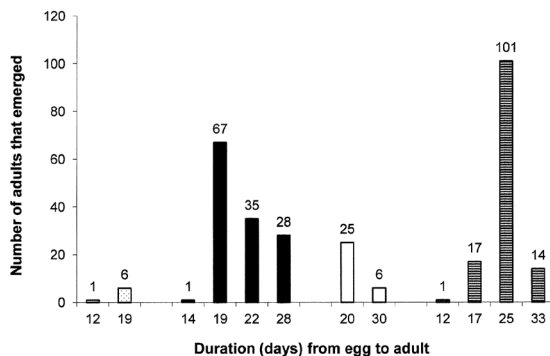
Fig. 1. Duration of the egg-to-adult period and number of emerged *Diaphorina citri* adults on *Citrus sinensis* in 4 generations between XI-2006 and V-2007.

from Araras and Piracicaba, as well as the populations from Japan and Florida had similar temperature requirements for the immature stages.

The estimates for survival in the field were much lower than those observed under laboratory conditions. On *Murraya paniculata* L. Jack at temperatures from 15 to 30 °C, egg-adult survival values were higher than 60% (Liu & Tsai 2000), while on *C. limonia* at temperatures from 18 to 30 °C, survival values were higher than 70% (Nava et al. 2007). Consequently, weather, host plant, interspecific and intraspecific competition factors, among others, may reduce survivorship in the field.

Although in this investigation the insect was studied for 4 generations in less than a yr, the study period comprised the spring, summer, and fall seasons, when the highest populations of this insect have been found. The observations that the highest mortalities occur in the initial life stages (eggs and initial nymphal instars) demonstrate that they are more susceptible to adverse weather and host conditions. Additional mortality rates for late-instar nymphs caused by the parasitoid *T. radiata* were low.

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