

Population Ecology and Phenology of *Diaphorina citri* (Hemiptera: Psyllidae) in Two Florida Citrus Groves

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ABSTRACT Studies were conducted to assess population densities and phenology of the psyllid *Diaphorina citri* Kuwayama at two citrus groves in east-central Florida. One grove contained young, irrigated grapefruit trees and the other contained mature, nonirrigated orange trees. The two groves were sampled weekly for eggs, nymphs, and adults on flush shoots; for adults on mature leaves; and for adults captured on yellow sticky card traps. Because infestations of immature *D. citri* develop strictly on young flush, the abundance of flush was assessed weekly. Overall means of 26.5, 16.8, and 0.27 eggs, nymphs, and adults per flush shoot, respectively, were observed in the young grapefruit trees. In the grove of mature orange trees, overall means of 16.0, 12.7, and 0.31 eggs, nymphs, and adults per flush shoot were observed, respectively. Flush abundance was an inconsistent indicator of the mean density of *D. citri* per flush shoot. Mean density per shoot by itself was an inconsistent indicator of overall population levels of *D. citri* at each study site because few shoots were sometimes present when mean densities per shoot were high. May, June, and July were periods of time when immature *D. citri* were consistently present and most abundant at each study site, but the study indicated large infestations could occur at any time of the year depending on environmental factors and flush availability. Yellow sticky traps were effective for both male and female *D. citri* and useful for gauging adult population trends.

KEY WORDS phenology, trapping, sampling, sticky traps, huanglongbing

The Asian citrus psyllid, *Diaphorina citri* Kuwayama, is an important pest of citrus because it transmits phloem-limited bacteria (*Candidatus Liberibacter* spp.) responsible for citrus greening disease (huanglongbing), one of the world's most serious diseases of citrus (McClean and Schwartz 1970, Halbert and Manjunath 2004, Bové 2006). *D. citri* was first found in Florida during June 1998 (Tsai et al. 2002) and is now established throughout the state's citrus-growing regions (Michaud 2004). Citrus greening attributed to *C. L. asiaticus* was found in southern Florida during late August 2005 and has since been detected at a number of locations across the state (FDACS 2008).

Infected adult *D. citri* transmit the phytopathogenic bacterium to healthy trees, and symptoms of the disease may appear within several months (Bové 2006). Empirical observations from around the world indicate that the progression of citrus greening in a grove can be reduced by controlling the vector (Bové 2006). For this reason, an intensive psyllid control program

coupled with aggressive removal of infected trees is the primary strategy for managing citrus greening disease. Knowledge of the epidemiology of the disease as it relates to infestation densities of *D. citri* is lacking; therefore, it is unclear how intensive a psyllid control program needs to be.

Population fluctuations of *D. citri* on citrus and other host plants are closely correlated with rhythm, quantity, and nutritional quality of plant flush because eggs and nymphs are exclusively associated with new growth (Catling 1970). For this reason, Hall and Albrigo (2007) developed a sampling method for assessing the abundance of flush shoots in a citrus grove and proposed an index of relative abundance for psyllids based on both flush abundance and mean numbers of insects per flush shoot. Tsai et al. (2002) speculated that population peaks in Florida would generally occur whenever new flush becomes available. In a study initiated several months after the psyllid was first discovered in Florida, populations of adult *D. citri* in orange jasmine (*Murraya paniculata* L. Jack) and potted grapefruit (*Citrus paradise* Macfadyen) were continually present with peak populations during June–July, September–October, December, and February–April (Tsai et al. 2002). Natural enemies were not considered important factors in regulating popu-

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lations of *D. citri* during the first year after its discovery in Florida (Tsai et al. 2002). An increase in populations of a native lady beetle, *Olla v-nigrum* Mulsant, apparently in response to infestations of *D. citri*, was noted in several counties during 2001 (Michaud 2001). Numerous other natural enemies of *D. citri* have since been identified in Florida (McFarland and Hoy 2001, Michaud 2004, Michaud and Olsen 2004, Meyer et al. 2007). Despite these natural enemies, notable infestations of *D. citri* have continued to occur.

The purpose of research presented here was to describe population densities and phenology of *D. citri* on citrus in two groves in east-central Florida: one grove containing young citrus trees and one containing mature trees. We conducted weekly sampling for eggs, nymphs, and adults on flush shoots (young developing leaves as described by Hall and Albrigo 2007) and for adults on mature leaves. We also assessed the phenology of adult *D. citri* based on weekly captures of adults on yellow sticky card traps (Hall et al. 2007) deployed directly in citrus trees.

Materials and Methods

The phenology of *D. citri* was assessed during 2005 and 2006 at two citrus groves: one near Fort Pierce in Saint Lucie County (27°26'08" N, 80°25'50" W) and one near Vero Beach in Indian River County (27°39'02" N, 80°28'02" W). The study locations were 25 km apart. The Saint Lucie County grove was located at a USDA-ARS research farm that contained a number of blocks of trees of various ages and scion/rootstock combinations, all regularly irrigated. The particular block (0.2 ha in size, 2.7-m tree spacing, 7.5-m row spacing) chosen for the study contained 90 'Marsh' grapefruit (*C. paradise*) trees (2.5 yr old, ≈1.3 m tall) on the rootstock 'Sun Chu Sha' mandarin (*C. reticulata* Blanco). Sampling was initiated during early January 2005 and continued until July 2006, when discovery of citrus canker disease [cause by the bacterium *Xanthomonas axonopodis* pv. *citri* (Hasse)] in the block forced us to abandon the study (tree removal was mandated by USDA-ARS). The Indian River County grove was a nonirrigated, 1.0-ha block (4.6-m tree spacing, 9.1-m row spacing) of 'Temple' orange (*C. reticulata* Blanco × *C. sinensis* L. Osbeck) trees (36 yr old, ≈3.4 m tall) on the rootstock 'Cleopatra mandarin' (*C. reshni* Hort. ex Tan.). Sampling was initiated during early January 2005 and continued until the end of December 2006. No hard pesticides were applied to either group of trees during the study. The young trees were subjected to a minimal plant disease program (spray oils and copper): spray oil (455) was applied on 20 May (16 liters/ha) and 12 August 2005 (42 liters/ha). Metallic copper was applied with the oil on 12 August 2005 (4 kg/ha). The young trees were fertilized monthly during the spring and summer (four to five applications of liquid fertilizer, 9-2-9, and one application of dry fertilizer, 10-10-10, each season), and nutritional sprays of macronutrients and micronutrients were applied two or three times each season. In the mature orange grove,

spray oil (435) was applied on 19 May 2005 (5 liters/ha per ha) and 3 April 2006 (2 liters/ha). Another spray oil, 470, was applied on 22 July 2005 (56 liters/ha), 29 June (70 liters/ha), and 27 July 2006 (28 liters/ha). Foliar applications of macronutrients and micronutrients were applied approximately monthly during the spring and summer. Liquid fertilizer (5-0-8) was applied to the soil beneath the trees periodically from February through October. No pruning or hedging of trees was conducted at either study site. Air temperature (hourly readings) was obtained at each location using a data logger (WatchDog model 100; Spectrum Technologies, Plainfield, IL) hung inside a tree canopy close to the trunk. Rainfall data for the young trees was obtained 3 km from the study site at a rain gauge operated by the University of Florida's Florida Automated Weather Network (FAWN). Rainfall data for the mature trees were obtained 0.4 km from the study site at a rain gauge operated by the Florida Research Center for Agricultural Sustainability.

Egg, Nymph, and Adult Psyllid Populations on Flush. Young citrus flush growth was sampled weekly for psyllid eggs, nymphs, and adults. Forty-five trees were randomly selected weekly at each study location, and the quantity of flush was assessed by counting the number of new flush shoots within a cubic square frame (15.2 by 15.2 by 15.2 cm = 3.5 dm³) placed into the outer canopy of each tree at three locations (Hall and Albrigo 2007). Samples were equally spaced around the tree canopies at ≈1 m above ground in the young trees and 1-2 m above ground in the mature trees. A flush shoot was defined as any flush shoot with developing leaves. Flush counted therefore ranged from newly breaking buds of just new, unexpanded (often called feather) flush leaves to shoots with expanded tender young leaves. Three flush shoots (same approximate locations as where quantity of flush was assessed) were examined on each of the 45 trees to determine the number of adults per shoot. Fewer shoots were examined when flush was scarce, and sometimes no flush was present to examine. Examinations of flush for adults were generally made between the hours of 0900 and 1130 in the young trees and 0900 and 1400 in the mature trees. In addition to examining flush shoots to count adults, the shoots were also searched for natural enemies of *D. citri*. One flush shoot from each of the 45 trees was excised, placed into an individual sample bag, and taken to a laboratory to count numbers of eggs and nymphs and to sex adults captured. Data were also collected from these flush shoots on shoot length (cm), number of expanded leaves per shoot, and number of unexpanded leaves per shoot. Numbers of nymphs parasitized by *T. radiata* were counted (2005 only) by examining the ventral side of fourth- and fifth-instar nymphs for parasitoid eggs and larvae. Mean numbers of eggs, nymphs, and adults per flush shoot were calculated each week (data for adults from shoots examined in the groves), and means and SEM were computed over all weekly means. The phenology of *D. citri* on flush was depicted graphically by plotting mean numbers of egg, nymph, and adult psyllids per shoot per week over

time. Numbers of males and females per flush shoot (data from flush shoots examined in the laboratory) were compared using a pooled *t*-test (in cases where heterogeneity was detected, the data were transformed to square roots). Weekly percentages of shoots with eggs, nymphs, and adults were calculated. The relationship between percentages of shoots infested by *D. citri* and mean density of *D. citri* per shoot was studied using correlation analyses. An index of abundance for eggs, nymphs, and adults (Hall and Albrigo 2007) was calculated each week by multiplying the mean number of flush shoots per sample by mean numbers of eggs, nymphs, or adults per flush shoot. Correlations were studied between *D. citri* densities on flush shoots and each of the following variables: shoot length, number of unexpanded leaves per flush shoot, number of expanded leaves per flush shoot, and total number of leaves per flush shoot. Stepwise regressions were conducted to determine whether egg density per flush shoot could be related to shoot length, number of unexpanded leaves per flush shoot, number of expanded leaves per flush shoot, and/or total number of leaves per flush shoot. The possible negative effect of the petroleum oil sprays was studied by comparing pre- and posttreatment densities of *D. citri* on flush shoots. Mean, maximum, and minimum daily air temperatures were determined and were averaged over 1-, 2-, and 3-wk periods preceding each sample date. Total rainfall over 1-, 2-, and 3-wk periods preceding each sample date was determined. Correlations were studied between these environmental variables and both numbers of flush shoots per sample and densities of *D. citri* per flush shoot.

Adult Psyllid Populations on Mature Leaves. Adult counts were made weekly on a pair of mature leaves (including the stem between the leaves) at each study location in the same 45 trees as above, 10 pairs of leaves per tree in the young trees, and 20 pairs of leaves per tree in the mature trees. The 10 or 20 leaf pairs were randomly chosen around the outer tree canopy 1–2 m above ground. The number of adults on each pair of leaves was counted without disturbing the leaves. The mean number of adults per pair of mature leaves was calculated each week, and an overall mean and SEM was computed over all weekly means. The seasonal abundance of adult psyllids on mature leaves was graphed by plotting the mean number of psyllids per pair of leaves per week over time. Weekly percentages of mature leaf samples infested by adults were calculated and plotted over time.

Sticky Trap Samples for Adult Psyllids. Yellow (a bright yellow hue similar to S-G-390 by Behr Process, Santa Ana, CA) sticky traps (7.62 by 12.7 cm; Great Lakes IPM, Vestaburg, MI) were used to monitor adult psyllid populations in 10 trees randomly selected at each study location (one trap per tree). Traps were suspended 1–1.5 m above ground near the outside of the canopy from a branch using a twist tie and replaced weekly from the same trees throughout the study. Adult psyllids collected on the traps were sexed and counted. In addition, on each day that traps were

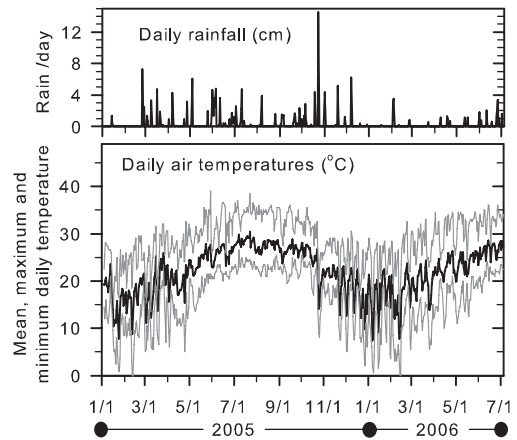


Fig. 1. Daily rainfall and mean, maximum, and minimum daily air temperatures at the young grapefruit grove.

deployed, adult psyllid counts were made on random pairs of mature leaves in each tree as described above taking 10 pairs per tree in the young trees and 20 pairs per tree in the mature trees. Numbers of males and females captured per trap at each study location were compared over all sample dates, and on individual sample dates when a total of five or more adults were captured among all traps, using pooled *t*-tests (in cases where heterogeneity was detected, the data were log-transformed). The seasonal abundance of adult psyllids according to trap captures was depicted graphically by plotting the mean number of psyllids per trap per week over time. Correlation analyses were conducted between mean number of adults per trap per week and mean number of adults per pair of mature leaves (the latter being the mean of data from both the beginning and end of each trapping period).

Statistical Analyses. All *t*-tests were conducted using PROC TTEST (SAS Institute 2002) ($\alpha = 0.05$) with the folded form *F* statistic option to test homogeneity of variances; correlation analyses using PROC CORR (SAS Institute 2002) (Spearman rank correlation co-

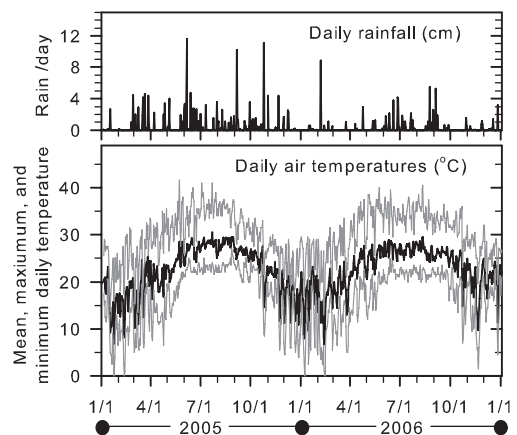


Fig. 2. Daily rainfall and mean, maximum, and minimum daily air temperatures at the mature orange grove.

Table 1. Air temperatures within the young grapefruit grove and the mature orange grove^a

Average daily temperatures ^b	Young grapefruit grove	Mature orange grove
Overall mean/7 d	21.9 ± 0.5	22.3 ± 0.4
Highest mean/7 d	28.9 ± 0.4	29.0 ± 0.2
Lowest mean/7 d	12.0 ± 0.9	11.2 ± 1.4
Highest mean/14 d	28.8 ± 0.2	28.9 ± 0.1
Lowest mean/14 d	13.7 ± 0.9	13.1 ± 1.1
Overall mean max./7 d	28.8 ± 0.5	29.8 ± 0.5
Highest mean max./7 d	35.5 ± 0.6	37.9 ± 0.8
Highest mean max./14 d	35.2 ± 0.4	36.5 ± 0.5
Overall mean min./7 d	16.1 ± 0.6	16.1 ± 0.5
Lowest mean min./7 d	4.3 ± 0.6	3.0 ± 1.0
Lowest mean min./14 d	6.2 ± 1.2	5.6 ± 1.2

Values are mean ± SEM (°C).

^a Air temperatures measured within tree canopies.

^b For overall mean, mean max., and mean min. daily temperatures, *n* = 79 7-d periods for the young grapefruit grove and *n* = 105 7-d periods for the mature orange grove. Means and SEM values for all other average daily temperature variables are based on the no. days of the period of interest, *n* = 7 or 14 d.

efficients, $\alpha = 0.05$); and stepwise regression analyses using PROC STEPWISE (SAS Institute 2002) (significance levels for variable entry and retention = 0.15).

Results

Seasonal air temperature and rainfall profiles at the young grapefruit and mature orange groves are presented in Figs. 1 and 2, respectively. Air temperature summaries are presented in Table 1. A mean of 2.3 ± 0.4 (SEM) cm of rainfall per week was recorded in the vicinity of the young grapefruit grove, and 2.4 ± 0.3 cm of rainfall per week was recorded at the mature orange grove. Mean densities of eggs, nymphs, or adults per flush shoot; mean percentages of flush shoots infested by each life stage; and mean indices of abundance for each life stage over the entire study at each location are presented in Table 2. Seasonal profiles of flush abundance and of population densities and phenology of *D. citri* on flush are presented in Figs. 3 (young grapefruit grove) and 4 (mature orange grove). Population densities and phenology of adult *D. citri* observed on mature leaves and captured on

traps are presented in Figs. 5 (young grapefruit grove) and 6 (mature orange grove).

The following beneficial insects were observed on flush at each study location: *Cycloneda s. sanguinae* L., *Curinus coeruleus* Mulsant, *Harmonia axyridis* Pallas, *Olla v-nigrum* Mulsant (Coleoptera: Coccinellidae); *Allograpta* sp. (probably *A. oblique* Say) (Diptera: Syrphidae); *Chrysopa* sp. (Neuroptera: Chrysopidae); an unidentified brown lacewing species (Neuroptera: Hemerobiidae); and *Zelus longipes* L. (Hemiptera: Reduviidae) (identifications made by M. Hentz). *C. s. sanguinae*, *H. axyridis*, and *O. v-nigrum* were common at each study location but primarily only from January through early June each year. Over all sample dates, means of 14 ± 4 and 4 ± 1% nymphs per sample date were observed to be parasitized by *T. radiata* at the young grapefruit and mature orange grove, respectively. Levels of 30% or more nymphs parasitized were occasionally observed in the young grapefruit trees during July, August, and September, with an observed maximum of 52.3%. No parasitized nymphs were observed in these trees from February through June. Parasitism of *D. citri* nymphs in the mature orange trees was low but consistent from July through October, with a maximum of 15% nymphs parasitized in October. Parasitized nymphs were observed in these trees on only one sample date from February through June. Cadavers of adult *D. citri* killed by the entomophagous fungus *Hirsutella citrififormis* Speare were occasionally observed on mature leaves from summer through winter each year but only at the mature orange grove (identification of *H. citrififormis* made by D. Boucias, University of Florida). Voucher specimens of these natural enemies were deposited in the USDA-ARS Subtropical Insects Research Unit collection in Fort Pierce, FL.

Young Grapefruit Grove. Foliar flush growth was almost continuously present in these young trees from January 2005 through July 2006 (Fig. 3). No significant correlations were found between mean number of flush shoots per sample and either air temperature or rainfall during the 7 d preceding a sample date (Table 3). Results similar to these were obtained when analyses were conducted using temperature and rainfall during 14 and 21 d preceding sample dates, except a

Table 2. Infestation densities (mean ± SEM) of *D. citri* in citrus in east-central Florida in one grove of young grapefruit trees and one grove of mature orange trees

Life stage	Mean/flush shoot/sample date	Highest density/single shoot	Mean index of abundance/sample date	Mean percent infested shoots/sample date
Young grapefruit grove ^a				
Eggs	26.5 ± 2.9	777	39.3 ± 6.6	51.7 ± 3.4
Nymphs	16.8 ± 2.3	405	24.2 ± 4.4	50.3 ± 3.2
Adults	0.27 ± 0.04	13	0.4 ± 0.1	13.3 ± 1.9
Mature orange grove ^b				
Eggs	16.0 ± 2.1	316	34.7 ± 8.2	49.9 ± 3.4
Nymphs	12.7 ± 1.5	319	21.0 ± 3.8	59.6 ± 2.8
Adults	0.31 ± 0.03	23	0.4 ± 0.1	11.0 ± 1.2

^a *N* = 77.

^b *N* = 88.

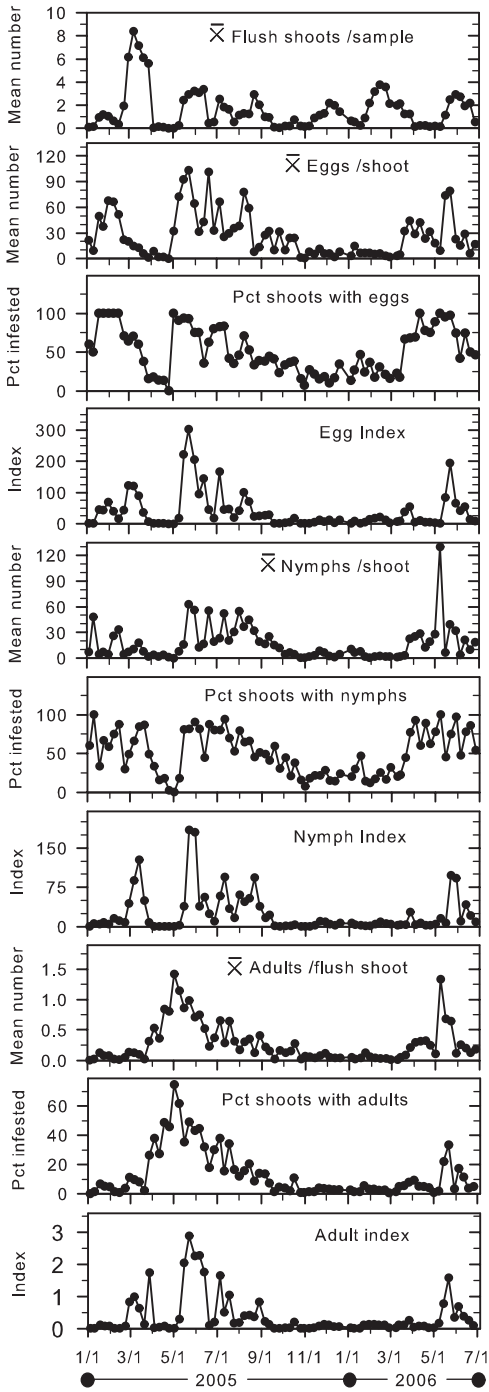


Fig. 3. Population dynamics of *D. citri* over time on flush shoots in a young grapefruit grove in east-central Florida. The index of abundance for each life stage is the product of the mean number of insects per shoot multiplied by the mean number of shoots per sample.

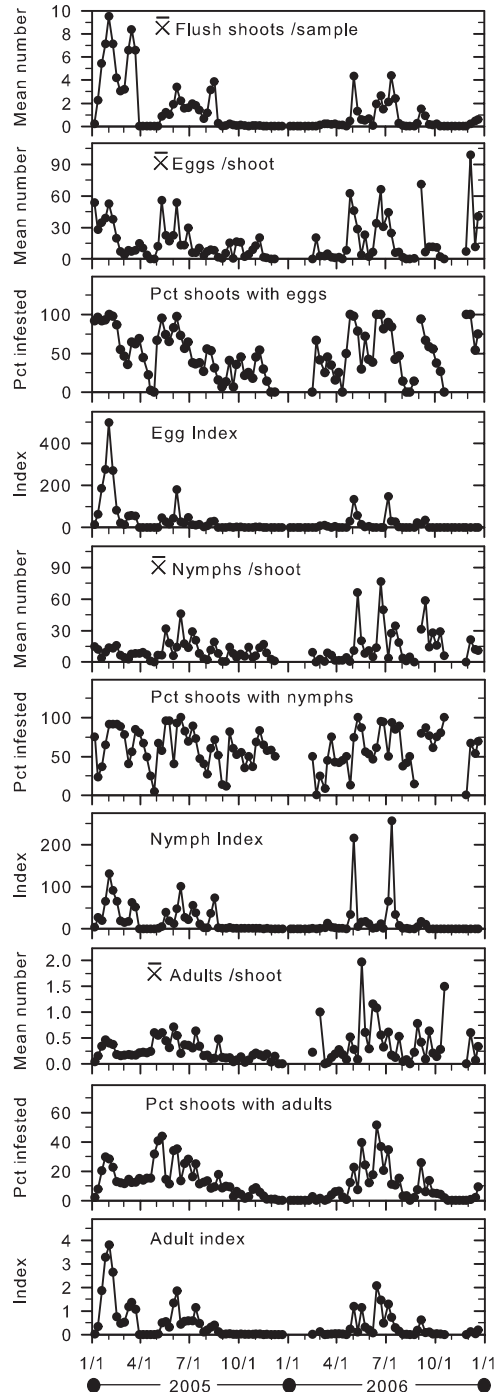


Fig. 4. Population dynamics of *D. citri* over time on flush shoots in a mature orange grove in east-central Florida. The index of abundance for each life stage is the product of the mean number of insects per shoot multiplied by the mean number of shoots per sample.

significant positive correlation was found between flush shoot density and total rainfall during the 14 d before a sample date ($r = 0.24, Pr > r = 0.04, n = 76$).

A mean length of 7.3 ± 0.1 cm per flush shoot was observed over all shoots sampled. Means of 4.3 ± 0.1 unexpanded, 6.7 ± 0.1 expanded, and 11.0 ± 0.1 total

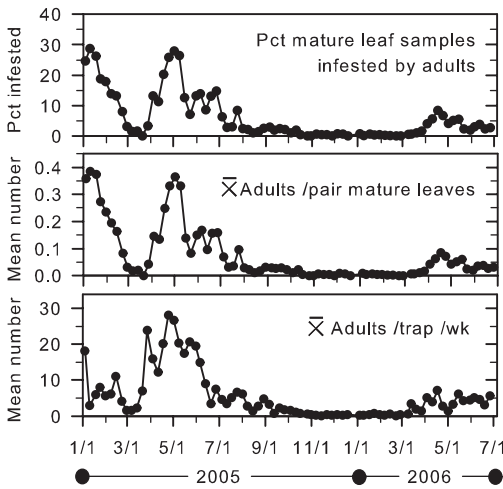


Fig. 5. Population densities and phenology of *D. citri* in a young grapefruit grove in east-central Florida based on adults observed on mature leaves and captured at yellow sticky traps.

leaves per flush shoot were observed over all flush shoots sampled.

Mean numbers of eggs per flush shoot were positively correlated with numbers of unexpanded leaves per shoot (Table 4). Nonsignificant correlations were found between mean number of flush shoots per sample and mean number of eggs, nymphs, or adults per flush shoot (Table 4). Stepwise regressions indicated that, among all of the flush variables measured, mean number of eggs per shoot (Y) was only related to the mean number of new, unexpanded leaves per shoot (X): $Y = 1.8 + 5.4X$ ($F = 26.7, Pr > F = <0.0001, r^2 = 0.26, 76$ df). Significant correlations were found between mean number of eggs, nymphs, or adults per

flush shoot and the percentage of shoots infested by eggs ($r = 0.70, Pr > r = <0.0001, n = 77$), nymphs ($r = 0.67, Pr > r = <0.0001, n = 77$), and adults ($r = 0.85, Pr > r = <0.0001, n = 77$), respectively.

Seasonal trends in the index of relative abundance were similar for eggs, nymphs, and adults (Fig. 3). The indices for eggs and nymphs reflected a sharper decline in population densities during May through August than was reflected by mean densities per shoot. Population levels of eggs and nymphs were low in the young grapefruit trees during April 2006 based on indices of abundance, although mean densities per flush shoot were relatively large.

Means of 92.6 ± 19.8 eggs, 15.9 ± 4.0 nymphs, and 1.1 ± 0.2 adults per shoot were present before the low-rate application of spray oil. Means of 65.4 ± 9.2 eggs, 59.4 ± 7.6 nymphs, and 1.0 ± 0.1 adults per shoot were present after this treatment. There were no significant differences between these pre- and postspray densities of eggs or adults (analyses not presented), but postspray densities of nymphs were significantly greater than prespray densities ($t = 5.1, Pr > t = <0.0001, 115$ df). With respect to the higher-rate application of spray oil, means of 78.0 ± 27.1 eggs, 36.7 ± 11.6 nymphs, and 0.5 ± 0.2 adults per shoot were present before the treatment and 31.9 ± 7.7 eggs, 38.2 ± 9.0 nymphs, and 0.4 ± 0.1 adults per shoot were present after the treatment. There were no significant differences between the pre- and postspray densities of eggs, nymphs, or adults.

A total of 744 adult *D. citri* from flush shoots at the young grapefruit grove were sexed during the study, and 54.2% of these were females. Means of 0.23 ± 0.05 females and 0.19 ± 0.03 males per flush shoot were observed over all sample dates. There was no significant difference between these means ($t = 0.79, Pr > t = 0.43, 152$ df).

Means of 29.0 ± 9.9 eggs and 20.7 ± 5.8 nymphs per shoot were observed during July 2005 before the hottest 7-d period during the study (Table 1), and 35.7 ± 12.5 eggs and 30.6 ± 11.5 nymphs per shoot were observed after this hot period. Means of 29.0 ± 9.9 eggs and 20.7 ± 5.8 nymphs per shoot were observed during July 2005 before the hottest 14 d period of the study, and 37.9 ± 13.3 eggs and 54.5 ± 18.2 nymphs per shoot were observed at the end of this hot period.

Means of 49.0 ± 6.4 eggs and 4.2 ± 2.8 nymphs per shoot were observed during late January 2005 just before the coldest 7-d period of the study (Table 1), and 37.0 ± 9.1 eggs and 6.7 ± 4.4 nymphs per shoot were observed at the end of the cold spell. The coldest 7- and 14-d periods based on mean minimum air temperatures occurred during February 2006, with air temperatures falling to 0°C for <1 h on 12 February and for >3 h on 13 February. Air temperatures fell to -0.5°C for >1 h on 14 February 2006. Means of 5.4 ± 3.3 eggs and 1.5 ± 0.9 nymphs per shoot were observed just before this cold spell, and 5.5 ± 1.8 eggs and 2.4 ± 1.2 nymphs per shoot were observed the day after this cold spell.

Mean numbers of eggs or nymphs per flush shoot at the young grapefruit grove were positively correlated

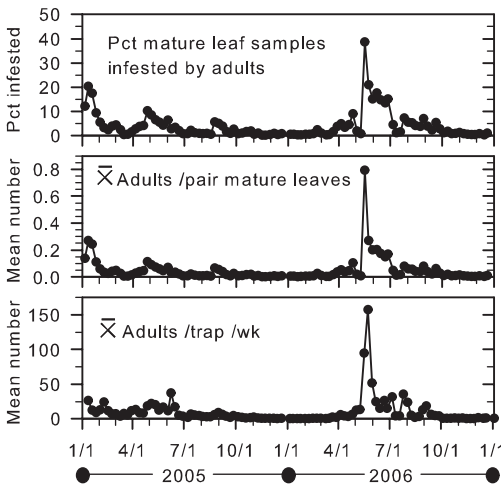


Fig. 6. Population densities and phenology of *D. citri* in a mature orange grove in east-central Florida based on adults observed on mature leaves and captured at yellow sticky traps.

Table 3. Spearman correlation coefficients between (1) mean numbers of *D. citri* per citrus flush shoot per sample date and various environmental factors during the wk before sampling and (2) mean no. of flush shoots per sample and the same environmental factors

Environmental variable	Eggs per shoot ^a	Nymphs per shoot ^a	Adults per shoot ^a	Flush shoots per sample ^b
Young grapefruit grove				
Mean daily air temp	0.34 ^c	0.48 ^c	0.54 ^c	-0.03
Mean max daily air temp	0.36 ^c	0.54 ^c	0.55 ^c	-0.03
Mean min. daily air temp	0.30 ^c	0.40 ^c	0.45 ^c	-0.01
Total rain	0.02	-0.04	0.23 ^d	0.09
Mean daily air temp × total rain	0.07	-0.01	0.26 ^d	0.07
Mature orange grove				
Mean daily air temp	-0.01	0.27 ^c	0.10	0.22 ^d
Mean max daily air temp	-0.01	0.26 ^d	0.16	0.20 ^d
Mean min. daily air temp	0.05	0.28 ^c	0.03	0.23 ^d
Total rain	0.17	-0.05	0.20	0.18
Mean daily air temp × total rain	0.17	-0.02	0.20	0.19

Data from a young grapefruit grove and a mature orange grove.

^a *N* = 77 for young tree data, 88 for mature tree data.

^b *N* = 77 for young tree data, 102 for mature tree data.

^c Significant at $\alpha = 0.01$.

^d Significant at $\alpha = 0.05$.

with air temperatures during the 7 d preceding a sample date but not correlated with rainfall (Table 3). Adult densities per flush shoot were positively correlated with both air temperature and rainfall. Results similar to these were obtained when analyses were conducted using temperature and rainfall during 14 and 21 d preceding sample dates.

A mean of 0.08 ± 0.01 adults per pair of mature leaves was observed over the entire study at the young grapefruit grove. The largest single number of adults observed per pair of mature leaves was six. Weekly percentages of mature leaf samples containing at least one adult averaged $6.2 \pm 0.9\%$ over all sample dates. The seasonal profile of adult densities on mature

leaves generally reflected the profile based on percentages of mature leaf samples infested (Fig. 4).

A total of 4,154 adults (45.3% female) were captured on sticky traps during the study, with a mean of 5.6 ± 0.8 adults per trap per week. The largest single number of adults observed for one trap was 78 per week. Means of 3.0 ± 0.4 males and 2.5 ± 0.4 females were observed per trap per week over all sample weeks. There was no significant difference between these means ($t = -0.86$, $Pr > t = 0.39$, 152 df). A correlation coefficient of $r = 0.73$ ($Pr > r = <0.0001$, $n = 76$) was found between mean number of adults per trap per week and mean number of adults per pair of mature leaves per tree per week. A correlation coefficient of $r = 0.39$ ($Pr > r = 0.0005$, $n = 76$) was found between mean number of eggs per flush shoot and mean number of adults per trap per week.

Table 4. Spearman correlation coefficients between mean no. of egg, nymph, and adult *D. citri* per citrus flush shoot and various flush shoot parameters in a young grapefruit grove and a mature orange grove^a

Flush parameter	Eggs per shoot	Nymphs per shoot	Adults per shoot
Young grapefruit grove			
Mean no. flush shoots per sample	0.02	0.05	-0.05
Mean shoot length (cm)	-0.17	0.26 ^b	0.16
Mean no. of unexpanded leaves per shoot	0.45 ^c	0.19	0.10
Mean no. of expanded leaves per shoot	-0.22	0.21	0.05
Mean total no. of leaves per shoot	0.11	0.39 ^c	0.16
Mature orange grove			
Mean no. flush shoots per sample	0.56 ^c	0.43 ^c	0.25 ^b
Mean shoot length (cm)	-0.51 ^c	-0.01	-0.30 ^c
Mean no. of unexpanded leaves per shoot	0.62 ^c	0.11	0.16
Mean no. of expanded leaves per shoot	-0.47 ^c	0.06	-0.27 ^c
Mean total no. of leaves per shoot	-0.13	0.22 ^b	-0.19

^a *N* = 77 for young tree data, 88 for mature tree data.

^b Significant at $\alpha = 0.05$.

^c Significant at $\alpha = 0.01$.

Mature Orange Grove. Foliar flush growth was periodically abundant in these trees (Fig. 4). Almost no flush was present in the trees from September 2005 through mid-April 2006. Significant correlations were found between mean number of flush shoots per sample and air temperatures during the 7 d preceding a sample date, but no significant correlations were found with rainfall (Table 3). Results similar to these were obtained when analyses were conducted using temperature and rainfall during 14 and 21 d preceding sample dates.

The mean length of flush shoots was 5.7 ± 0.1 cm over all shoots sampled. Means of 2.9 ± 0.1 unexpanded, 5.8 ± 0.1 expanded, and 8.7 ± 0.1 total leaves per flush shoot were observed over all flush shoots sampled. Mean number of flush shoots per sample was correlated with mean numbers of eggs, nymphs, and adults per shoot (Table 4). Regression analysis indicated that the relationship between mean egg density per flush shoot (*Y*) and number of new flush shoots per sample (*X*) was described by $Y = 12.1 + 2.9X$ ($F = 9.24$, $Pr > F = 0.003$, $r^2 = 0.10$, 87 df). Stepwise regression indicated that egg densities were better described by a model consisting of the independent

variables shoot length (X_1) and number of new, unexpanded leaves per shoot (X_2): $Y = 14.1 - 1.4X_1 + 3.3X_2$ ($F = 18.8$, $Pr > F = <0.0001$, $r^2 = 0.31$, 87 df). The partial r^2 associated with mean number of unexpanded leaves per shoot contributed 80% to the final model r^2 . A regression of mean number of eggs per flush shoot (Y) on mean number of unexpanded leaves per shoot (X) indicated $Y = 1.9 + 4.7X$ ($F = 29.0$, $Pr > F = <0.0001$, $r^2 = 0.25$, 87 df). Significant correlations were found between mean number of eggs, nymphs or adults per flush shoot and the percentage of shoots infested by eggs ($r = 0.80$, $Pr > r = <0.0001$, $n = 88$), nymphs ($r = 0.64$, $Pr > r = <0.0001$, $n = 88$), and adults ($r = 0.56$, $Pr > r = <0.0001$, $n = 89$), respectively.

Seasonal trends in the index of relative abundance at the mature orange grove were similar for eggs, nymphs, and adults (Fig. 4). The indices of abundance showed a large increase in populations of nymphs and adults during January 2005 that was not shown by mean densities per flush shoot. Population densities of *D. citri* per flush shoot were high on many sample dates during late summer and fall 2006, but the indices of abundance indicated overall population levels were relatively low.

No significant reductions were observed in *D. citri* densities per flush shoot after either of the two low-rate applications of spray oil. Over all three of the higher-rate applications of spray oil, there were means of 14.9 ± 2.5 eggs, 24.0 ± 3.0 nymphs, and 0.1 ± 0.04 adults per shoot before the treatments and 15.2 ± 2.2 eggs, 7.9 ± 1.3 nymphs, and 0.1 ± 0.02 adults per shoot after the treatments. There were no significant differences between these pre- and postspray densities of eggs or adults (analyses not presented), but postspray densities of nymphs were significantly lower than pre-spray densities ($t = -4.97$, $Pr > t = <0.0001$, 174 df).

A total of 809 adult *D. citri* from flush shoots at the mature orange grove were sexed during the study, and 60.3% were female. Means of 0.18 ± 0.03 females and 0.11 ± 0.02 males per flush shoot were observed over all sample dates. There was no significant difference over all sample dates between mean numbers of males and females per flush shoot ($t = 1.89$, $Pr > t = 0.06$, 174 df).

Mean densities of 8.7 ± 2.7 eggs and 11.6 ± 2.8 nymphs per shoot were observed during August 2005 just before the hottest week of the study based on mean daily temperatures (Table 1), and 7.8 ± 3.3 eggs and 19.1 ± 4.5 nymphs per shoot were observed after this hot period. The warmest 7-d period based on maximum daily temperatures occurred during early July 2005; means of 29.4 ± 5.4 eggs and 13.4 ± 2.4 nymphs per shoot were observed just before this warm period, and 6.0 ± 2.1 eggs and 29.0 ± 5.0 nymphs per shoot were observed at the end of the period. Means of 1.8 ± 0.8 eggs and 3.9 ± 2.2 nymphs per shoot were observed in mid-August 2006 before the warmest 14-d period of the study, and 0.3 ± 0.3 eggs and 0.1 ± 0.1 nymphs per shoot were observed 1 wk after this hot period. By early September 2006, mean densities exceeded 70 eggs and 30 nymphs per shoot.

Mean densities of 34.1 ± 4.1 eggs and 3.5 ± 1.1 nymphs per shoot were observed in late January 2005 just before a cold spell, during which air temperatures fell to 0°C for >1 h. On the sample date after this cold spell, means of 38.7 ± 3.9 eggs and 9.1 ± 1.9 nymphs per shoot were observed. The coldest 7- and 14-d periods preceding a sample date based on mean daily and mean minimum daily temperatures occurred in February 2006, and means of 0.0 eggs and 9.0 ± 9.0 nymphs per shoot were observed after this cold period. Air temperatures averaged -0.9°C for >5 h during this period, with a low of -1.5°C for >1 h.

Air temperatures during the 7-d period preceding a sample date at the mature orange grove were correlated with mean numbers of nymphs per flush shoot but not with mean numbers of eggs (Table 3). Results similar to these were obtained when analyses were conducted using temperature and rainfall during 14 and 21 d preceding sample dates. No significant correlations were found between rainfall and mean numbers of eggs, nymphs, or adults per flush shoot.

A mean of 0.05 ± 0.01 adults per pair of mature leaves was observed over the entire study at the mature orange grove. The largest single number of adults observed per pair of mature leaves was 13. Weekly percentages of mature-leaf samples containing at least one adult averaged $4.1 \pm 0.6\%$ over the entire study. The seasonal profile of adult densities on mature leaves during 2005 and 2006 reflected the profile based on percentages of mature leaf samples infested (Fig. 6).

A total of 9,831 adults (46.4% female) were captured on sticky traps during the study, with a mean of 9.8 ± 1.9 adults per trap per week. The largest single number of adults observed on one trap per week was 361. Large increases in numbers of adults trapped occurred over a 3-wk period during late May 2006, peaking at a mean of 155 adults per trap per week (Fig. 6). Means of 5.2 ± 1.0 males and 4.5 ± 0.9 females were observed per trap per week over all sample weeks. There was no significant difference between these means ($t = -0.51$, $Pr > t = 0.61$, 202 df). Significantly more males than females were captured during 6 of 82 wk during which at least five adults were captured among all 10 traps (sample weeks ending 19 and 26 January, 2 and 9 February, 2 March 2005, and 3 May 2006). Mean numbers of males and females per trap per week for these trapping periods averaged 9.1 ± 1.4 and 3.8 ± 1.0 , respectively. The first four of these six periods occurred successively when means of 12.4 ± 2.8 , 9.0 ± 1.7 , 12.7 ± 2.0 , and 23.8 ± 4.3 adults per trap per week were observed. The mean number of adults on traps observed during the May trapping period was 12.5 ± 1.8 . A correlation coefficient of $r = 0.90$ ($Pr > r = <0.0001$, $n = 102$) was found between mean number of adults per trap per week and mean number of adults per pair of mature leaves per tree per week. A non-significant correlation ($r = 0.15$, $Pr > r = 0.16$, $n = 87$) was found between mean number of eggs per flush shoot and mean number of adults per sticky trap per week.

Discussion

Seasonal profiles of citrus vegetative flush growth influence the phenology of *D. citri* because adults oviposit on unexpanded flush leaves and nymphs develop on young flush. Flush was consistently most abundant at the young grapefruit grove during March and May–June but almost continually. In the nonirrigated, mature orange grove, flush was consistently most abundant each year during May–July. A large flush occurred in these trees during late January–early February 2005, which we attributed to tree recovery from defoliation caused by hurricanes during September 2004 in conjunction with environmental conditions favorable for flush development. A typical spring flush (Hall and Albrigo 2007) occurred in these trees during March 2005 but not during 2006. We suspect that this difference may have been related to a lack of rainfall during early 2006, but we were unable to relate flush abundance to rainfall. Our data showed that air temperature was correlated with numbers of flush shoots produced at the mature orange grove but not at the young grapefruit grove, probably because young trees tend to flush continually across a wider range of air temperatures (Hall and Albrigo 2007). No pruning or hedging of trees was made during these studies. Hedging promotes flush, thus the seasonal profile of flush would have looked different had we hedged trees and this could have affected the phenology and abundance of *D. citri*.

Coinciding increases in mean number of flush shoots per sample and mean density of *D. citri* per flush shoot consistently occurred at each grove particularly during late April and May but also during June, July, and September. At other times of the year, mean number of flush shoots per sample was sometimes a poor indicator of the presence or abundance of eggs, nymphs, or adults. The index of abundance provided a more realistic measurement of overall population levels of psyllids than mean density per flush shoot because it took into account both mean density per flush shoot and the abundance of flush. The indices sometimes indicated overall population levels in each grove were low even though moderate to high mean densities were present per flush shoot.

Spray oils are conventionally used in Florida citrus primarily for the control of greasy spot (*Mycosphaerella citri* Whiteside) and other citrus diseases. The spray oils applied during our study negatively affected population densities of nymphs at one study location, at least for short periods of time. Other researchers have noted that petroleum oils suppress nymphs of *D. citri* (Childers et al. 2002, Stansly and Qureshi 2007). Spray oils are not currently recommended for managing *D. citri* in Florida citrus (Rogers and Stansly 2007), probably because petroleum oils are less effective than a number of conventional insecticides unless applied repetitively. Although few oil sprays were applied to either grove, population densities could have been different had we not applied the sprays, at least for short periods of time. There was no evidence that the application of copper to the young grapefruit

grove had any negative effect on population densities of the psyllid.

May, June, and July were periods of time when *D. citri* eggs and nymphs were consistently most abundant at the two groves. Large infestations of *D. citri* in Florida citrus may usually be most common during May–July but, as exemplified by a great abundance of immature *D. citri* at the mature orange grove in late January 2005, outbreaks can occur at any time of the year depending on environmental factors and the availability of flush. This conclusion is supported by observations made by other researchers (Atwal et al. 1968, Aubert and Hua 1990, Tsai et al. 2002). Growers using foliar applications of insecticides against infestations of eggs and nymphs should benefit by scouting year-round and applying insecticide sprays when both immature psyllids and flush begin to increase in abundance. A model to predict when citrus trees are going to produce flush would be helpful, particularly for timing applications of soil-applied systemic insecticides. Our research indicated a model for predicting a flush would involve more than just temperature and rainfall data. Adult *D. citri* were scarce at our mature tree study site for an extended period of time during winter 2005–2006. Growers using foliar insecticides against infestations of adults should benefit by scouting beforehand to determine whether enough are present to justify control.

Environmental conditions at our study locations were generally favorable for populations of *D. citri*. The optimum temperature range for *D. citri* population growth lies between 24 and 28°C, whereas a constant temperature of 16°C is detrimental to adult *D. citri* (Liu and Tsai 2000, Fung and Chen 2006). Average daily air temperatures consistently fell within 24–28°C during May, June, and September, coinciding with peak populations of *D. citri*. During winter, air temperatures in east-central Florida often fell well below the optimum range for *D. citri*. Cold weather seemed to suppress oviposition and, based on Fung and Chen (2006), probably prolonged the development of immatures. A freeze that kills a flush shoot would be expected to result in the death of any eggs and nymphs present because of their close association with flush. Freeze damage to flush shoots only occurred during one cold spell during our studies: in the mature orange trees during February 2005. Temperatures within the tree canopy during this particular event were not as cold as during some other cold events. The most significant freeze during the study occurred in February 2006 at the mature tree location. Live nymphs and adults were observed the day after the freeze, and newly oviposited eggs were found the following week. Therefore, although we do not know to what extent this freeze negatively affected population levels of *D. citri*, we know that there was survival. Temperatures during the hottest 7- and 14-d periods during the study were well above the optimal range for *D. citri*, but these did not seem to have any negative effect on numbers of eggs or nymphs based on data from the young grapefruit grove. A decline in egg and nymph densities at the mature orange grove

during August 2006 coincided with similar hot spells, but this decline may have been a consequence of low densities of flush appropriate for oviposition in combination with declining numbers of adults. Fung and Chen (2006) reported that the longevity of adult *D. citri* on *M. paniculata* dropped from 84 d at 20°C to 36 d at 28°C.

Tsai et al. (2002) speculated that minimum daily air temperature and rainfall might be key factors affecting adult population increases. We found significant positive correlations between mean, maximum, and minimum air temperatures and population levels of nymphs and adults at the young grapefruit tree grove. In the mature orange grove, positive correlations were found between air temperatures and nymph densities, but no correlations were found between egg or adult population levels and temperature. The fact that egg and adult densities were correlated with air temperature at the young grapefruit grove and not at the mature orange grove may have been because the young trees tended to flush continually allowing psyllid population growth over longer periods of time across a wider range of air temperatures. There was no evidence during the study that rainfall had any effect on population levels of eggs or nymphs. However, at the young grapefruit grove, adult densities on shoots were positively correlated with rainfall and temperature. Definite conclusions regarding the effects of rainfall on *D. citri* populations in the young grapefruit grove could not be made because of the distance of the rain gauge from the trees.

Our study was not designed to investigate the effects of citrus nutritional programs on the population ecology of *D. citri*. However, the population dynamics of *D. citri* might be influenced by tree nutrition. Pfeiffer and Burts (1983) reported that egg and nymph densities of the pear psylla, *Cacopsylla pyricola* Foerster, increased faster and reached higher levels on pear, *Pyrus communis* L., trees receiving higher nitrogen applications.

The seasonal profile of adult *D. citri* based numbers captured on yellow sticky traps was similar to the profile based on numbers of adults on mature leaves. Sticky traps hung in trees were effective for monitoring both sexes of *D. citri*. Aubert and Quilici (1988) reported yellow sticky traps to be effective for *D. citri* with a slight bias toward males. Although nonsignificant over all sample dates, we observed a similar trap bias for males based on *D. citri* populations having an $\approx 50\%$ sex ratio (Tsai et al. 2002). There were some weeks at each of our study sites when significantly greater numbers of males were captured. At the young grapefruit grove, instances of more males being captured were erratic over time, and the magnitude of differences in numbers of each sex captured was small. However, at the mature orange grove, there were 4 consecutive wk beginning mid January 2005 when considerably more males were trapped. Population levels of adult psyllids in these mature trees during this time period were the largest observed during the study at either location, and this population outbreak coincided with a large peak in flush abundance. The in-

creased captures of males might have been related to increased flight activity by males as discussed by Aubert and Quilici (1988) and/or decreased flight activity by ovipositing females.

The largest peak in numbers of adults on mature leaf samples and on yellow sticky card traps at the mature orange grove occurred during May 2006, but there was no corresponding large peak in egg or nymph numbers on flush preceding this adult peak. This occurred because large populations of eggs and nymphs developed during April 2006 on floral shoots, and we had restricted our samples to foliar flush. The fast disappearance of the adults associated with this population peak could not be attributed to biological control, spray oils, rainfall, adverse air temperatures, or lack of flush for oviposition. Therefore, we speculate that they migrated away from the trees. In support of this hypothesis, the highest mean density of adult psyllids per pair of mature leaves in trees with sticky traps (1.0 adults per sample) was observed the week before the largest peak in trap captures occurred. At the end of the week that this large peak in trap captures was observed, the mean number of adults per pair of leaves had dropped to 0.29. Aubert and Hua (1990) reported a peak period of adult flight activity during the month of May in plantings of *M. paniculata* in China. Whether or not adult *D. citri* migrate away from areas of large infestations or if they sometimes make seasonal, long-distance migrations remains to be determined.

We present observational information on biological control agents present at each study location but made no attempt to show direct effects of the natural enemies on population fluctuations of *D. citri*. *C. s. sanguinae*, *C. coeruleus*, *H. axyridis*, *O. v-nigrum*, *A. oblique*, and *Chrysopid* spp. had previously been reported as natural enemies of *D. citri* (Michaud 2004, Michaud and Olsen 2004). We observed *Z. longipes* attacking adult psyllids in the field and successfully maintained some individuals on adult psyllids in the laboratory. The fungus *H. citriformis* had previously been reported to attack *D. citri* in Florida (Meyer et al. 2007). Cadavers of adult *D. citri* killed by this fungus were consistently observed during late summer through winter at the mature orange grove, but none were observed at the young grapefruit grove.

This was a descriptive sampling project in which general information on the population ecology of *D. citri* was obtained by sampling two different citrus groves over time. The study provided insight into population densities of *D. citri* that may currently occur in citrus in east-central Florida, information useful for comparison purposes. Information from this study also provided insight into sampling approaches to detect and estimate densities of *D. citri*. Because significant correlations were found between mean densities of *D. citri* per flush shoot and percentages of flush shoots infested, binomial approaches of estimating densities without actually counting insects could be investigated.

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