

# Seasonal Population Dynamics of *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in Sweet Orange Trees Maintained Under Continuous Deficit Irrigation

RODRIGO KRUGNER,<sup>1,2</sup> RUSSELL L. GROVES,<sup>3</sup> MARSHALL W. JOHNSON, ARNEL P. FLORES, JAMES R. HAGLER,<sup>4</sup> AND JOSEPH G. MORSE

Department of Entomology, University of California, 3401 Watkins Dr., Riverside, CA 92521

J. Econ. Entomol. 102(3): 960–973 (2009)

**ABSTRACT** A 2-yr study was conducted in a citrus orchard (*Citrus sinensis* L. Osbeck cultivar Valencia) to determine the influence of plant water stress on the population dynamics of glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar). Experimental treatments included irrigation at 100% of the crop evapotranspiration rate ( $ET_c$ ) and continuous deficit-irrigation regimens at 80 and 60%  $ET_c$ . Microclimate and plant conditions monitored included temperature and humidity in the tree canopy, leaf surface temperature, water potential, and fruit quality and yield. Glassy-winged sharpshooter population densities and activity were monitored weekly by a combination of visual inspections, beat net sampling, and trapping. Glassy-winged sharpshooter populations were negatively affected by severe plant water stress; however, population densities were not linearly related to decreasing water availability in plants. Citrus trees irrigated at 60%  $ET_c$  had significantly warmer leaves, lower xylem water potential, and consequently hosted fewer glassy-winged sharpshooter eggs, nymphs, and adults than trees irrigated at 80%  $ET_c$ . Citrus trees irrigated at 100%  $ET_c$  hosted similar numbers of glassy-winged sharpshooter stages as trees irrigated at 60%  $ET_c$  and a lower number of glassy-winged sharpshooter nymphs than the 80%  $ET_c$  treatment, specifically during the nymphal density peak in mid-April to early July. Irrigation treatments did not affect populations of monitored natural enemies. Although the adult glassy-winged sharpshooter population was reduced, on average, by 50% in trees under severe water stress, the total number of fruit and number of fruit across several fruit grade categories were significantly lower in the 60%  $ET_c$  than in the 80 and 100%  $ET_c$  irrigation treatments.

**KEY WORDS** plant stress, citrus, glassy-winged sharpshooter, insect-plant interactions

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is a xylem fluid-feeding leafhopper native to the southeastern United States and northeastern Mexico (Triapitsyn and Phillips 2000) that was first detected in California in 1990 (Sorensen and Gill 1996). Glassy-winged sharpshooter transmits the bacterium *Xylella fastidiosa* Wells et al. into peach (Turner 1959), almond (Almeida and Purcell 2003a), oleander (Costa et al. 2000), citrus (Damsteegt et al. 2006), and grapevines (Purcell and Saunders 1999, Almeida and Purcell 2003b), where it causes Pierce's disease (PD) (Davis et al. 1978). Grapes are one of the most economically important crops in California, with an estimated value of \$4.1 billion per year (CDFA 2006). Currently there are  $\approx 335,000$  ha of vineyards

distributed throughout the state (CDFA 2006), which are now threatened by the introduction and establishment of glassy-winged sharpshooter.

Glassy-winged sharpshooter is a polyphagous leafhopper with >100 known hosts (Turner and Pollard 1959, Hoddle et al. 2003, Redak et al. 2004). Citrus is considered to be a key overwintering and first generation reproductive host (Blua et al. 1999) and plays an important role in PD incidence in adjacent vineyards in the Temecula (Perring et al. 2001) and Coachella Valleys of California (Park et al. 2006).

To date, the primary PD management tactic used has been implementation of an area-wide insecticide program to reduce glassy-winged sharpshooter populations in citrus groves, urban areas, and vineyards (Wendel et al. 2002, Hix et al. 2003, Park et al. 2006). This management effort has been focused in regions of the state where grape production is concentrated and glassy-winged sharpshooter populations are recurrent and high. However, over-reliance on insecticide applications to suppress glassy-winged sharpshooter populations in citrus orchards could potentially elim-

<sup>1</sup> Corresponding author, e-mail: Rodrigo.Krugner@ars.usda.gov.

<sup>2</sup> Present address: USDA-ARS, San Joaquin Valley Agricultural Sciences Center, 9611 S. Riverbend Ave., Parlier, CA 93648.

<sup>3</sup> Department of Entomology, University of Wisconsin, 1630 Linden Dr., Madison, WI 53706.

<sup>4</sup> USDA-ARS, Arid-land Agricultural Research Center, 21881 N. Cardon Lane, Maricopa, AZ 85238.

inate glassy-winged sharpshooter egg parasitoids such as *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae) (Lauziere and Elzen 2007). Moreover, area-wide applications of insecticide on these neighboring citrus orchards may also interfere with biological control agents important in regulating cottony cushion scale, *Icerya purchasi* (Williston) (Homoptera: Margarodidae) (Grafton-Cardwell and Gu 2003). In short, ecologically sustainable, integrated management tactics that are less reliant on area-wide insecticide applications are warranted (CDFA 2006).

A significant amount of research has been generated to characterize the impact of plant stress on insect outbreaks and regulation of insect population dynamics. Two hypotheses were developed in an attempt to explain the effects of plant quality on insect performance: the plant stress hypothesis (White 1969, 1974, 1984) and the plant vigor hypothesis (Price 1991). The plant stress hypothesis predicts that many herbivores will preferentially feed and perform better on stressed plants because abiotic stresses result in increased levels of nitrogenous compounds in plants (White 1969, 1974, 1984; Mattson and Haack 1987a) along with reduced concentrations of plant defensive chemicals (Rhoades 1979). Conversely, the plant vigor hypothesis predicts that herbivores will preferentially oviposit and feed on vigorous plants because they provide a better food source (Price 1991). In general, resulting responses often seem to be insect feeding guild dependent (Larsson 1989, Koricheva et al. 1998).

In a recent review of the literature, Huberty and Denno (2004) found strong negative effects of plant water stress on phloem, xylem, and mesophyll feeders. However, available evidence suggests that the effect of plant water stress on phloem feeders is nonlinear; that is, phloem feeders benefit from increases in soluble nitrogen caused by certain water stress levels (see Huberty and Denno 2004). Among the selected studies included in the review, only one study investigated the effect of plant water stress on the performance of a xylem feeder (Andersen et al. 1992). In that study, the rate of glassy-winged sharpshooter feeding on water stressed grape myrtle plants, *Lagerstroemia indica* L., was observed to decrease exponentially with incremental increases in water stress and glassy-winged sharpshooter feeding ceased below a xylem water potential of about  $-2.1$  MPa. Nadel et al. (2009) examined the effect of plant water status on host plant selection behavior and utilization by adult glassy-winged sharpshooter in laboratory choice tests and found that insects settled, oviposited, and fed significantly more on surplus-irrigated sweet orange plants (*Citrus sinensis* L.) than on plants under moderate deficit irrigation. In another laboratory study, the feeding rate and survival of the xylem-feeding sharpshooter, *Oncometopia facialis* (Signoret) (Hemiptera: Cicadellidae), a vector of *X. fastidiosa* in citrus in Brazil (Krugner et al. 2000), were significantly reduced in sweet orange seedlings that were maintained under continuous water deficit irrigation (Pereira et al. 2005). Although plant water stress seems to be deleterious to xylem feeding sharpshooters, deficit

irrigation during less vulnerable phenological stages of citrus fruit development caused little to no impact, and in some instances, increased gross yields, fruit loads, and fruit quality (Peng and Rabe 1998, González-Altozano and Castel 1999, Goldhamer and Salinas 2000). The most vulnerable stage of citrus fruit development (e.g., flowering and fruit set, initial fruit enlargement, and final fruit enlargement and maturation) vary among citrus species, cultivars, and climate (see references above for examples).

Although new information is available regarding the host preference of xylem feeding leafhoppers, little is known about the effect of plant water stress on glassy-winged sharpshooter behavior. Here, we studied the effects of continuous deficit irrigation regimens in citrus trees on the population dynamics of glassy-winged sharpshooter and several natural enemies. The goal of this research was to generate information that can be used to develop sustainable management strategies for glassy-winged sharpshooter control.

## Materials and Methods

**Experimental Site and Irrigation Treatments.** The study was conducted at Agricultural Operations on the campus of the University of California, Riverside (AO-UCR), from April 2005 to June 2007 in 5.4 ha of a 38-yr old citrus orchard (*C. sinensis* cultivar Valencia; AO-UCR Field 5) grafted on six different rootstocks: *Poncirus trifoliata* L. Raf. cultivars Pomeroy (96 trees) and Rubidoux (44 trees), *C. taiwanica* Tan. and Shim (68 trees), 'Koethen sweet orange' (60 trees), and two hybrids of *C. sinensis*  $\times$  *Poncirus trifoliata*: 'Carrizo' citrange (160 trees) and 'Troyer' citrange (148 trees). Trees were planted in a stripped block design. Each block consisted of 30 rows of six trees per row, with rootstock type nonrandomly assigned within each group of six trees per row. The position of each group of trees was randomly assigned to 1 of the 30 rows of each block. Thus, each block consisted of the same number of trees on each of six rootstocks. Trees were planted at a spacing of 6.8 by 5.9 m and were maintained under micro-sprinkler irrigation. The soil type is a fine sandy loam with 0–2% slope. Fertilizers were applied to the soil in January ( $K_2SO_4$  at 340 kg/ha) and February ( $NH_4NO_3$  at 280 liters/ha) 2005; foliar applications were in April 2006 (urea at 28 kg/ha,  $KNO_3$  at 13 kg/ha, and Zn/Mn at 5.5 kg/ha). Glyphosate, diuron, and simazine were used for weed control, and chlorpyrifos was sprayed around and on the lower 60 cm of the trunk of each tree in September 2005 and again in May 2006 to control infestations of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae). The experimental site was bordered by a lemon orchard (south), a 4-yr-old tangerine orchard (north), a commercial ornamental plant nursery (west), and a similar aged Valencia orchard (east). The experiment was designed as a 3 by 3 Latin square with three irrigation treatments: (1) trees irrigated at 100% of the crop evapotranspiration rate ( $ET_c$ ), (2) a continuous deficit-irrigated treatment maintained at 80%  $ET_c$ , and (3) a continuous

deficit-irrigated treatment maintained at 60% of  $ET_c$  throughout the 2 yr of the experiment. Each of the nine plots consisted of 120 trees (23.6-m<sup>2</sup> canopy cover). Crop coefficient ( $K_c$ ) values used to calculate  $ET_c$  were 0.5 (November to February), 0.8 (March to May), 0.85 (June and October), and 1.0 (July to September) in both study years.

**Microclimate and Plant Conditions.** Temperature and humidity in the tree canopy were monitored using two data loggers (HOBOH8; Onset Computer, Bourne, MA) per plot. Data loggers were installed at mid-canopy (trunk to outer leaf) at 2 m height on the north side of the trees. Leaf surface temperatures were monitored using an infrared thermometer (Spectrum Technologies, Plainfield, IL) according to the manufacturer's instructions, held 12 cm from the leaf. Leaf surface temperature readings were recorded weekly from three randomly selected trees per plot. To account for rootstock  $\times$  irrigation treatment effects on plant condition, a map of the plots was used to identify trees grafted on similar rootstocks, which were again randomly selected. The same trees, selected each week, were resampled for measurements described herein (i.e., leaf temperature, water potential, and insect density). From each tree, leaf surface temperature was recorded between 1130 and 1200 hours from three leaves located at a 2 m height in the southeast, south, and southwest corners of the tree (i.e., sunny side of the tree). The severity of water stress was also characterized weekly by measurements of predawn (0400–0530 hours) stem water potential ( $\Psi$ ) using a pressure chamber (model 610; PMS Instrument Company, Albany, OR), except for the period between mid-May to late July 2005 when water potential was measured at mid-day. To monitor the water potential at mid-day and predawn, the fourth leaf from the tip of two mature branches per tree was covered with a bag made of foil-laminate material for 30 min before being excised from the branch. Leaves were excised from the branch and immediately processed.

**Fruit Quality and Yield.** In early June 2006 and 2007, measurements of fruit sugar solids ("Brix") were collected from 16 randomly selected trees within each plot using a Reichert hand-held refractometer (Reichert, Depew, NY). One orange per tree was randomly selected from the north side of the tree to be sampled. All oranges were harvested in mid-June 2006 and 2007 and immediately taken to a local commercial packing house where oranges were mechanically counted, sized, and color graded. At the packing house, oranges were initially separated as either "juice" or "fruit" grade, where the "juice" grade designation refers to small and/or defective oranges to be delivered to a juice processing plant and "fruit" grade refers to oranges packed for the fresh fruit market. A final grading by hand was conducted on fruit-graded oranges to identify quality parameters such as sunburn, wind damage, and puff and creasing, which is often caused by an irrigation deficit. Based on this final grading, fresh market oranges were categorized as "first" (higher quality) or "second" (lower quality) grade—this is standard practice for citrus production

in California. Because of the high energy costs to operate the sorting machinery and time required to process the oranges, concomitant with a high volume of oranges sent to the packing house by numerous growers in the region, we were unable to collect data from individual trees. Thus, in 2006, all oranges harvested from individual trees were combined in bins by plot and treatment before grading. In 2007, all oranges harvested from individual trees were combined in bins by row, plot, and treatment before grading. In both years, oranges harvested from border trees located on the edge of the plots were not included in the analysis.

**Insect Populations.** Populations of glassy-winged sharpshooter and associated natural enemies within experimental plots were sampled on three trees, selected as described above (see Plant Conditions), weekly from April 2005 to December 2005 and February 2006 to December 2006. Various sampling techniques were used to survey different glassy-winged sharpshooter stadia. A 3-min visual inspection of leaves and branches around sample trees was conducted to monitor for glassy-winged sharpshooter egg masses, nymphs, adults, and natural enemies. Glassy-winged sharpshooter egg masses were collected and held in the laboratory in petri dishes for glassy-winged sharpshooter nymph (i.e., because of a lack of parasitism) or parasitoid emergence. The same trees were sampled 48 h later for glassy-winged sharpshooter adults, nymphs, and natural enemies by collecting a beat net sample from each tree. One beat net sample consisted of insects collected from 10 branches beaten four times. Collected material was placed into paper bags and taken to the laboratory for inspection under a dissecting scope. Yellow sticky traps (14 by 23 cm in size), with Stickem on both sides (Seabright, Emeryville, CA), were used to monitor insect activity. Six traps were placed on the south side of three rows per plot (two traps per row placed five trees apart) using 2-m-long wooden sticks inserted vertically into the soil. Traps were replaced weekly and placed into a freezer until inspection. The numbers of glassy-winged sharpshooter nymphs, adults, predators, and parasitoids were recorded on each trap.

**Data Analysis.** Two-way analysis of variance (ANOVA) was used to evaluate the significance of rootstock  $\times$  irrigation treatment interactions relative to "Brix, leaf surface temperature, plant water potential, and numbers of glassy-winged sharpshooter found during visual inspection. For leaf surface temperature, plant water potential, and number of glassy-winged sharpshooter per tree, a two-way ANOVA was performed separately for each sampling date (week) throughout the experiment. Because glassy-winged sharpshooter populations rapidly increased in late spring to early summer, declined, and peaked again in late summer, insect density data such as numbers of glassy-winged sharpshooter egg masses, nymphs, and adults were subdivided into groups according to periods of insect presence (i.e., generations) and subjected to a repeated-measures ANOVA (SPSS 15.0; SPSS, Chicago, IL) ( $\alpha = 0.05$ ). Periods between generations, when no insects were found, were excluded

**Table 1.** Mean  $\pm$  SEM leaf surface temperature, canopy temperature, and humidity of citrus trees irrigated with 60, 80, and 100% of the crop evapotranspiration rate (ET<sub>c</sub>)

Irrigation treatment	May to Oct. 2005	Oct. to Nov. 2005	Nov. to Feb. 2005/2006	Feb. to May 2006	May to Oct. 2006	Oct. to Nov. 2006
<b>Leaf surface temperature (°C)</b>						
60% ET <sub>c</sub>	23.85 $\pm$ 0.09a	16.10 $\pm$ 0.17a	—	14.40 $\pm$ 0.20a	22.42 $\pm$ 0.09a	19.26 $\pm$ 0.16a
80% ET <sub>c</sub>	23.15 $\pm$ 0.08b	15.88 $\pm$ 0.18a	—	13.65 $\pm$ 0.24b	21.90 $\pm$ 0.09b	18.72 $\pm$ 0.15ab
100% ET <sub>c</sub>	22.89 $\pm$ 0.09b	15.67 $\pm$ 0.17a	—	13.57 $\pm$ 0.21b	21.56 $\pm$ 0.08c	18.43 $\pm$ 0.15b
F value =	28.35	1.48	—	5.18	20.29	7.06
P value =	<0.01	0.248	—	0.01	<0.01	<0.01
<b>Canopy temperature (°C)</b>						
60% ET <sub>c</sub>	21.45 $\pm$ 0.05a	14.67 $\pm$ 0.09a	10.81 $\pm$ 0.12a	12.39 $\pm$ 0.06a	23.53 $\pm$ 0.08a	15.84 $\pm$ 0.07a
80% ET <sub>c</sub>	21.32 $\pm$ 0.05ab	14.56 $\pm$ 0.09a	10.44 $\pm$ 0.12a	12.31 $\pm$ 0.06a	23.49 $\pm$ 0.09a	15.81 $\pm$ 0.08a
100% ET <sub>c</sub>	21.20 $\pm$ 0.06b	14.62 $\pm$ 0.11a	10.73 $\pm$ 0.16a	12.26 $\pm$ 0.06a	23.27 $\pm$ 0.09a	15.68 $\pm$ 0.07a
F value =	4.19	0.35	2.19	1.07	2.21	1.21
P value =	0.04	0.71	0.17	0.38	0.17	0.34
<b>Canopy relative humidity (%)</b>						
60% ET <sub>c</sub>	62.19 $\pm$ 0.57a	61.27 $\pm$ 2.54a	61.15 $\pm$ 3.07a	66.37 $\pm$ 3.61a	54.02 $\pm$ 3.72a	56.46 $\pm$ 3.67a
80% ET <sub>c</sub>	63.34 $\pm$ 0.49a	63.38 $\pm$ 2.50a	65.94 $\pm$ 3.07a	68.93 $\pm$ 3.15a	56.34 $\pm$ 3.72a	58.96 $\pm$ 3.67a
100% ET <sub>c</sub>	63.32 $\pm$ 0.62a	64.13 $\pm$ 2.79a	64.32 $\pm$ 4.35a	70.17 $\pm$ 4.93a	57.85 $\pm$ 5.25a	60.41 $\pm$ 4.74a
F value =	1.39	0.33	0.62	0.24	0.20	0.24
P value =	0.30	0.73	0.57	0.79	0.82	0.79

Means within a column followed by the same letter are not significantly different ( $P > 0.05$ ).  
ET<sub>c</sub>, crop evapotranspiration.

from the analysis. Repeated-measures analyses were performed using measurements of plant condition (i.e., leaf surface temperature and humidity in the tree canopy) recorded during the following periods: (1) late May to early October 2005; (2) early October to late November 2005; (3) late November 2005 to February 2006; (4) February to mid-May 2006; (5) mid May to early October 2006; (6) early October to late November 2006; and (7) late November 2006 to February 2007. When results indicated a significant difference among treatments, treatment means were separated using Tukey's honestly significant difference (HSD) test ( $\alpha = 0.05$ ).

## Results

**Microclimate and Plant Conditions.** In main effect and two-way analyses of fruit sugar solids, leaf surface temperatures, plant water potentials, and numbers of glassy-winged sharpshooter per tree, there were no significant differences among the rootstock types and no significant rootstock type  $\times$  irrigation treatment interactions, respectively. Therefore, rootstock type was excluded from further statistical analyses. Ambient temperatures were higher inside the tree canopy during late May to early October 2005 (period 1) in the 60% ET<sub>c</sub> treatment compared with the 100% ET<sub>c</sub> treatment ( $F = 4.19$ ;  $df = 2,10$ ;  $P = 0.047$ ; Table 1). However, canopy temperatures in trees located in the 80% ET<sub>c</sub> treatment were not significantly different from those from other treatments. There were no significant differences in canopy temperatures among treatments during periods beyond October 2005. Throughout the study, there were no significant differences in canopy relative humidity among the treatments (Table 1).

Leaf surface temperatures were significantly different among treatments across all periods throughout the study, except from October to November 2005 (Table 1). Leaf surface temperatures of trees irrigated with 60% ET<sub>c</sub> were significantly higher (0.5–1.0°C) than those of trees irrigated with 80 and 100% ET<sub>c</sub>, except during the winter periods. Leaf surface temperatures of trees irrigated with 80% ET<sub>c</sub> were significantly higher than those of trees irrigated with 100% ET<sub>c</sub> only during the period from late May to early October 2006 (Table 1).

In 2005, mid-day water potential measurements taken from mid-May to late July were significantly different among treatments ( $F = 4.46$ ;  $df = 2,47$ ;  $P = 0.016$ ). The water potential in the 100% ET<sub>c</sub> treatment was  $\approx 8\%$  higher than in the 60 and 80% ET<sub>c</sub> treatments (Fig. 1A). There was no difference in mid-day water potential between the 60 and 80 ET<sub>c</sub> treatments ( $P = 0.99$ ; Fig. 1A). Predawn water potential measurements were consistently lower in the 60% ET<sub>c</sub> treatment than in the 80 or 100% ET<sub>c</sub> treatments at all time periods after late July 2005 (Fig. 1A and B); late July to early October 2005 ( $F = 12.18$ ;  $df = 2,19$ ;  $P < 0.001$ ); early October to late November 2005 ( $F = 6.56$ ;  $df = 2,43$ ;  $P < 0.001$ ); February to mid-May 2006 ( $F = 6.50$ ;  $df = 2,30$ ;  $P < 0.01$ ); mid-May to early October 2006 ( $F = 151.67$ ;  $df = 2,40$ ;  $P < 0.001$ ); and early October to late November 2006 ( $F = 15.89$ ;  $df = 2,45$ ;  $P < 0.001$ ). There were no differences in leaf water potential between the 80 and 100% ET<sub>c</sub> treatments during these periods.

**Fruit Quality and Yield.** Mean ( $\pm$ SEM) concentrations of fruit sugar solids immediately before the 2006 harvest were  $13.81 \pm 0.18$ ,  $13.66 \pm 0.20$ , and  $13.45 \pm 0.15$  °Brix in the 60, 80, and 100% ET<sub>c</sub> treatments, respectively. However, no differences in fruit



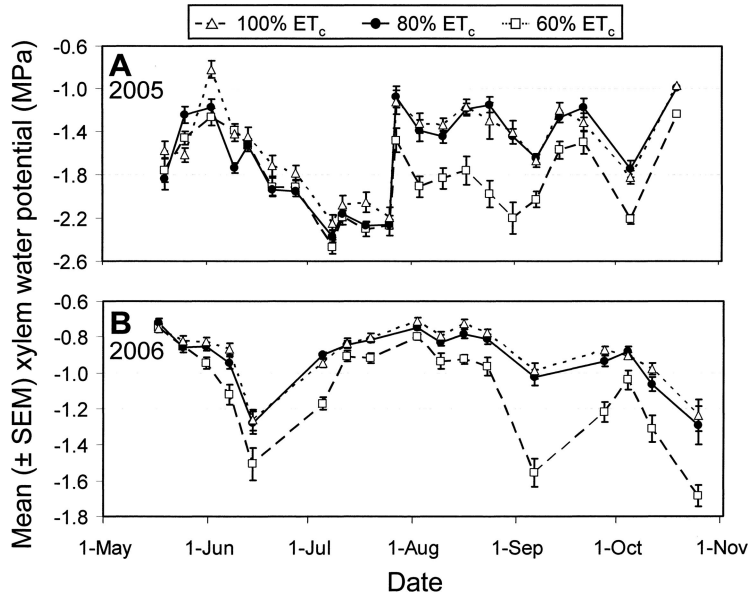


Fig. 1. Mean ( $\pm$ SEM) xylem water potential in 2005 (A) and 2006 (B) in citrus trees continuously irrigated at 60, 80, and 100% of the crop evapotranspiration rate. Water potential measurements were taken at predawn throughout the study, except for the period between mid May to late July 2005, when measurements were taken mid-day.

sugar solid content were detected among the irrigation treatments ( $F = 0.91$ ;  $df = 2,134$ ;  $P = 0.404$ ) and no significant rootstock  $\times$  irrigation interaction effect was observed ( $F = 0.61$ ;  $df = 8,134$ ;  $P = 0.763$ ). In 2007, fruit sugar concentrations were  $14.22 \pm 0.19$ ,  $14.31 \pm 0.17$ , and  $13.56 \pm 0.15$ °Brix in the 60, 80, and 100%  $ET_c$  treatments, respectively. Fruit sugar solid contents were higher in trees irrigated at 60 and 80%  $ET_c$  than at 100%  $ET_c$  ( $F = 6.63$ ;  $df = 2,134$ ;  $P = 0.001$ ). Again, no significant rootstock main effect ( $F = 0.58$ ;  $df = 1,134$ ;  $P = 0.444$ ) or rootstock  $\times$  irrigation interaction effect was observed ( $F = 1.59$ ;  $df = 2,134$ ;  $P = 0.207$ ).

In 2006, there were no differences in total numbers of harvested fruit or in the number of fruit per grade

category among irrigation treatments (Table 2). However, the percentage of first grade fruit was higher in the 80%  $ET_c$  treatment ( $F = 274.31$ ;  $df = 2,2$ ;  $P = 0.003$ ). Moreover, the percentage of first grade fruit was significantly lower in the 60% than in the 100%  $ET_c$  treatment. There were no differences in the percentages of low-quality, nonjuice (second grade) fruit among treatments. Overall, the percentage of fruit rejected for the fresh market and thus, delivered to a juice processing plant, was not different among irrigation treatments. Furthermore, the percentage of discarded fruit (i.e., rots, smashed) was not different among treatments. In 2007, the total number of harvested fruit in the 60%  $ET_c$  treatment was significantly

Table 2. Number of oranges harvested in 2006 from citrus trees under continuous deficit irrigation regimens and percentage of oranges across fruit grade categories ranging from the highest (first grade) to lowest quality (discarded)

Treatment	Fruits per ha ( $\times 10^3$ )	Fruit grade <sup>a</sup>					
		First grade	Second grade	Juice sized <sup>b</sup>	Juice	Juice total	Discarded
No. fruits per ha ( $\times 10^5$ )							
60% ET <sub>c</sub>	3.81 ± 0.30a	0.01 ± 0.00a	0.13 ± 0.03a	0.00 ± 0.00a	3.58 ± 0.28ab	3.58 ± 0.28a	0.08 ± 0.01a
80% ET <sub>c</sub>	4.64 ± 0.23a	0.35 ± 0.08a	0.74 ± 0.34a	1.08 ± 0.43a	2.31 ± 0.14b	3.44 ± 0.43a	0.11 ± 0.00a
100% ET <sub>c</sub>	4.49 ± 0.27a	0.09 ± 0.02a	0.46 ± 0.08a	0.01 ± 0.01a	3.83 ± 0.24a	3.84 ± 0.24a	0.10 ± 0.01a
F value =	9.26	13.48	2.92	6.3	19.86	6.15	11.44
P value =	0.097	0.069	0.254	0.136	0.047	0.139	0.08
% fruit per grade							
60% ET <sub>c</sub>	—	0.17 ± 0.11c	3.45 ± 0.71a	0.00 ± 0.00b	94.11 ± 0.84a	94.0 ± 0.84a	2.25 ± 0.03a
80% ET <sub>c</sub>	—	7.53 ± 1.58a	15.99 ± 7.64a	23.33 ± 9.74a	50.78 ± 0.73b	74.1 ± 9.16a	2.35 ± 0.04a
100% ET <sub>c</sub>	—	1.95 ± 0.41b	10.30 ± 1.68a	0.17 ± 0.17ab	85.20 ± 1.92ab	85.4 ± 2.09a	2.35 ± 0.02a
F value =	—	274.31	2.97	23.25	125.53	7.73	2.98
P value =	—	0.003	0.251	0.04	0.007	0.11	0.25

<sup>a</sup> Means and fractions of fruit across fruit grades followed by the same letter are not significantly different ( $P > 0.05$ ).

<sup>b</sup> The juice sized oranges refers to fruits initially accepted for the fresh market by sorting machinery but rejected after final grading by hand because of scars, wind damage, deformities, etc.

$ET_c$ , crop evapotranspiration.

**Table 3.** Number of oranges harvested in 2007 from citrus trees under continuous deficit irrigation regimens and percentages of oranges across fruit grade categories ranging from the highest (first grade) to lowest quality (discarded)

Treatment	Fruits per ha (×10 <sup>5</sup> )	Fruit grade <sup>a</sup>					
		First grade	Second grade	Juice sized <sup>b</sup>	Juice	Juice total	Discarded
No. fruits per ha (× 10 <sup>5</sup> )							
60% ET <sub>c</sub>	1.13 ± 0.16b	0.16 ± 0.04b	0.13 ± 0.02b	0.08 ± 0.03b	0.74 ± 0.11b	0.83 ± 0.13b	0.00 ± 0.00b
80% ET <sub>c</sub>	2.24 ± 0.18a	0.38 ± 0.06a	0.37 ± 0.05a	0.20 ± 0.03a	1.26 ± 0.06a	1.47 ± 0.08a	0.02 ± 0.01a
100% ET <sub>c</sub>	2.33 ± 0.22a	0.48 ± 0.13a	0.39 ± 0.07a	0.15 ± 0.03ab	1.27 ± 0.08a	1.42 ± 0.08a	0.03 ± 0.01a
F value =	24.83	12.86	8.12	4.96	10.92	12.86	8.12
P value =	<0.001	<0.001	0.002	0.017	<0.001	<0.001	0.002
% fruit per grade							
60% ET <sub>c</sub>	—	14.15 ± 2.61a	18.40 ± 3.91a	6.73 ± 2.18a	66.73 ± 5.49a	73.47 ± 4.03a	0.00 ± 0.00b
80% ET <sub>c</sub>	—	16.72 ± 1.74a	24.94 ± 2.93a	8.90 ± 0.85a	58.04 ± 3.59a	66.95 ± 3.31a	0.90 ± 0.20a
100% ET <sub>c</sub>	—	18.47 ± 2.91a	28.99 ± 5.81a	6.63 ± 1.29a	57.25 ± 5.19a	63.89 ± 4.91a	1.22 ± 0.43a
F value =	—	1.02	1.54	1.36	1.42	1.63	10.12
P value =	—	0.377	0.237	0.278	0.263	0.219	<0.001

<sup>a</sup> Means and fractions of fruit across fruit grades followed by the same letter are not statistically different ( $P > 0.05$ ).

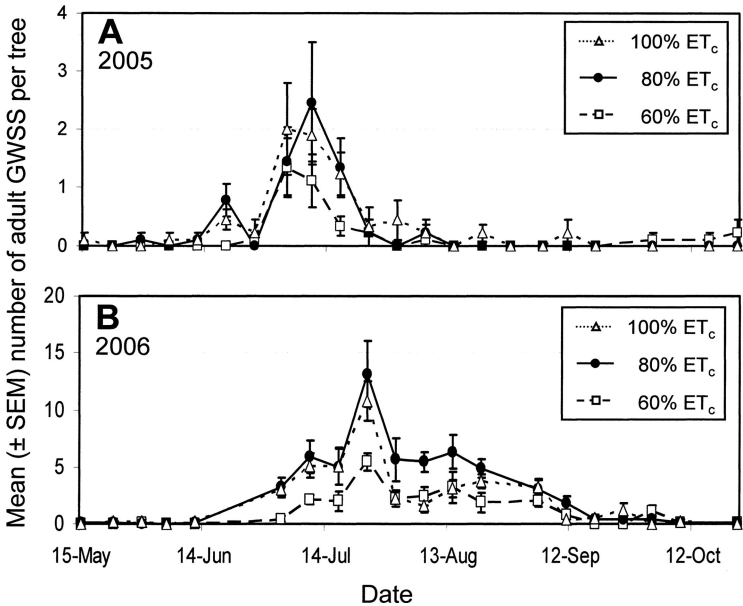
<sup>b</sup> The juice sized oranges refers to fruits initially accepted for the fresh market by sorting machinery but rejected after final grading by hand because of scars, wind damage, deformities, etc.

ET<sub>c</sub>, crop evapotranspiration.

lower than in the 80 and 100% ET<sub>c</sub> treatments (Table 3). The numbers of fruit across all fruit grade categories were lower in the 60% ET<sub>c</sub> treatment than in the 80 and 100% ET<sub>c</sub> irrigation treatments. There were no differences in total number of fruit and number of fruit per grade category between the 80 and 100% ET<sub>c</sub> irrigation treatments. Among the irrigation treatments, there were no differences in percentages of marketable fruit across all fruit grade categories in 2007.

**Insect Populations.** Visual counts in 2005 showed an increase in adult glassy-winged sharpshooter levels from late June to a peak in mid-July (Fig. 2A) consistent with the appearance of first generation adult emergence. During this period,  $\approx 50\%$  fewer adults

were counted on trees irrigated with 60% of the ET<sub>c</sub> than with 80 and 100% ET<sub>c</sub> ( $F = 4.95$ ;  $df = 2,20$ ;  $P = 0.017$ ). There was no difference in the number of glassy-winged sharpshooter adults observed per tree between the 80 and 100% ET<sub>c</sub> treatments ( $P = 0.96$ ). On average ( $\pm$ SEM),  $1.1 \pm 0.4$ ,  $2.4 \pm 1.0$ , and  $1.9 \pm 0.4$  glassy-winged sharpshooter adults were observed per tree at the population peak in mid-July 2005 in the 60, 80, and 100% ET<sub>c</sub> treatments, respectively. In 2006, there was a substantial increase in the overall number of adult glassy-winged sharpshooter observed per tree during the same period of first generation eclosion in early July to the population peak in late July (Fig. 2B). Up to the peak of glassy-winged sharpshooter num-



**Fig. 2.** Mean ( $\pm$ SEM) number of glassy-winged sharpshooter adults observed per tree during 3-min visual inspections around citrus trees continuously irrigated at 60, 80, and 100% of the crop evapotranspiration rate in 2005 (A) and 2006 (B).

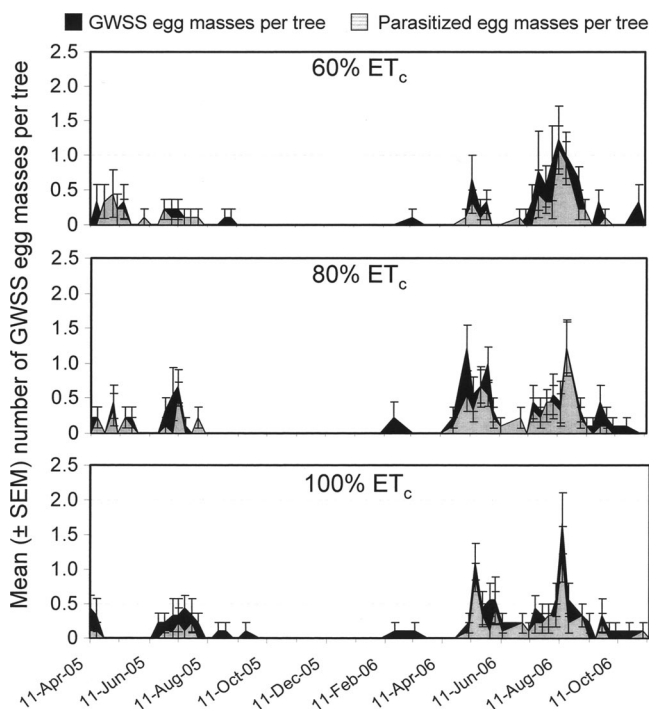


Fig. 3. Mean ( $\pm$ SEM) number of fresh glassy-winged sharpshooter egg masses (black areas behind the gray areas) and glassy-winged sharpshooter egg masses from which *G. ashmeadi* (gray area) emerged after rearing in the laboratory. Egg masses were found and collected from trees during a 3-min visual inspection around citrus trees continuously irrigated at 60, 80, and 100% of the crop evapotranspiration rate.

bers in late July, fewer adults were found on trees irrigated at 60%  $ET_c$  than at 80 and 100%  $ET_c$  ( $F = 7.20$ ;  $df = 2, 20$ ;  $P = 0.004$ ). There was no difference in the number of glassy-winged sharpshooter adults observed per tree between 80 and 100%  $ET_c$  treatments ( $P = 0.78$ ). Averaging over the early July to early October interval, fewer adult glassy-winged sharpshooter were found in trees irrigated at 60%  $ET_c$  than at 80%  $ET_c$  ( $F = 10.08$ ;  $df = 2, 20$ ;  $P < 0.001$ ). The number of adult glassy-winged sharpshooter counted in the 100%  $ET_c$  treatment was not different from those observed in the 60 ( $P = 0.07$ ) or 80%  $ET_c$  ( $P = 0.11$ ) irrigation treatments. On average ( $\pm$ SEM),  $5.4 \pm 0.7$ ,  $13.1 \pm 2.8$ , and  $10.8 \pm 1.7$  adult glassy-winged sharpshooter were observed in visual counts per tree at the peak period of second generation adult emergence in late July 2006 in the 60, 80, and 100%  $ET_c$  treatments, respectively. Note, however, that an approximate six-fold increase in mean peak density of glassy-winged sharpshooter adults was observed in the irrigation treatments between 2005 and 2006, presumably because of the applications of chlorpyrifos for control of Argentine ants that were applied in September 2005 and again in May 2006 (see below).

During visual inspections in 2005 and 2006,  $<1.0$  and  $2.2$  glassy-winged sharpshooter egg masses, respectively, were found per tree each week (Fig. 3). During the 2005 sampling period, there were two peaks of glassy-winged sharpshooter oviposition (mid-May and mid-July). However, there were no differences in

the mean number of glassy-winged sharpshooter egg masses observed among the irrigation treatments throughout either the mid-April to mid-May ( $F = 0.36$ ;  $df = 2, 20$ ;  $P = 0.701$ ) interval or during the second, and highest, egg mass peak lasting from mid-June to early August ( $F = 0.64$ ;  $df = 2, 20$ ;  $P = 0.537$ ). In 2006, there seemed to be four discrete periods of glassy-winged sharpshooter oviposition (Fig. 3). The first period, resulting from oviposition by overwintering adults, occurred from late February to early March. A second and more prominent peak occurred from late April to early June, and the third and largest peak occurred from early July to early September. The fourth discrete oviposition period occurred from late September to late October. In only one of the four periods were any differences in glassy-winged sharpshooter egg masses observed as a result of deficit irrigation treatment. Specifically, fewer egg masses were found in the 60% than in the 80 and 100%  $ET_c$  treatments during the second peak ovipositional period of 2006 ( $F = 12.22$ ;  $df = 2, 20$ ;  $P < 0.001$ ).

Temporal patterns in adult glassy-winged sharpshooter counts collected in the beat nets were similar to those observed from the visual counts. That is, a nearly six-fold increase in the number of glassy-winged sharpshooter nymphs and adults was observed between the 2005 and 2006 seasons (Fig. 4A and B). In 2005, relatively few glassy-winged sharpshooter nymphs and adults were collected in the beat net samples versus levels in 2006. There were no differ-

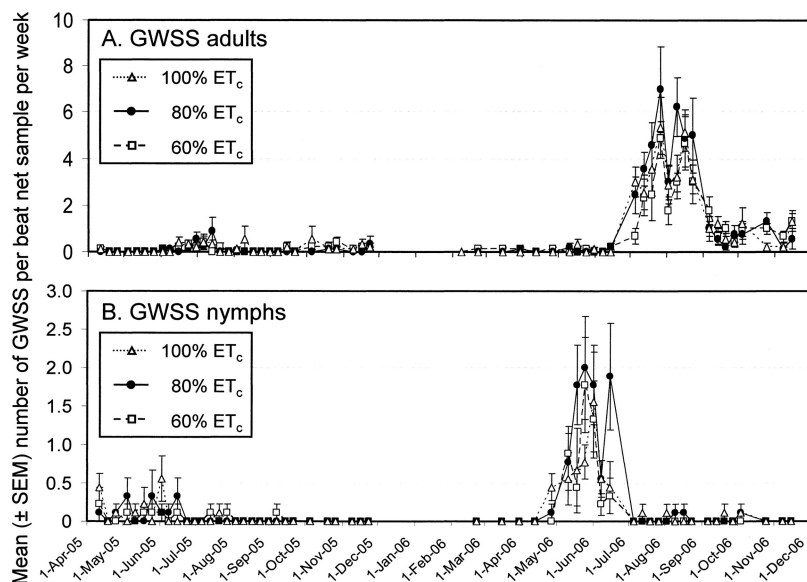


Fig. 4. Mean ( $\pm$ SEM) number of glassy-winged sharpshooter adults (A) and nymphs (B) collected in beat net samples from citrus trees continuously irrigated at 60, 80, and 100% of the crop evapotranspiration rate.

ences in the number of glassy-winged sharpshooter nymphs ( $F = 0.77$ ;  $df = 2,20$ ;  $P = 0.472$ ) or adults ( $F = 0.48$ ;  $df = 2,20$ ;  $P = 0.622$ ) among the irrigation treatments. In 2006, however, significant increases in the number of adult glassy-winged sharpshooter were observed during the mid-June to late July peak (Fig. 4A) and more glassy-winged sharpshooter adults were collected in the 80% than in the 60% ET<sub>c</sub> treatment ( $F = 7.11$ ;  $df = 2,20$ ;  $P = 0.004$ ). Population numbers in the 100% ET<sub>c</sub> treatment were not different from either the 80% ( $P = 0.10$ ) or the 60% ET<sub>c</sub> ( $P = 0.26$ ) treatments during the same interval. A peak in the number of glassy-winged sharpshooter nymphs collected occurred from mid-April to early July (Fig. 4B) with more nymphs collected from the 80% ET<sub>c</sub> treatment than in the 60 and 100% ET<sub>c</sub> treatments ( $F = 5.26$ ;  $df = 2,20$ ;  $P = 0.014$ ). The number of nymphs collected from the 60 and 100% ET<sub>c</sub> treatments did not differ ( $P = 1$ ).

Yellow sticky trap counts identified the relative movement of adult glassy-winged sharpshooter among the various irrigation treatments throughout the 117-wk study. A steady increase in insect activity was observed in late July 2005 and July 2006 (Fig. 5) and peaked with an average ( $\pm$ SEM) of  $11.96 \pm 1.16$  and  $95.22 \pm 4.81$  adults per trap per week, respectively. These peaks in adult capture were followed by a sharp decrease in the numbers of insects caught in all treatments. During the periods of highest adult glassy-winged sharpshooter activity from early July to mid-August, there were no differences in numbers of glassy-winged sharpshooter adults per trap per week among the irrigation treatments in 2005 ( $F = 0.39$ ;  $df = 2,46$ ;  $P = 0.673$ ) and 2006 ( $F = 0.24$ ;  $df = 2,44$ ;  $P = 0.783$ ). Similarly, no differences in the number of adult glassy-winged sharpshooter collected per trap each week were observed among irrigation treatments during periods of low insect activity from late August to

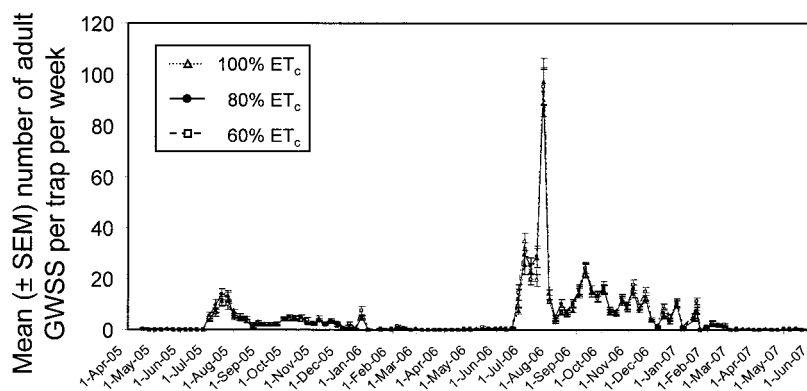


Fig. 5. Mean ( $\pm$ SEM) number of glassy-winged sharpshooter adults captured per yellow sticky trap per week installed in citrus blocks continuously irrigated at 60, 80, and 100% of the crop evapotranspiration rate.



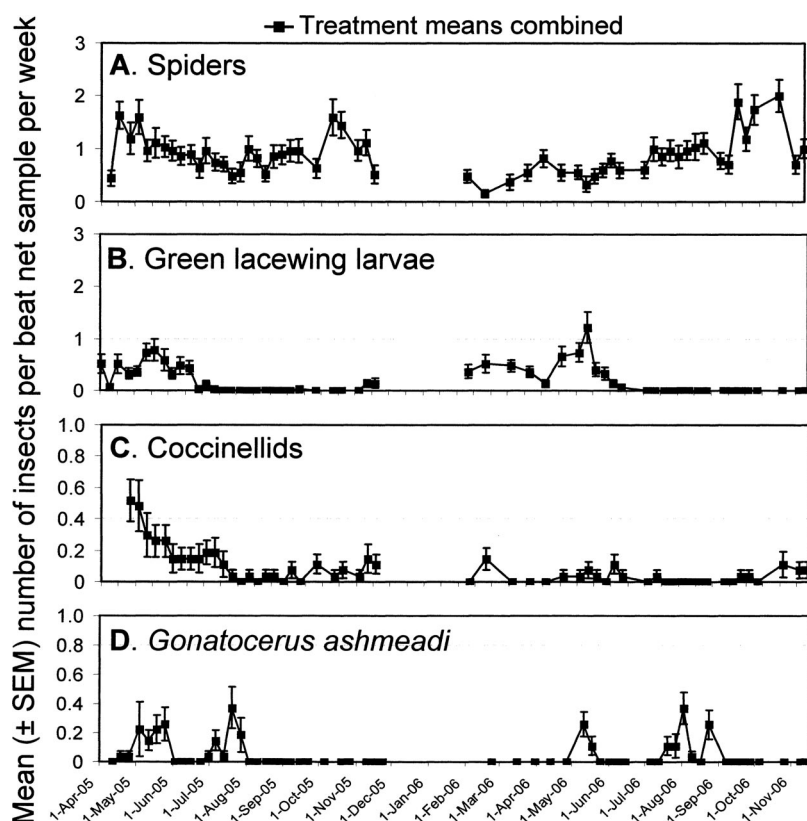


Fig. 6. Mean ( $\pm$ SEM) numbers of spiders (A), green lacewing larvae (B), coccinellids (C), and *G. ashmeadi* (D) collected in beat net samples, showing the seasonal population dynamics of selected predators and parasitoid.

mid-December 2005 ( $F = 0.40$ ;  $df = 2,43$ ;  $P = 0.669$ ) and 2006 ( $F = 0.51$ ;  $df = 2,45$ ;  $P = 0.603$ ). However, a consistent and significant row effect (i.e., three plots [one of each irrigation treatment] located in the same row) in glassy-winged sharpshooter numbers per trap per week was detected each year. Specifically, more glassy-winged sharpshooter adults were caught on sticky traps located in the southernmost row or edge of the experimental site than in the center and northernmost rows of irrigation treatment plots. In both years, edge effects were observed during the high (2005:  $F = 5.49$ ;  $df = 2,46$ ;  $P = 0.007$ ; 2006:  $F = 6.05$ ;  $df = 2,44$ ;  $P = 0.004$ ) and low (2005:  $F = 6.67$ ;  $df = 2,43$ ;  $P = 0.003$ ; 2006:  $F = 3.71$ ;  $df = 2,45$ ;  $P = 0.032$ ) glassy-winged sharpshooter activity periods.

Beat net samples identified the presence of numerous beneficial arthropods. Among them, jumping spiders (Salticidae), green lacewing larvae [*Chrysoperla carnea* (Stephens)], and coccinellids [*Hippodamia convergens* Guérin-Ménéville, *Harmonia axyridis* (Pallas), and *Cryptolaemus montrouzieri* Mulsant] were the most common. No differences in the numbers of spiders (2005:  $F = 0.31$ ;  $df = 2,20$ ;  $P = 0.732$ ; 2006:  $F = 0.79$ ;  $df = 2,20$ ;  $P = 0.469$ ), green lacewing larvae (2005:  $F = 1.14$ ;  $df = 2,20$ ;  $P = 0.435$ ; 2006:  $F = 0.09$ ;  $df = 2,20$ ;  $P = 0.912$ ), or coccinellids (2005:  $F = 0.05$ ;  $df = 2,20$ ;  $P = 0.949$ ; 2006:  $F = 2.53$ ;  $df = 2,20$ ;  $P = 0.104$ )

were observed among the irrigation treatments across all sample dates. Spiders were the most common predator collected throughout the study (Fig. 6A), whereas the number of green lacewing larvae (Fig. 6B) and coccinellids (Fig. 6C) decreased through the interval from mid-April to early June, after which both groups were practically absent over both years. Population densities of these beneficial arthropods did not seem to be affected by severe plant water stress similar to the response of glassy-winged sharpshooter. In general, predator populations did not respond numerically to increased or reduced glassy-winged sharpshooter populations among and within irrigation treatments, which suggests that glassy-winged sharpshooter were not their primary prey.

*Gonatocerus ashmeadi* was the most common glassy-winged sharpshooter egg parasitoid collected in the beat net samples. Two adult population peaks of this species were observed per year (Fig. 6D). In 2005, an initial peak occurred around mid-May and a second peak around mid-July, which corresponded with glassy-winged sharpshooter oviposition peaks (Fig. 3). There were no differences among irrigation treatments in the number of adult *G. ashmeadi* collected during the first ( $F = 1.03$ ;  $df = 2,20$ ;  $P = 0.373$ ) or second egg mass peak ( $F = 16.33$ ;  $df = 2,20$ ;  $P = 0.0259$ ). In 2006, an initial peak of this parasitoid appeared in

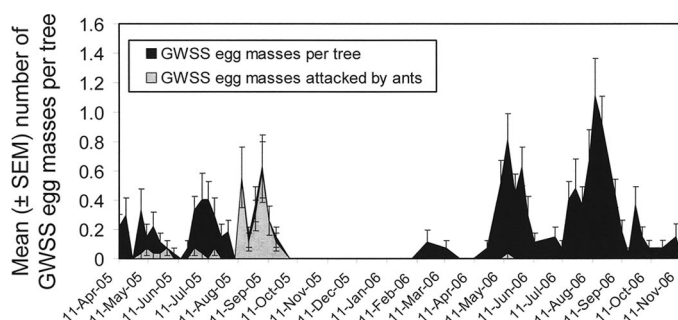


Fig. 7. Mean ( $\pm$ SEM) number of viable and preyed on glassy-winged sharpshooter egg masses (black areas behind the gray areas) and glassy-winged sharpshooter egg masses showing signs of Argentine ant attack (gray area) found in trees during a 3-min visual inspection.

early May and a second peak was observed in late July. Among the irrigation treatments in 2006, no differences in the numbers of collected *G. ashmeadi* adults were detected during either the first ( $F = 0.82$ ;  $df = 2,20$ ;  $P = 0.453$ ) or second egg mass peak ( $F = 14.43$ ;  $df = 2,20$ ;  $P = 0.800$ ). Similarly, the number of glassy-winged sharpshooter egg masses parasitized by *G. ashmeadi* did not differ among irrigation treatments during the first ( $F = 1.41$ ;  $df = 2,20$ ;  $P = 0.266$ ) or second ( $F = 0.04$ ;  $df = 2,20$ ;  $P = 0.958$ ) glassy-winged sharpshooter ovipositional periods in 2005. In 2006, no glassy-winged sharpshooter egg masses were parasitized during the first ovipositional period (late February to late March) in any of the irrigation treatment plots. During the second glassy-winged sharpshooter ovipositional peak, more parasitized egg masses were found in the 80%  $ET_c$  treatment than in the 60 and 100%  $ET_c$  treatments ( $F = 5.04$ ;  $df = 2,20$ ;  $P = 0.017$ ). No differences in the number of parasitized eggs occurred between the 60 and 100%  $ET_c$  treatments. Similarly, no differences in the number of collected and parasitized egg masses were observed during either the third ( $F = 0.20$ ;  $df = 2,20$ ;  $P = 0.814$ ) or the fourth ( $F = 0.63$ ;  $df = 2,20$ ;  $P = 0.545$ ) glassy-winged sharpshooter ovipositional periods.

Argentine ants were commonly found on the trees from April to September 2005. They were actively tending populations of black scale, *Saissetia oleae* (Olivier), and brown soft scale, *Coccus hesperidum* L. Ant infestations became extremely heavy throughout the entire orchard in early June 2005. Visual inspections documented predation rates of glassy-winged sharpshooter egg masses by ants that ranged from 35% in mid-May to 70–100% between early August to late September 2005 (Fig. 7). Observations of ants attacking glassy-winged sharpshooter egg masses in the field, coupled with subsequent laboratory dissections, showed that ants initially chewed egg masses from the point of egg deposition into the leaf (i.e., the side of the leaf epidermis serrated by the female glassy-winged sharpshooter during oviposition). Typical signs of ant predation on glassy-winged sharpshooter egg masses included irregular longitudinal chewed depressions extending across several eggs. A single chlorpyrifos insecticide application around the trunk

of the trees in September 2005 reduced ant densities within the tree canopies until May 2006, when a second application was necessary. No glassy-winged sharpshooter egg masses were found in 2006 with visible signs of ant attack.

### Discussion

Our measurements of microclimate and plant condition indicate that continuous water stress throughout the growing season increased leaf surface temperatures and stem water potential. The higher leaf surface temperatures of trees irrigated at 60%  $ET_c$  in comparison to the 80 and 100%  $ET_c$  treatments suggests that water stress reduced transpiration and thus leaf cooling. Because of the smaller soil moisture reserve, transpiration was perhaps reduced in stressed trees because they were unable to extract enough water from the soil to meet the increasing demand for water during warm periods. Imposed water stress treatments also reduced the plant water potential in vascular tissues. During the first year, small differences in pressure bomb measurements taken at mid-day until late July showed that trees irrigated at 60 and 80%  $ET_c$  were water-stressed relative to trees irrigated at 100%  $ET_c$ . However, measurements taken at predawn showed no difference between the 80 and 100%  $ET_c$  treatments. One reason for this discrepancy is that mid-day and predawn measurements reflect differences in plant condition during periods of high and low plant transpirative demand, respectively. Thus, differences in water potential between 80 and 100%  $ET_c$  treatments are expected to be high in the former and lower during the latter period of measurement. Nevertheless, the two irrigation deficit regimens, 60 and 80%  $ET_c$ , differentially affected the population dynamics of glassy-winged sharpshooter in the experimental citrus plots.

Glassy-winged sharpshooter populations were negatively affected by severe host plant water stress, but glassy-winged sharpshooter population density was not linearly correlated with decreasing water availability in plants. Trees irrigated at 60%  $ET_c$  were host to fewer glassy-winged sharpshooter eggs, nymphs, and adults than trees irrigated at 80%  $ET_c$ . Interest-

ingly, the 100% ET<sub>c</sub> treatment hosted similar numbers of glassy-winged sharpshooter eggs, nymphs, and adults as the 60% ET<sub>c</sub> treatment in some periods of the study and lower numbers of glassy-winged sharpshooter nymphs than the 80% ET<sub>c</sub>. Moderate water stress in trees (e.g., 80% ET<sub>c</sub>) may increase solute concentrations used for osmotic adjustment (i.e., carbohydrates, amino acids, and organic acids) that may also serve as feeding stimulants and nutritional substrates (Mattson and Haack 1987a, Büssis and Heineke 1998, Showler 2002). However, reduced water potential beyond a certain threshold in more severely water stress irrigation treatments (60% ET<sub>c</sub>) might impede glassy-winged sharpshooter feeding because more energy would be needed to extract xylem fluid (Andersen et al. 1992). Conversely, well-watered plants (100% ET<sub>c</sub>) with higher mean water potentials may facilitate extraction of xylem fluid. However, because the energy required for extracting xylem fluid was reduced in well-watered trees, more fluid would have to be ingested and filtered to compensate for a more dilute xylem food source. The feeding behavior of glassy-winged sharpshooter has previously been linked to plant nutritional status (Andersen et al. 1989; Bi et al. 2005, 2007): in particular, the relative concentration of xylem amino acids including glutamine and asparagine (Brodbeck et al. 1990), and specifically, the ratio of glutamine to proline (Andersen et al. 2005). Thus, citrus trees irrigated at 80% ET<sub>c</sub> may combine two important plant characteristics for glassy-winged sharpshooter: (1) a nutrient-concentrated food source and (2) a water potential above acceptable thresholds for glassy-winged sharpshooter xylem fluid extraction, at least during periods of low transpirative demand by plants. Using a pressure chamber apparatus, we were unable to detect differences in water potential between trees irrigated at 100 and 80% ET<sub>c</sub>.

In Florida, Andersen et al. (1992) observed that feeding by glassy-winged sharpshooter on water-stressed cape myrtle plants ceased at water potentials below  $-2.1$  MPa. In this study, glassy-winged sharpshooter adults and nymphs were found in citrus trees with water potentials that reached, on average,  $-2.3$  MPa at mid-day, but were sometimes as low as  $-2.6$  MPa tension. Predawn measurements, however, indicated that the water potential in severely stressed plants barely exceeded  $-2.0$  MPa, suggesting that glassy-winged sharpshooter remained able to feed on stressed plants until the warmest periods of the day. Recently, Nadel et al. (2009) reported that adult glassy-winged sharpshooter settled, oviposited (71% of egg masses), and fed significantly more on surplus-irrigated citrus plants than on plants under continuous deficit irrigation. When provided with a choice of a surplus-irrigated plant and one undergoing drought, glassy-winged sharpshooter began to preferentially settle ( $\approx 70\%$ ) on surplus-irrigated plants on the eighth day after initiation of drought, at a point when water potential began decreasing rapidly (no more than  $-0.9$  MPa) below the control level. Diurnal water potential measurements from stressed citrus trees un-

der field conditions coupled with a quantitative measure of glassy-winged sharpshooter feeding, either by electropenetration graph recordings or excreta collections, could determine whether and how periodic fluctuations in plant water potential are correlated with glassy-winged sharpshooter feeding activity and dispersal.

In Brazil, survival of the sharpshooter *O. facialis* was reduced in sweet orange seedlings maintained under continuous water deficit irrigation (Pereira et al. 2005). However, glassy-winged sharpshooter adults and nymphs are highly mobile as indicated by shifts among a diversity of host species during their lifetime (Mizzel and French 1987). This alternation among or between host plants seems to be an important survival mechanism of the vector species in Brazil (Milanez et al. 2001). In fact, Brodbeck et al. (1995) found that host switching decreased the glassy-winged sharpshooter amino acid deficiencies found in a single plant and was consistent with both the distribution and survivorship of different developmental stages of glassy-winged sharpshooter. The mechanisms used by glassy-winged sharpshooter in host location and selection behavior, including the use of visual and olfactory cues, are still being studied (Patt and Sétamou 2007). Past research suggests that plant spectral qualities (i.e., greater infrared reflectance), leaf color (i.e., yellowing), higher (canopy or leaf) temperature, and qualitative and quantitative changes in chemical blends emitted by water-stressed plants could be behavioral modifiers for insects locating suitable feeding or oviposition hosts (Mattson and Haack 1987a, b). Further analyses (R.K., unpublished data) are underway to determine whether differences in glassy-winged sharpshooter population densities among irrigation treatments result from negative effects of plant water stress on insect population performance (i.e., developmental time, fecundity, and longevity) or insect dispersal within treatment plots.

Yellow sticky trap data indicated that glassy-winged sharpshooter adults were equally active among the irrigation treatments. Although visual inspections and beat net samples documented higher glassy-winged sharpshooter population densities (e.g., eggs, nymphs, and adults) in the 80% versus 60% ET<sub>c</sub> treatment in specific periods of the study, sticky traps showed no differences among the irrigation treatments. One explanation for the lack of correlation between insect density estimates and adult activity is that the lowest deficit irrigation regimen (60% ET<sub>c</sub>) may have been a less than preferable site for glassy-winged sharpshooter settling, feeding, and oviposition, and thus, increased levels in adult captures may have resulted from movement into and out of the three areas with this treatment.

Comparatively fewer numbers of glassy-winged sharpshooter egg masses, nymphs, and adults were observed in 2005 compared with 2006. Other studies in this vicinity also documented substantial declines in glassy-winged sharpshooter and natural enemy populations (Luck 2005, Hoddle 2006). The cause of the decline is unknown, but is likely because of a high

population of Argentine ants during this time. Argentine ants, which are mainly sugar feeders, were seen tending the large population of scale insects infesting our plots during 2005. When a sugar-based diet is scarce, they may obtain energy by consuming other insects (DeBach and Rosen 1991), including glassy-winged sharpshooter eggs (Daane and Johnson 2005, Morse 2006, Fournier et al. 2006) or may even become a significant avian nest predator (Suarez et al. 2005). The role of Argentine ants as potential regulators of glassy-winged sharpshooter populations in citrus orchards warrants further study.

Our data showed that a water saving of 20% (i.e., irrigation at 80% ET<sub>c</sub>) over 2 yr did not induce significant reduction in yield and fruit quality compared with full irrigation (100% ET<sub>c</sub>). Moreover, significantly higher concentrations of fruit sugar solids were observed from moderately water-stressed trees than from fully irrigated trees, which occurred independently of fruit size. The 20% water saving practice improved water use efficiency (yield per unit water) and thus seems a viable option for commercial practice to maintain productivity and reduce irrigation costs in areas with scarce water resources. However, long-term effects of this deficit irrigation regimen on plant vegetative growth needs further study.

Findings from this study have generated significant new information regarding the host selection behavior of glassy-winged sharpshooter in California. Trees under severe water stress had warmer leaves, lower water potential, and consequently hosted fewer glassy-winged sharpshooter than trees maintained under moderate water stress. Moderate water stress increased the glassy-winged sharpshooter nymphal population but did not affect the adult population density compared with levels in fully irrigated plots. Although the adult glassy-winged sharpshooter population was reduced, on average, by 50–65% in citrus plots maintained under continuous severe water stress, the negative economic impacts to citrus growers reflected by lower yield and fruit quality (50% overall reduction), especially after 2 consecutive yr of severe water stress, impedes the adoption of this management strategy to reduce glassy-winged sharpshooter populations in Valencia orchards in southern California. Nevertheless, regulated deficit irrigation (RDI) regimens (i.e., shorter water stress periods) are widely practiced over millions of hectares worldwide to reduce use of irrigation water and increase farmer's profits (Ferreira and Soriano 2007). In recent years, various RDI strategies in citrus in the San Joaquin Valley of California have been adopted for 10–15% of the citrus acreage in Kern and Tulare counties. An additional 10% of the acreage is probably deficit irrigated during the peak of the season because of lack of adequate scheduling (B. Sanden, personal communication). A more complete understanding of the effect of RDI applied during less vulnerable phenological stages of citrus fruit development and the operative host plant cues that influence glassy-winged sharpshooter host selection behavior may result in the deployment of strategies to improve control efforts and contribute to

limiting the spread of *X. fastidiosa* to susceptible crops and/or lowering the costs of current control measures by reducing insecticide applications.

### Acknowledgments

We thank M. Sisterson, K. M. Daane, and R. F. Luck for useful comments on an earlier version of this manuscript; L. Morrison and T. Ortega from the UCR Agriculture Operations Unit for the installation and maintenance of the irrigation system; and Redlands Foothill Groves for processing the harvested oranges. Funding for this project was provided in part by the University of California, Division of Agriculture and Natural Resources, Pierce's Disease and Glassy-winged Sharpshooter Research Grants Program, the USDA-ARS, and through a Specific Cooperative Agreement between the USDA-ARS and UC Riverside.

### References Cited

- Almeida, R.P.P., and A. H. Purcell. 2003a. *Homalodisca coagulata* (Hemiptera: Cicadellidae) transmission of *Xylella fastidiosa* to almond. Plant Dis. 87: 1255–1259.
- Almeida, R.P.P., and A. H. Purcell. 2003b. Transmission of *Xylella fastidiosa* to grapevines by *Homalodisca coagulata* (Hemiptera: Cicadellidae). J. Econ. Entomol. 96: 264–271.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizzell III. 1989. Metabolism of amino acids, organic acids and sugars extracted from the xylem fluid of four host plants by adult *Homalodisca coagulata*. Entomol. Exp. Appl. 50: 149–159.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizzell III. 1992. Feeding by the leafhopper, *Homalodisca coagulata*, in relation to xylem fluid chemistry and tension. J. Insect Physiol. 38: 611–622.
- Andersen, P. C., B. V. Brodbeck, R. F. Mizzell III, and S. Oden. 2005. Abundance and feeding of *Homalodisca coagulata* (Hemiptera: Auchenorrhyncha: Cicadellidae) on *Vitis* genotypes in North Florida. Environ. Entomol. 34: 466–478.
- Bi, J. L., S. J. Castle, F. J. Byrne, S. J. Tuan, and N. C. Toscano. 2005. Influence of seasonal nitrogen nutrition fluctuations in orange and lemon trees on population dynamics of the glassy-winged sharpshooter (*Homalodisca coagulata*). J. Chem. Ecol. 31: 2289–2308.
- Bi, J. L., S. J. Castle, and N. C. Toscano. 2007. Amino acid fluctuations in young and old orange trees and their influence on glassy-winged sharpshooter (*Homalodisca vitripennis*) population densities. J. Chem. Ecol. 33: 1692–1706.
- Blua, M. J., P. A. Phillips, and R. A. Redak. 1999. A new sharpshooter threatens both crops and ornamentals. Calif. Agric. 53: 22–25.
- Brodbeck, B. V., P. C. Andersen, and R. F. Mizzell. 1995. Differential utilization of nutrients during development by the xylophagous leafhopper, *Homalodisca coagulata*. Entomol. Exp. Appl. 75: 279–289.
- Brodbeck, B. V., R. F. Mizzell III, W. J. French, P. C. Andersen, and J. H. Aldrich. 1990. Amino acids as determinants of host preference for xylem feeding leafhopper, *Homalodisca coagulata* (Homoptera: Cicadellidae). Oecologia (Berl.) 83: 338–345.
- Büssis, D., and D. Heineke. 1998. Acclimation of potato plants to polyethylene glycol-induced water deficit. II. Contents and subcellular distribution of organic solutes. J. Exp. Bot. 49: 1361–1370.



- [CDFA] California Department of Food and Agriculture. 2006. County agricultural commissioner's data, calendar year 2005. California Department of Food and Agriculture, Sacramento, CA.
- Costa, H. S., M. S. Blua, J. A. Bethke, and R. A. Redak. 2000. Transmission of *Xylella fastidiosa* to oleander by the glassy-winged sharpshooter, *Homalodisca coagulata*. Hortscience 35: 1265-1267.
- Daane, K. M., and M. W. Johnson. 2005. Biology and ecology of the glassy-winged sharpshooter in the San Joaquin Valley, pp. 97-100. In M. A. Tariq, P. Blincoe, M. Mochel, S. Oswalt, and T. Esser (eds.), Proceedings, 2005 Pierce's disease research symposium. California Department of Food and Agriculture, San Diego, CA, 5-7 December 2005, Copeland Printing, Sacramento, CA.
- Damsteegt, V. D., R. H. Brlansky, P. A. Phillips, and A. Roy. 2006. Transmission of *Xylella fastidiosa*, causal agent of citrus variegated chlorosis, by the glassy-winged sharpshooter, *Homalodisca coagulata*. Plant Dis. 90: 567-570.
- Davis, M. J., A. H. Purcell, and S. V. Thompson. 1978. Pierce's disease of grapevines: isolation of the causal bacterium. Science 199: 75-77.
- DeBach, P., and D. Rosen. 1991. Biological control by natural enemies, 2nd ed. Cambridge University Press, New York.
- Fereres, E., and M. A. Soriano. 2007. Deficit irrigation for reducing agricultural water use. J. Exp. Bot. 58: 147-159.
- Fournier, V., J. R. Hagler, K. M. Daane, J. de Léon, R. L. Groves, H. S. Costa, and T. J. Henneberry. 2006. Development and application of a glassy-winged and smoke-tree sharpshooter egg-specific predator gut content ELISA. Biol. Control 37: 108-118.
- Goldhamer, D. A., and M. Salinas. 2000. Evaluation of regulated deficit irrigation on mature orange trees grown under high evaporative demand, pp. 227-231. In L. G. Albrigo [ed.], Proceedings of the international society of citricult. IX Congr. ASHS Press, Alexandria, VA.
- González-Altozano, P., and J. R. Castel. 1999. Regulated deficit irrigation in "Clementine de Nules" citrus trees. I. Yield and fruit quality effects. J. Hortic. Sci. Biotechnol. 74: 706-713.
- Grafton-Cardwell, E. E., and P. Gu. 2003. Conserving vedalia beetle, *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae), in citrus: a continuing challenge as new insecticides gain registration. J. Econ. Entomol. 96: 1388-1398.
- Hix, R., N. Toscano, and C. Gispert. 2003. Area-wide management of the glassy-winged sharpshooter in the Temecula and Coachella Valleys, pp. 292-294. In M. A. Tariq, S. Oswalt, P. Blincoe, R. Spencer, L. Houser, A. Ba, and T. Esser (eds.), Proceedings, 2003 Pierce's disease research symposium. California Department of Food and Agriculture, Coronado, CA, 8-11 December 2003, Copeland Printing, Sacramento, CA.
- Hoddle, M. S. 2006. Are glassy-winged sharpshooter populations regulated in California? Long-term phenological studies and construction of multi-cohort life tables for the glassy-winged sharpshooter in citrus orchards, pp. 73-77. In T. Esser, M. A. Tariq, R. Medeiros, M. Mochel, and S. Veling (eds.), Proceedings, 2006 Pierce's disease research symposium. California Department of Food and Agriculture, San Diego, CA, 27-29 November 2006, Copeland Printing, Sacramento, CA.
- Hoddle, M. S., S. V. Triapitsyn, and D.J.W. Morgan. 2003. Distribution and plant association records for *Homalodisca coagulata* (Hemiptera: Cicadellidae) in Florida. Fla. Entomol. 83: 89-91.
- Huberty, A., and R. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85: 1383-1398.
- Koricheva, J., S. Larsson, and E. Haukioja. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. Annu. Rev. Entomol. 43: 195-216.
- Krugner, R., M.T.V. de C. Lopes, J. S. Santos, M.J.G. Beretta, and J.R.S. Lopes. 2000. Transmission efficiency of *Xylella fastidiosa* by sharpshooters and identification of two new vector species. In Proceedings, XIV conference of the international organization of citrus virologists, 13-18 September 1998, Campinas, SP, 2000, Brazil. IOCV, Riverside, CA.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. Oikos 56: 277-283.
- Lauziere, L., and G. Elzen. 2007. Effect of formulated insecticides on *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) and its parasitoid *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae). J. Entomol. Sci. 42: 11-19.
- Luck, R. F. 2005. Glassy-winged sharpshooter's (glassy-winged sharpshooter) population dynamics as a means of gaining insight into the management of glassy-winged sharpshooter populations, pp. 359-363. In M. A. Tariq, P. Blincoe, M. Mochel, S. Oswalt, and T. Esser (eds.), Proceedings, 2005 Pierce's disease research symposium. California Department of Food and Agriculture, San Diego, CA, 5-7 December 2005, Copeland Printing, Sacramento, CA.
- Mattson, W. J., and R. A. Haack. 1987a. The role of drought stress in provoking outbreaks of phytophagous insects, pp. 365-408. In P. Barbosa and J. C. Schultz (eds.), Insect outbreaks. Academic, San Diego, CA.
- Mattson, W. J., and R. A. Haack. 1987b. The role of drought in outbreaks of plant-eating insects. Bioscience 37: 110-118.
- Milanez, J. M., J.R.P. Parra, and D. C. Magri. 2001. Alteration of host plants as a survival mechanism of leafhoppers *Dilobopterus costalimai* and *Oncometopia facialis* (Hemiptera: Cicadellidae), vectors of the citrus variegated chlorosis (CVC). Scientia Agricola 58: 699-702.
- Mizzel, R. F., and W. J. French. 1987. Leafhopper vectors of phony peach disease: feeding site preference and survival on infected and uninfected peach, and seasonal response to selected host plants. J. Entomol. Sci. 22: 11-22.
- Morse, J. G. 2006. Seasonal population dynamics of glassy-winged sharpshooter egg parasitoids: variability across sites and host plants, pp. 92-94. In T. Esser, M. A. Tariq, R. Medeiros, M. Mochel, and S. Veling (eds.), Proceedings, 2006 Pierce's disease research symposium. California Department of Food and Agriculture, San Diego, CA, 27-29 November 2006, Copeland Printing, Sacramento, CA.
- Nadel, H., R. Seligmann, M. W. Johnson, J. R. Hagler, D. C. Stenger, and R. L. Groves. 2009. Effects of citrus and avocado irrigation and nitrogen-form soil amendment on host selection by adult glassy-winged sharpshooter, *Homalodisca vitripennis*. Environ. Entomol. 37: 787-795.
- Park, Y. L., T. M. Perring, C. A. Farrar, and C. Gispert. 2006. Spatial and temporal distribution of two sympatric *Homalodisca* spp. (Hemiptera: Cicadellidae): implications for areawide pest management. Agric. Ecosyst. Environ. 113: 168-174.
- Patt, J. M., and M. Sétamou. 2007. Olfactory and visual stimuli affecting host plant detection in *Homalodisca coagulata* (Hemiptera: Cicadellidae). Environ. Entomol. 36: 142-150.



- Peng, T. H., and E. Rabe. 1998. Effect of differing irrigation regimes on fruit quality, yield, fruit size and net CO<sub>2</sub> assimilation of "Mihowase" Satsuma. *J. Hortic. Sci. Biotechnol.* 73: 229–234.
- Pereira, É. F., J. R. S. Lopes, D. T. Turati, C. Munhoz, and J. E. Corrente. 2005. Influência das condições hídricas do solo e da temperatura na sobrevivência e alimentação de *Oncometopia facialis* (Hemiptera: Cicadellidae) em "seedlings" de citrus. *Arq. Inst. Biol. São Paulo* 72: 343–351.
- Perring, T. M., C. A. Farrar, and M. J. Blua. 2001. Proximity to citrus influences Pierce's disease in Temecula Valley vineyards. *Calif. Agric.* 55: 13–18.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62: 244–251.
- Purcell, A. H., and S. R. Saunders. 1999. Glassy-winged sharpshooter expected to increase plant disease. *Calif. Agric.* 53: 26–27.
- Redak, R. A., A. H. Purcell, J. R. S. Lopes, M. J. Blua, R. F. Mizell III, and P. C. Andersen. 2004. The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annu. Rev. Entomol.* 49: 243–270.
- Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores, pp. 3–54. *In* G. A. Rosenthal and D. H. Janzen (eds), *Herbivores: their interaction with secondary plant metabolites*. Academic, New York.
- Showler, A. T. 2002. Effects of water deficit stress, shade, weed competition, kaolin particle film on selected foliar free amino acid accumulations in cotton, *Gossypium hirsutum* (L.). *J. Chem. Ecol.* 28: 631–651.
- Sorensen, J. T., and R. J. Gill. 1996. A range extension of *Homalodisca coagulata* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California. *Pan-Pac. Entomol.* 72: 160–161.
- Suarez, A. V., P. Yeh, and T. J. Case. 2005. Impacts of Argentine ants on avian nesting success. *Insectes Soc.* 52: 378–382.
- Triapitsyn, S. V., and P. A. Phillips. 2000. First record of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae) from eggs of *Homalodisca coagulata* (Homoptera: Cicadellidae) with notes on the distribution of the host. *Fla. Entomol.* 83: 200–203.
- Turner, W. F. 1959. Insect vectors of phony peach disease. *Science* 109: 87–88.
- Turner, W. F., and H. N. Pollard. 1959. Life histories and behavior of five insect vectors of phony peach disease. *U.S. Dep. Agric. Tech. Bull.* 1188: 1–28.
- Wendel, L., M. Ciomperlik, D. Bartels, D. Luvisi, and D. Elms. 2002. The area-wide pest management of glassy-winged sharpshooter in Kern County, pp. 302–307. *In* M. A. Tariq, S. Oswalt, P. Blincoe, and T. Esser (eds.), *Proceedings, 2002 Pierce's disease research symposium*. California Department of Food and Agriculture, Coronado, CA, 15–18 December 2002, Copeland Printing, Sacramento, CA.
- White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50: 905–909.
- White, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia (Berl.)* 16: 279–301.
- White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stresses food plants. *Oecologia (Berl.)* 63: 90–105.

Received 30 July 2008; accepted 27 January 2009.