DISPERSAL AND MOVEMENT OF THE GLASSY-WINGED SHARPSHOOTER AND ASSOCIATED NATURAL ENEMIES IN A CONTINUOUS, DEFICIT-IRRIGATED AGRICULTURAL LANDSCAPE

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ABSTRACT

Host-plant water status is thought to influence dispersal of the glassy-winged sharpshooter (GWSS). Preference of adult GWSS for citrus plants maintained under different water deficit regimes was studied under laboratory and field conditions. In laboratory studies, settling and oviposition preference were studied on potted 'Washington navel' orange in cage choice tests, and feeding activity was estimated via insect excreta production. A field study was conducted in a citrus orchard ('Valencia') to determine the influence of plant water stress on population dynamics of GWSS. Experimental treatments in this study included irrigation at 100% of the crop evapotranspiration (ET_c) and continuous deficit-irrigation (CDI) regimes at 80% and 60% ET_c. Plant conditions were monitored by measurements of leaf surface temperature, water potential, and fruit quality and yield. GWSS population density and activity were monitored weekly by visual inspections, beat net sampling, and trapping. In laboratory tests, insects settled, oviposited, and fed significantly more on surplus-irrigated plants than on plants under moderate CDI. Plants under gradual deficit irrigation became less preferred after 7 d. Citrus water consumption at this point declined to 40% of the control and xylem-fluid tension was estimated at 9.3 Bar. GWSS populations in the field study were negatively affected by severe plant water stress; however, population density was not linearly related to decreasing water availability in plants. Citrus trees irrigated at 60% ET_c had significantly warmer leaves, higher xylem matrix potential, and consequently hosted smaller numbers of GWSS eggs, nymphs, and adults than trees irrigated at 80% ET_c. Citrus trees irrigated at 100% ET_c hosted the same number of insects as trees irrigated at 60% and 80% ET_c. Although the adult GWSS population was reduced, on average, by 35% 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.

INTRODUCTION

The GWSS is a highly polyphagous leafhopper with over 100 known hosts (Turner and Pollard 1959). Citrus is the most common overwintering and first generation reproductive host found in southern California (Blua et al. 1999) and plays an important epidemiological role in Pierce's disease incidence in adjacent vineyards (Perring et al. 2001) because it influences the spatial distribution of GWSS populations (Park et al. 2006). Therefore, with over 109,384 ha of citrus distributed throughout the state and nearly 13.1% of these hectares (14,356 ha) treated with imidacloprid in 2006 alone (CDFA 2006), integrated management tactics that are considered more ecologically sustainable and have less overall reliance on area-wide insecticide applications are warranted.

During the last 40 years, a considerable volume of information has been generated to characterize the impact of plant water stress on insect outbreaks and regulation of insect population dynamics. In general, resulting responses often appear to be insect feeding-guild dependent (Larsson 1989). In a recent analysis, which included results from 116 published studies, Huberty and Denno (2004) found strong negative effects of water stress on phloem-, xylem-, and mesophyll-feeders. Among the selected studies, only one study investigated the effect of plant water stress on the performance of a xylem feeder. Andersen et al. (1992) found that rates of GWSS adult feeding on water-stressed crape myrtle plants, *Lagerstroemia indica* L., were observed to decrease exponentially with increases in water stress and GWSS feeding ceased above a xylem tension of about 2.1 MPa. In further laboratory studies, the feeding rate and survival of the xylem-feeding sharpshooter *Oncometopia facialis* (Signoret), one of the vectors of *Xylella fastidiosa* (*Xf*) in citrus in Brazil (Krugner et al. 2000), were significantly reduced in sweet orange seedlings (cv. 'Caipira'), that were maintained under continuous water deficit irrigation

(Pereira et al. 2005). While the effect of plant water stress appears to be deleterious to xylem feeding sharpshooters, deficit irrigation regimes applied during less vulnerable phenological stages of citrus fruit development have caused little to no impact, and in some instances, increased gross yields, fruit loads, and fruit quality (Goldhamer and Salinas 2000).

Although significant new information is becoming available regarding the host selection behavior of xylem feeding cicadellids, little is understood regarding the effect of plant water stress on GWSS host selection behavior and population dynamics, which is critical to improving our understanding of vector ecology. The goal of this research was to generate novel information useful in the development of sustainable management strategies for control of GWSS populations, which might limit the spread of *Xf* into susceptible crops.

OBJECTIVES

1. To evaluate host-plant factors utilized by adult GWSS and associated natural enemies as long-range cues to locate feeding and ovipositional hosts in a complex agricultural landscape.
2. Investigate the effects of continuous deficit irrigation regimes in citrus trees on the population dynamics of GWSS and associated natural enemies.

Objective 1

Olfactometer

An olfactometer system for studying the response of GWSS to host-plant volatiles was built and the airflow dynamics adjusted to equally integrate odor fields from humidity or volatile sources. Bioassays were performed using adult GWSS collected from Bakersfield and Fillmore, CA. However, data analysis showed no conclusive differences among a variety of treatments, suggesting that GWSS may not use olfactory cues during host location. Responses of female *Gonatocerus ashmeadi* to humid air and to potential volatile cues in the excreta of gravid female GWSS were tested in a Y-tube olfactometer, but preliminary analysis indicates no detectable response to these stimuli.

Laboratory choice bioassays

Field-collected adult GWSS were caged with a choice of two potted sweet orange (cv 'Washington navel') plants receiving different nutritional treatments or different water-deficit treatments. GWSS showed no apparent settling or ovipositional preference for plants receiving nutritional treatments of 1:1 or 26:1 nitrate-N: ammonium-N. However, GWSS preferred to settle (average of 62%) and oviposit (71% of egg masses) on surplus-irrigated citrus compared to plants under CDI during the weeklong study. Stressed plants received about 25% of the water applied to the surplus-irrigated plants, which imposed an evapotranspiration rate of about 40% of the control. Xylem-fluid tension was estimated at about 7.3 bars in the CDI-stressed plants compared with 3.53 ± 0.19 bars in the controls. When provided with a choice of a surplus-irrigated plant and one undergoing drought, GWSS began to preferentially settle (about 70%) on surplus-irrigated plants on the eighth day after initiation of drought, at a point when xylem-fluid tension began increasing rapidly ($\geq$ 9.5 bars) beyond the control level.

Laboratory no-choice feeding bioassays

Results from GWSS confined in sachets on citrus receiving the two nutritional treatments revealed no significant differences in excreta production, suggesting similar feeding rates on plants of either treatment. As expected, GWSS produced more excreta on surplus-irrigated plants than on plants under CDI (0.80 ± 0.10 vs. 0.09 ± 0.02 ml per day, respectively). When confined on non-watered citrus, excreta production was similar to the control for eight days, and decreased significantly thereafter. Unexpectedly, a single day of surplus irrigation applied to drought-stressed plants on the 14th day resulted in significantly higher excreta production on these plants than on the control plants for about four days, after which it again fell below the control level.

Objective 2

A study conducted at Agricultural Operations at the University of California, Riverside, from April 2005 to June 2007 in a citrus orchard (cv. 'Valencia') was designed as a 3 x 3 Latin square with three irrigation treatments: 1) trees irrigated at 100% of the crop evapotranspiration (ET_c), 2) a continuous deficit-irrigated treatment maintained at 80% ET_c, and 3) a continuous deficit-irrigated treatment at 60% of ET_c. We monitored the temperature and humidity in the tree canopy, leaf surface temperatures, and pre-dawn trunk water potential. In June 2006 and 2007, all oranges were harvested and immediately taken to a local commercial packing house where oranges were mechanically counted, sized, and color graded. Measurements of fruit sugar solids (°Brix) were also recorded. Populations of GWSS were sampled weekly from April 2005 to Dec 2005 and Feb 2006 to Dec 2006. A 3-min visual inspection of leaves and branches around sample trees was conducted to monitor for GWSS egg masses, nymphs, adults, and natural enemies. GWSS population density was also monitored by collecting beat net samples. Yellow sticky traps were used to monitor insect activity. Repeated measures analyses were performed using measurements of plant condition and insect density data.

Effect of irrigation deficit on microclimate and plant conditions

Higher temperatures inside the tree canopy were recorded during May to September 2005 in the 60% ET_c treatment than in the 100% ET_c treatment. Throughout the study, there were no significant differences in canopy relative humidity among the treatments. In general, leaf surface temperatures of trees irrigated with 60% ET_c were higher than those of trees irrigated with 80% and 100% ET_c. There was no difference between the 80% and 100% ET_c treatments ($P = 0.23$). Pre-dawn water potential measurements were higher in the 60% ET_c treatment than in the 80% or 100% ET_c treatments recorded among all time periods. There were no differences in water potential between the 80% and 100% ET_c treatments. In 2006, no differences in fruit sugar solid content were detected among the irrigation treatments ($F = 0.91$; df = 2, 134; $P = 0.404$). In 2007, fruit sugar solid contents were higher in trees irrigated at 60% (14.22 ± 0.19 °Brix) and 80% ET_c (14.31 ± 0.17) than at 100% ET_c (13.56 ± 0.15) ($F = 6.63$; df = 2, 134; $P = 0.001$). In 2006, there were no differences in total numbers of harvested fruit and number of fruit per grade category among irrigation treatments. In 2007, the total number of harvested fruit and numbers of fruit across all fruit grade categories in the 60% ET_c treatment were significantly lower than in the 80% and 100% ET_c treatments. There were no significant differences in total number of fruit and number of fruit per grade category between the 80% and 100% ET_c irrigation treatments.

Effect of irrigation deficit on GWSS populations
During the visual inspections in 2005, fewer GWSS adults were found on trees irrigated with 60% of the ET_c than with 80% and 100% ET_c ($F = 4.95$; df = 2, 20; $P = 0.017$). There was no difference in the number of GWSS adults found per tree between the 80% and 100% ET_c treatments ($P = 0.96$). On average (± SEM), 1.1 ± 0.4, 2.4 ± 1.0, and 1.9 ± 0.4 GWSS adults were found per tree at the population peak in mid-July 2005 in the 60%, 80%, and 100% ET_c treatments, respectively. In 2006, up to the peak of GWSS numbers in late-July, fewer adults were found on trees irrigated at 60% of the 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 GWSS adults found per tree between 80% and 100% ET_c treatments ($P = 0.78$). In the early-July to early-Oct interval, fewer adult GWSS were found in trees irrigated at 60% of the ET_c than at 80% ET_c ($F = 10.08$; df = 2, 20; $P < 0.001$). The number of adult GWSS was not different in the 100% ET_c treatment vs. those in the 60% ($P = 0.07$) or the 80% ET_c ($P = 0.11$) treatments. On average (± SEM), 5.4 ± 0.7, 13.1 ± 2.8, and 10.8 ± 1.7 adult GWSS were observed in visual counts per tree at the peak period in late-July 2006 in the 60%, 80%, and 100% ET_c treatments, respectively. In 2005 and 2006, less than 1.0 and 2.2 GWSS egg masses were found per sampled tree per week, respectively. In 2005, no differences in the mean number of GWSS egg masses were observed among the irrigation treatments. In 2006, there appeared to be four peaks of GWSS oviposition. The first peak occurred between late-February to early-March. A second peak occurred from late-April to early-June and the third peak occurred between early-July to early-September. A discrete fourth peak occurred between late-September to late-October. Fewer GWSS egg masses were found in the 60% ET_c treatment in comparison to the 80% or 100% ET_c treatments during the second peak oviposition period of 2006 ($F = 12.22$; df = 2, 20; $P < 0.001$).

In 2005, there were no differences among irrigation treatments in the number of GWSS nymphs ($F = 0.77$; df = 2, 20; $P = 0.472$) or adults ($F = 0.48$; df = 2, 20; $P = 0.622$) collected in beat net samples. In 2006, however, significantly more GWSS adults were collected in the 80% than in the 60% ET_c treatment ($F = 7.11$; df = 2, 20; $P = 0.004$). Population numbers in the 100% ET_c treatment were not different from either the 80% ($P = 0.10$) or the 60% ET_c ($P = 0.26$) treatments. Significantly more nymphal GWSS were collected from the 80% ET_c treatment than in the 60% and 100% ET_c treatments ($F = 5.26$; df = 2, 20; $P = 0.014$) between mid-April to early-July. Yellow sticky traps documented the presence of adult GWSS throughout the 117 weekly trapping periods, except for two and one trapping periods in late-June 2005 and early-June 2006, respectively, when no adult GWSS were caught on any of the traps. The following trapping periods showed a steady increase in insect activity to a peak in late July 2005 and 2006, with an average (± SEM) of 11.96 ± 1.16 and 95.22 ± 4.81 adults caught per trap per week, respectively. There were no differences in numbers of GWSS adults per trap per week among the irrigation treatments.

DISCUSSION
When given a choice, adult GWSS appear to select among host plants based on water stress, both for feeding and oviposition. The results indicate that GWSS begin to move off citrus when xylem-fluid tension exceeds 0.7 MPa, but GWSS feed normally on crape myrtle at levels up to 1.2 MPa (Andersen et al. 1992). The discrepancy may due to reduced vigor of the test insects under laboratory conditions. The increased feeding observed in citrus after drought was broken for a day may indicate a reduction in xylem-fluid tension below the level of the control. Although this was not detected in our test, such an extreme post-stress phenomenon was recorded in another citrus species when irrigation resumed after drought (Kaufmann and Levy 1976). This may be further evidence for the hypothesis that GWSS move into citrus directly after irrigation is applied, and warrants further study.

Our measurements of microclimate and plant conditions in the field experiment indicated that water stress increased leaf surface temperatures and trunk water potential. The two irrigation deficit regimes, 60% and 80% ET_c, differentially affected the population dynamics of GWSS in the experimental citrus plots. Severe to moderate water-stressed trees (60% and 80% ET_c) perhaps had increased solute concentrations used for osmotic adjustment (i.e., carbohydrates, amino acids, and organic acids) that might serve as feeding stimulants and primary nutrients of insects (Mattson and Haack 1987). However, increased water potential in more severe water-stress irrigation treatments (60% ET_c) might have been an impediment to GWSS feeding because more energy would be required to extract xylem fluid out of the xylem vessels (Andersen et al. 1992). In contrast, well-watered plants (100% ET_c) had lower mean water potentials that potentially facilitated extraction of xylem fluid, but more fluid would have to be ingested and filtered to compensate for a more dilute xylem food source. Thus, citrus trees irrigated with 80% ET_c may combine two important plant characteristics for GWSS: 1) a nutrient-concentrated food source and 2) a water potential at acceptable levels for GWSS xylem fluid extraction, at least during periods of low transpirative demand by plants.

CONCLUSIONS

Findings from this study have generated significant new information regarding the host selection behavior of GWSS in California. Trees under severe water stress hosted fewer GWSS than trees maintained under moderate water stress. A more complete understanding of the effect of shorter water stress periods (i.e., regulated deficit irrigation regimes) and the operative host-plant cues that influence GWSS host selection behavior may result in the deployment of strategies to improve control efforts and contribute to limiting the spread of *Xf* induced diseases to susceptible crops.

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