Effects of Citrus and Avocado Irrigation and Nitrogen-Form Soil Amendment on Host Selection by Adult *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

H. NADEL,[1] R. SELIGMANN,[2] M. W. JOHNSON,[3] J. R. HAGLER,[4] D. C. STENGER,[1] AND R. L. GROVES[5]

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ABSTRACT Host plant water status is thought to influence dispersal of the xylophagous leafhopper *Homalodisca vitripennis* Germar, especially where plants are grown under high evaporative demand. Preference by adult *H. vitripennis* for plants grown under different water deficit and nitrogen form fertilization regimens was studied under laboratory conditions. Leafhopper abundance and ovipositional preference were studied on potted 'Washington navel' orange and 'Haas' avocado in cage choice tests, and feeding rate was estimated using excreta produced by insects confined on plants. A similar study compared responses to citrus treated with 1:1 and 26:1 ratios of fertigated nitrate-N to ammonium-N. The insects were more abundant, oviposited, and fed significantly more on surplus-irrigated plants than on plants under moderate continuous deficit irrigation except avocado feeding, which was nearly significant. Plants exposed to drought became less preferred after 3 and 7 d in avocado and citrus, respectively. Citrus xylem fluid tension at this point was estimated at 0.93 MPa. A corresponding pattern of decline in feeding rate was observed on citrus, but on avocado, feeding rate was low overall and not statistically different between treatments. No statistical differences in abundance, oviposition, or feeding were detected on citrus fertigated with 26:1 or 1:1 ratios of nitrate-N to ammonium-N. Feeding occurred diurnally on both plant species. Discussion is provided on the potential deployment of regulated deficit irrigation to manage *H. vitripennis* movement as part of a multitactic effort to minimize the risk of disease outbreaks from *Xylella fastidiosa* Wells et al. in southern California agriculture.

KEY WORDS regulated water deficit, glassy-winged sharpshooter, *Xylella fastidiosa*, choice tests

The glassy-winged sharpshooter, *Homalodisca vitripennis* Germar (Hemiptera: Cicadellidae), is an important vector of the bacterium *Xylella fastidiosa* Wells et al. The bacterium is the causal agent of many economically important plant diseases including Pierce's disease of grape, phony peach disease, and numerous leaf scald and scorch diseases affecting plum, almond, sycamore, oak, and elm (Brlansky et al. 1983, Hopkins and Purcell 2002). A xylem fluid feeder native to southeastern United States and northern Mexico, *H. vitripennis* was inadvertently introduced into California in the late 1980s, probably from Texas (Smith 2005), resulting in increased prevalence and severity of Pierce's disease in Riverside County (Almeida and Purcell 2003). This insect is highly mobile and polyphagous, feeding and ovipositing on a broad range of cultivated and wild host plants (Turner and Pollard 1959, Adlerz and Hopkins 1979, Daane and Johnson 2003, Groves and Chen 2003, Hoddle et al. 2003). Spatial aggregations of *H. vitripennis* in southern California landscapes are often associated with citrus orchards bordering vineyards, a situation that heightens the risk of Pierce's disease epidemics (Perring et al. 2001, Blua and Morgan 2003, Park et al. 2006). Citrus is a common host that supports breeding and overwintering of *H. vitripennis* (Adlerz 1980, Blua et al. 1999, Blua and Morgan 2003, Hoddle et al. 2003, Groves and Chen 2005).

Development of comprehensive management strategies to limit disease outbreaks requires a complete understanding of factors that influence vector preference and dispersal. Insect herbivores generally forage for food hosts that optimize nutrient uptake (Mitchell 1981). Although host utilization by *H. vitripennis* is

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[1] USDA–ARS, San Joaquin Valley Agricultural Sciences Center, 9611 S. Riverbend Ave., Parlier, CA 93648.

[2] Smith Institute of Plant Sciences, Faculty of Agriculture, Hebrew University of Jerusalem, PO Box 12, Rehovot 76100, Israel.

[3] Department of Entomology, University of California, Riverside, CA 92521.

[4] USDA–ARS, U.S. Arid Land Agricultural Research Center, 21881 Cardon Ln., Maricopa, AZ 85238.

[5] Corresponding author: Department of Entomology, University of Wisconsin, Madison, WI 53706 (e-mail: groves@entomology.wisc.edu).

broadly dictated by factors such as host species and phenology (Adlerz 1980, Mizell and French 1987, Daane and Johnson 2003, Bi et al. 2005, Groves and Chen 2005), the underlying factor for host selection is nutrient content of xylem fluid (Brodbeck et al. 1990, 1995, 1996, Andersen et al. 1992). Xylem fluid is especially poor in carbon energy resources (Redak et al. 2004) and futhermore requires energy to extract, because it is usually held under tension in vascular elements (Raven 1983, Andersen et al. 1992). Plant water deficit increases xylem tension (Andersen et al. 1992, 2005), and a tension threshold exists above which feeding becomes energetically unprofitable (Andersen et al. 1992). Plant water status is therefore a factor that may potentially affect *H. vitripennis* host selection and movement. Soil-applied fertilizer amendments may also affect xylem fluid tension (Guo et al. 2007) and nutrient composition (Brodbeck et al. 2004) and may further influence *H. vitripennis* foraging behavior. In addition, *H. vitripennis* movement may be influenced by its choice of plant species favored for adult feeding versus those selected for oviposition and nymphal development (Adlerz 1980, Brodbeck et al. 1995, 1996, Bi et al. 2005).

Research on *H. vitripennis* host preference has focused on nutrition-mediated patterns of host utilization by adults, whose seasonal shifts correlate with concentrations of preferred amino acids in citrus and other plants (Brodbeck et al. 1990, Andersen et al. 2005, Bi et al. 2005). However, spatial and temporal differences in plant water status may also motivate dispersal from water-stressed to adequately watered hosts. Replicated field plots of mature 'Valencia' sweet orange (*Citrus sinensis* L. Osbeck) held under continuous deficit irrigation were found to support lower populations of adult *H. vitripennis* compared with citrus irrigated to evapo-transpiration demand of the crop (ET_c) (Groves et al. 2006), and peak periods of *H. vitripennis* flight in citrus groves were recorded around mid-day when evaporative demand was presumably highest (Blackmer and Hagler 2003, Blackmer et al. 2006). Andersen et al. (1992) showed that fluctuations in *H. vitripennis* feeding rate on water stressed crape-myrtle, *Lagerstroemia indica* L., are associated with both xylem fluid tension and chemistry. Because the mid-day flight peak corresponds to periods when most nutrients in xylem fluid are at their highest concentration in many plants (Andersen et al. 1993, 1995), and nutrient peaks may produce cues used by leafhoppers searching for optimal hosts (Brodbeck et al. 1990, 1993, Andersen et al. 1992), mid-day dispersal may also be an orientation response toward other host plants.

The first objective of this study was to examine how plant water status affects host selection behavior and utilization by adult *H. vitripennis.* Because citrus has been characterized as an important feeding host and breeding reservoir for adult *H. vitripennis* in California, we monitored adult *H. vitripennis* abundance, feeding, and ovipositional behavior on sweet orange (cultivar 'Washington navel') under regulated levels of deficit irrigation, noting that regulated deficit irrigation of citrus orchards is already under study as a profitable and water-conserving production practice (Goldhamer and Salinas 2000, Fereres and Soriano 2006). Citrus is considered a relatively drought tolerant species (Castel and Buj 1990), reducing stomatal conductance and transpiration only after several days of drought (Gomes et al. 2004). In parallel tests, we examined *H. vitripennis* responses to regulated deficit irrigation treatments in avocado (*Persea americana* P. Miller), another common but less preferred perennial host crop in southern California that is not considered drought tolerant (Whiley and Schaffer 1994).

The second objective of this study was an exploratory investigation of *H. vitripennis* preference for citrus fertigated with two ratios of ammonium (NH_4^+-N) and nitrate (NO_3^--N) forms of nitrogen. These commonly used nutrients are both readily absorbed by plants (Serna et al. 1992) but differentially affect several physiological and biochemical plant processes (Guo et al. 2007). Ammonium-N soil amendment is thought to increase xylem fluid tension in higher plants (Guo et al. 2007) and therefore may be less favorable than nitrate-N for sharpshooters. Nitrate increases xylem fluid amide concentration and was shown to be more favorable than urea amendment for adult *H. vitripennis* performance on a legume (Brodbeck et al. 1999). Significant differences in adult performance on the two nitrogen forms, if found, may provide an option for managing *H. vitripennis* populations and movements through fertilizer choice.

Confirmation of *H. vitripennis* preference for hydrated host plants, estimation of water deficit threshold at which adults disperse, and determination of the effects of commonly used fertilizers on host selection will provide information to assist prediction of movement patterns of this economically influential insect in complex agricultural landscapes. A more complete understanding of cultural management practices that influence *H. vitripennis* population dynamics may ultimately result in deployment of strategies to focus control efforts, enhance efficacy of biological control, and effectively limit spread of *X. fastidiosa*–induced diseases to susceptible crops.

Materials and Methods

Insect Collection and Maintenance. Adult *H. vitripennis* were collected from a variety of landscape ornamental shrubs in Bakersfield (Kern County), CA, and from commercial citrus groves grown near Fillmore (Ventura County), CA, from April 2006 to February 2007. Adult insects were maintained in cages on potted cowpeas, *Vigna unguiculata* L., in combination with at least one of the following perennial plant species: *Citrus sinensis, Pittosporum tobira* (Thunberg ex Murray) Aiton, or *Euonymus japonicus* Thunberg. Insects used in a particular test were acclimated on the same set of host species.

Plants, Irrigation, and Environmental Conditions. The plants were potted, 2-yr-old *C. sinensis* cultivar 'Washington navel' oranges grafted on trifoliate orange (*Poncirus trifoliata* L. Rafinesque) rootstock, and

Persea americana Mill. cultivar 'Hass' avocado were grafted on cultivar 'Mexican' rootstock. Experiments were conducted under high-pressure sodium vapor lamps (14 L: 10 D) in a room cycling at day-night conditions of 32–20°C, 33–68% RH, and 3.2–0.9 kPa vapor pressure deficit. Light intensity at the plant canopy ranged from 5,500 to 8,550 lux. Experimental replicates were randomized on two growth racks on each of two shelves, with one lamp centered above each shelf.

Deficit irrigation treatments were monitored and controlled by six scale lysimeters (3733LP; 50-kg maximum, 10-g resolution; Avery Weigh-Tronix, Fairmont, MN) and a measurement and control unit (CR10X; Campbell Scientific, Logan, UT) that measured every minute and averaged and recorded various parameters at 10-min intervals. Two scales monitored control (surplus-irrigated, I_c) citrus, two monitored I_c control avocados, and one scale monitored each of the deficit-irrigated citrus treatments (space was insufficient for an additional scale lysimeter to measure deficit-irrigated avocado, and deficit irrigation levels were imposed by withholding a percentage of I_c avocado irrigation). A pair of plants was monitored on each scale when possible, although in some cases only one plant was monitored during the studies because of space limitations. Irrigation was applied three times daily to each pot by pressure-compensating drip emitters (Netafim, Kibbutz Hazerim, Israel) using a relay controller operating electric valves (Bermad, Kibbutz Evron, Israel). Daily irrigation quantities were adapted to real-time weight loss through water consumption (evapo-transpiration) of control I_c plants receiving surplus irrigation to ensure leaching of salts, resulting in I_c delivery to citrus and avocado of ≈ 175 and 250 ml/d, respectively. The fertigation system, in which nutrient solution was combined and injected with irrigation water, consisted of a set of water-powered pumps (D250RE10; Dosatron, Tresses, France) delivering final nutrient concentrations of 120 N, 20 P, 75 K, 86 Ca, and 36 Mg ppm, along with a microelement mix. The standard nitrogen delivery was a 26:1 ratio of nitrate nitrogen (NO_3-N) to ammonium nitrogen (NH_4-N).

Deficit Irrigation Treatments. In addition to the I_c control, two types of deficit irrigation treatments were imposed on citrus and avocado to induce experimental water stress: continuous deficit irrigation (CDI) and gradual deficit irrigation (GDI). Under CDI, plants were irrigated only a portion of I_c at each of the three daily irrigation events. Citrus received 25% of I_c, whereas avocado, which is less tolerant of water deficit, received 50% of I_c. Insect preference and feeding tests began when water consumption stabilized at ≈25% of the I_c consumption rate under CDI in the citrus. The CDI tests in avocado were performed on the same days as citrus, although no weight measurements were taken on CDI avocado because of the previously noted space limitations. Under GDI, plants were irrigated to the point of drainage during days 0 and 14 of the study, but otherwise received no water between irrigation events to create gradually increasing water deficit.

When the studies ended and plants were surplus irrigated for >2 mo, water deficit treatments were reimposed on citrus, and stem xylem fluid tension was measured between 1130 and 1230 hours with a pressure chamber apparatus (Soilmoisture Equipment, Santa Barbara, CA). A single leaf from each of three citrus plants per treatment was measured on each sample date. Leaf blades chosen for tension determination were covered with an aluminum-foiled plastic bag for 2 h, after which they were excised at the petiole and transferred to the pressure chamber within 45 s. Measurements on avocado were made on surplus irrigated and CDI treatments only.

N-form Treatments. The study was conducted on citrus. The standard N-form ratio of NO_3-N to NH_4-N (26:1) was designated the nitrate-N treatment. This pronounced nitrate nutrition was compared with a treatment designated the ammonium-N treatment, in which the delivery ratio of NO_3-N to NH_4-N was 1:1. The NH_4-N proportion was restricted to 50% to avoid potential inhibitory effects on plant growth associated with higher concentrations (Guo et al. 2007). Leafhopper abundance, ovipositional preference and feeding tests started after N-form treatments were imposed for at least 1 wk. Stem xylem fluid tension was measured on a single day on one leaf of each of 10 plants per treatment as described above. Because plant position relative to the overhead lamp may have affected xylem fluid tension among plants, measurements were recorded for paired plants of each treatment at each position.

Cage Choice Tests. Preference studies were conducted separately on citrus and avocado in cages placed on the previously described growth racks. Cages were composed of aluminum floors and frames, 61 by 61 cm at the base and 81 cm high, with two opposing sides of amber nylon mesh for air flow, and the remainder and top consisted of clear polyethylene sheeting for viewing. A pair of woven cotton sleeves on one side allowed manipulation of plants and insects. Cages were placed on racks equidistant from the lamps. During preliminary trials, we found that a large proportion of *H. vitripennis* oriented toward the light and remained on the cage ceiling until severely weakened. To reduce this problem, we placed a sheet of 21 by 28-cm white paper at the corner of each cage directly under the lamps. This reduced light intensity directly below the paper but still allowed unfiltered light to reach a major portion of each plant canopy (≈5,000 lux). A pair of plants, one per treatment, was placed inside each cage equidistant to the lamp and fed by dripper lines inserted through one of the sleeves. The CDI tests began when the target water stress level was reached in citrus. In the GDI study, insects were introduced on the first day of drought. Between 1000 and 1100 hours on day 1 of each test, 30–40 adult *H. vitripennis* (≈50% female) were released into each cage from collecting vials placed on the cage floor equidistant from the plants at the corner farthest away from the lamp. The number of *H. vit-*

ripennis on each plant was recorded daily at 1600 hours. After the first set of trials (four replicates), treatments were switched between the two plants by exchanging dripper lines, and the plants were allowed to acclimate for at least 1 wk before a second trial was conducted. This was done to confirm that preference was caused by treatment and not plant effects. When CDI and N-form trials ended, the number of egg masses was recorded for each plant. Because the insects were recently collected from the field and may have had different nutritional histories, we quantified only oviposition choice (egg masses per plant) and not the number of eggs per mass.

Feeding Rate. Excreta production for *H. vitripennis* confined on plants was quantified as a measure of feeding rate (Andersen et al. 1992). Insects were confined individually in flat, semirectangular Parafilm "M" (Pechiney Plastic Packaging, Chicago, IL) sachets, 7 cm high by 5 cm long by 1 cm wide, wrapped at one end around the plant stem and secured with a plastic clip. The sachet walls were pierced with a needle for air flow. The design was modified by R. Seligmann from Pathak et al. (1982) to allow drainage and collection of excreta through a 16- or 20-gauge needle into a 2-ml screw-cap tube. The caps were impaled on the needles and loosely screwed onto the tubes to allow air displacement. Two *H. vitripennis* per plant were confined along the main stem above the graft union in citrus and on separate branches in avocado. Excreta volumes were measured in a graduated cylinder. When droplets were visible on the sachet walls but were insufficient to enter the tube, the amount was recorded as 0.01 ml to indicate that minimal excretion occurred. Collections were made daily in the morning and late afternoon during the N-form and CDI studies to determine whether feeding is diurnal or nocturnal on the two host species. Diurnal excreta (0800–1600 hours) and nocturnal excreta (1600–0800 hours) were measured at 1600 and 0800 hours, respectively. During the GDI study, 24-h excreta production was measured daily at 1600 hours. To compare sex differences in feeding rate, one male and one female were confined per plant in the N-form and GDI studies. Only females were used in the CDI study. Mortality was high during the week-long N-form study, so subsequent deficit irrigation studies were modified to include replacement insects and were extended to 16 d.

Data Analysis. Proportions of egg masses laid on a choice of plants under two treatments were analyzed by χ^2, testing the hypothesis that the proportion of egg masses is equally distributed (0.5) between the treatments.

Deficit irrigation studies were designed as random blocks in a balanced factorial split-split-plot design, with 4 blocks (cages), 2 plots (trial periods), 2 subplots (treatments), and 7–14 sub-subplots (observation days). After the first trial period (four replicates), treatments were switched between each pair of plants, and after at least 1 wk of acclimation, the trial was repeated. Studies were analyzed separately for citrus and avocado. The N-form study was similar to the

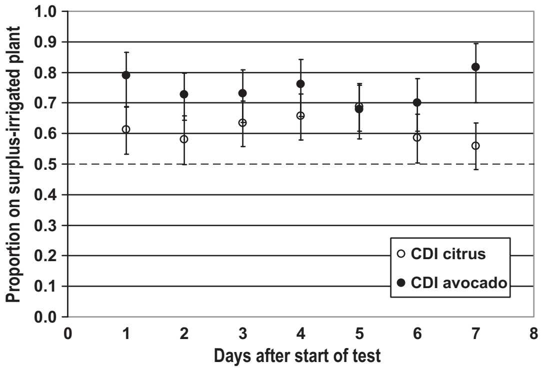

Fig. 1. Proportion (mean ± 95% CI) of *H. vitripennis* that settled on surplus-irrigated (I_c) plants when given a choice of a pair of citrus or avocado plants, one under CDI and the other under surplus irrigation (logistic regression analysis, excluding within-cage and treatment-position effects).

deficit irrigation study, but with randomized (unbalanced) treatment positions and 12 replicates equally divided among three trial periods. Daily proportions of *H. vitripennis* on plants under each treatment were fitted to a logistic regression model to exclude between-cage effects and within-cage effects caused by plant position in cages.

Daily excreta volumes were normalized by square-root transformation. N-form treatment data were analyzed by factorial analysis of variance (ANOVA) to examine effects of N-form, sex, time of day, plant effects, and the interaction effects of N-form × sex and N-form × time of day. Daily excreta production within GDI and CDI studies was compared by repeated-measures ANOVA, with sex nested within treatment in GDI tests. Xylem fluid tension in plants under N-form treatments was compared by paired *t*-test. All analyses were performed using SAS (SAS Institute 2003).

Results

Deficit Irrigation. Xylem fluid tension of citrus increased from an average of 0.35 ± 0.02 MPa in the I_c controls to 0.73 ± 0.05 MPa in the CDI treatment after measurements stabilized. Tension in CDI avocado increased from 0.18 ± 0.02 to 0.92 ± 0.17 MPa. In all cage studies, some *H. vitripennis* were daily observed off plants on cage walls, indicating repeated opportunities to select between host plants throughout each study. Adult *H. vitripennis* were more abundant on I_c citrus than on CDI citrus throughout the study (62% overall mean), with significant preference for I_c citrus on days 1, 3, 4, and 5 of the 7-d experimental interval, whereas on avocado, leafhopper abundance was significantly higher on I_c plants during all 7 d (74% overall mean; Fig. 1). Insects laid significantly more egg masses on I_c plants of both species (Table 1) and produced significantly more excreta on I_c citrus plants (daily mean ± SEM: I_c, 0.80 ± 0.10 ml; CDI, 0.09 ± 0.02 ml; $F = 6.73$; df = 1,18; $P = 0.0183$). Excreta production was lower

Table 1. Number of *H. vitripennis* egg masses laid on a choice of two plants under different N-form or water-deficit treatments

Plant species	Treatment[a]	No. egg masses	χ^2	P
Citrus	Nitrate-N	39		
	Ammonium-N	32	0.690	0.4061
Citrus	I_c	57		
	CDI	23	14.450	<0.0001
Avocado	I_c	20		
	CDI	9	4.172	<0.0411

Thirty to 40 adult *H. vitripennis*, ≈50% females, were introduced into a cage for 7 d.

The χ^2 goodness-of-fit test was used to test if proportions were equal (0.5) on each treatment. $P < 0.05$ is statistically significant.

[a] The nitrate-N and ammonium-N treatments consisted of NO_3:NH_4 at 26:1 and at 1:1 ratios, respectively.

I_c, surplus irrigation; CDI, continuous deficit irrigation.

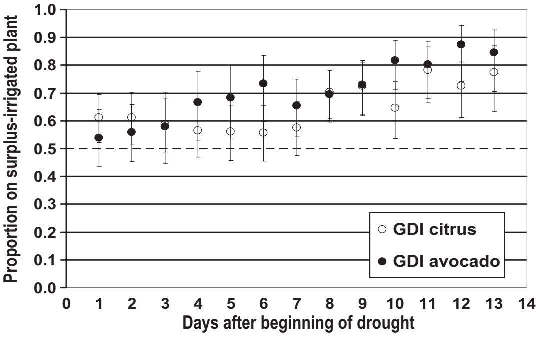

Fig. 3. Proportion (mean ± 95% CI) of *H. vitripennis* that settled on surplus-irrigated (I_c) plants when given a choice of a pair of citrus or avocado plants, one under GDI and the other under surplus irrigation (logistic regression analysis, excluding within-cage and treatment-position effects).

on avocado, with a nearly significantly higher level on I_c (daily mean ± SEM: I_c, 0.25 ± 0.07 ml; CDI, 0.03 ± 0.01 ml; $F = 4.39$; df = 1,18; $P = 0.0506$).

During drought (GDI), xylem fluid tension increased rapidly in citrus after day 7 from ≈0.50 to 0.95 MPa and continued to rise to >1.2 MPa (Fig. 2), while water consumption measurements indicated a 60% decrease relative to the control on day 7, stabilizing at that level until irrigation on day 14. The host choice pattern on citrus closely corresponded to xylem fluid tension and plant water consumption, declining as tension rose and water consumption declined. The proportion of adult *H. vitripennis* on the two plants was nearly equal through the first 6 d after onset of drought, after which adults began significantly preferring the I_c plant beginning on day 8 (Fig. 3). In avocado, the proportion of adults on both plants was similar on days 1–3, and preference for I_c plants began on day 4. Thereafter, sharpshooters showed an increasing preference for I_c plants of both species until the study ended.

Sex differences in excreta production were not statistically significant, so the data were pooled for further analysis. Excreta production on I_c avocados was always higher than GDI for the first 11 d, but volumes were highly variable, and no statistical differences were found between treatment means on any day (Fig. 4A). After day 11, excreta production was near zero on both avocado treatments. On citrus, however, the effects of day ($F = 2.44$; df = 25,400; $P = 0.012$) and day × treatment ($F = 2.40$; df = 25,400; $P = 0.014$) were significant. The relative trend in excreta production on GDI and I_c plants fell into four distinct phases: similar in days 1–7, GDI lower than I_c between days 8–14 and days 25–30, and GDI higher than I_c on days 15–20 (Fig. 4B). During days 1–14, the pattern of GDI excreta production corresponded roughly to the degree of water deficit as indicated by xylem fluid tension (Fig. 2) and leafhopper abundance (Fig. 3). After irrigation on day 14, however, feeding rate on GDI plants rose rapidly, significantly exceeding the rate on I_c between days 16 and 20, and fell again to below I_c levels around day 23. No dramatic rise in feeding on GDI plants was evident after plants were irrigated again on day 28.

N-form. Adult *H. vitripennis* showed no significant differences in abundance or oviposition rate on citrus fertigated with either the pronounced nitrate-N or ammonium-N treatments. N-form treatment also had no significant effect on excreta production. Although females generally produced more excreta than males, sex differences were not significant, as in the GDI

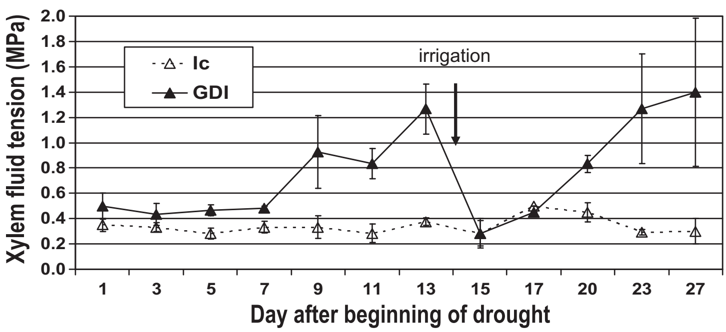

Fig. 2. Xylem-fluid tension (mean ± SEM) in potted citrus plants under GDI and control, with surplus irrigation provided to GDI plants on day 14. Measurements began 1 d after drought was imposed. One leaf was measured on each of three plants per treatment per sample.

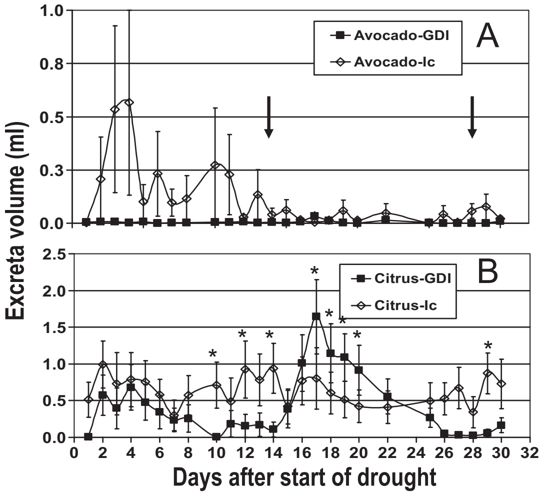

Fig. 4. Excreta volume (mean ± SEM) produced by *H. vitripennis* on surplus-irrigated (I_c) and GDI plants over 30 d after drought was imposed on GDI. Arrows indicate when GDI plants were surplus-irrigated for 1 d. (A) Avocado. (B) Citrus. Daily excreta production was averaged from one male and one female *H. vitripennis* caged separately on each plant, with five plants per treatment. Dead *H. vitripennis* were replaced. *Significantly different treatment means (repeated-measures ANOVA, $P < 0.05$).

study. Time of day had a significant effect on excreta production, with higher feeding activity during diurnal (0800–1600 hours) rather than nocturnal (1600–0800 hours) periods ($F = 16.84$; df = 1,56; $P < 0.001$). Nocturnal production among treatments averaged between 0.02 ± 0.01 and 0.08 ± 0.05 ml/insect/night, whereas diurnal production averaged between 0.21 ± 0.13 and 0.47 ± 0.22 ml/insect/d. Plant effects were significant in the N-form experiment ($F = 3.32$; df = 18,56; $P < 0.001$), indicating variability that may have been caused by distance from the grow lamp (excreta production was observed to decrease with increasing distance from the light source).

Mean ± SEM xylem fluid tension of citrus plants treated with nitrate-N was 0.21 ± 0.02 MPa, which was significantly lower than in plants treated with ammonium-N (2.73 ± 0.21; paired *t*-test; *t* value = 2.487; df = 9; $P = 0.035$).

Discussion

The abundance of *H. vitripennis* was higher on adequately watered plants than on plants experiencing a moderate degree of water deficit. The most likely explanation for this preference is the higher capacity of sharpshooters to feed on adequately watered rather than water-deficient plants, which is supported in this study and elsewhere (Andersen et al. 1992, Redak et al. 2004). Oviposition was also higher on adequately watered plants, but whether this predicts better nymphal performance on such plants is unknown. Leafhoppers fed diurnally on both citrus and avocado, as is the case on most host species studied (Andersen et al. 1989, 1992, Brodbeck et al. 1993), indicating that concentration of xylem nutrients favored by the sharpshooter (organic and nitrogen constituents) is higher during the day in both tested host species (Andersen and Brodbeck 1989). Nocturnal feeding has been recorded on *Catharanthus roseus* L., which corresponds to higher nighttime nutrient concentrations (Brodbeck et al. 1993).

Peak feeding in citrus irrigated after a drought cycle (Fig. 4) provides a possible explanation for the observation (R. Groves, unpublished data) that *H. vitripennis* move toward recently irrigated citrus when it is grown under high evaporative demand. An extreme poststress decrease in xylem fluid tension was noted by Kaufmann and Levy (1976) in potted rough lemon (*Citrus jambhiri* Lush.) seedlings when they were watered for a day after 3- to 8-d drought cycles. That study showed that xylem fluid tension in stressed plants decreased rapidly below control levels for ≈3 d after irrigation, later rising again to above the control tension level. Such a marked reduction in xylem fluid tension should enhance *H. vitripennis* feeding by reducing the energy required to extract the fluid (Scholander et al. 1965, Raven 1983, Andersen et al. 1992, Redak et al. 2004). Although we did not detect a poststress reduction in xylem fluid tension below the control, such a phenomenon may have occurred while the feeding studies were under way and may have contributed to the significant feeding peak recorded on water stressed citrus directly after irrigation was applied (Fig. 4).

The level of xylem fluid tension at which adult *H. vitripennis* leave or avoid potted sweet orange plants can be broadly estimated from Fig. 2 to occur near or above 0.90 MPa, corresponding to the level recorded after day 7. The rapid rise in xylem fluid tension corresponds to the shift in relative proportions of *H. vitripennis* from equal on GDI and surplus-irrigated citrus toward a preference for surplus-irrigated plants, which intensified as tension continued to rise under deficit irrigation. The shift also corresponded to an imposed evapo-transpiration rate of ≈40% of surplus-irrigated citrus. Relative feeding rates on GDI citrus also begin to decline at around the same level. These results help explain distribution patterns observed in *H. vitripennis* populations in southern California, where blocks of citrus continuously irrigated at 60% ET_c support lower *H. vitripennis* populations than blocks irrigated at 80 or 100% ET_c (Krugner 2007). The results are somewhat consistent with stress levels in potted 'Pêra' oranges subjected to drought, in which xylem fluid tension begins showing a significant rise after 5 d (Gomes et al. 2004). Feeding on *L. indica* proceeds normally at xylem fluid tension of up to 1.20 MPa (Andersen et al. 1992), higher than the threshold estimated on sweet orange in this study. This difference may be caused in part by host plant species and experimental conditions but is also likely to reflect differences in rearing history and vigor of the experimental insects.

Although the higher nitrate-N treatment was expected to be favored for adult feeding, the two tested ratios of nitrate-N to ammonium-N amendments elicited no detectable responses in feeding choice by adult *H. vitripennis.* Ammonium may, under certain conditions and in certain species, restrict water uptake by roots of higher plants, which would result in increased xylem fluid tension relative to nitrate (Guo et al. 2007). Nitrate nutrition promotes higher concentrations of amides in xylem sap of a legume (Brodbeck et al. 1999), which is favorable for the adults but not the nymphs (Brodbeck et al. 1995, 1996, 1999). Although we detected a slight increase in xylem tension in ammonium-treated plants, it seemed insufficient to cause a measurable short-term response by adult *H. vitripennis,* which can regularly feed on xylem fluid at tensions as high as 1.8 MPa (Andersen et al. 1992). We also noted no oviposition preference for ammonium-treated plants, although they might be favored for nymphal development. Brodbeck et al. (2007) found no linkage between adult *H. vitripennis* oviposition preference and nymphal performance among host species, and this likely extends to intraspecific variation in host quality. Although the data thus far do not support a dramatic short-term influence of nitrogen form on adult *H. vitripennis* host selection and movement in citrus, comparison of the amendments over multiple generations may demonstrate differences on sharpshooter populations by affecting both adult and nymphal fitness. This is an area for future research.

The response by *H. vitripennis* to plant water status provides an opportunity for manipulation of irrigation practices to manage Pierce's disease outbreaks at citrus–grape interfaces. A regulated deficit irrigation strategy has good economic potential in citrus (Hilgeman and Sharp 1970, Domingo et al. 1996, Goldhamer and Salinas 2000) and is regularly used in fruit trees to control canopy size and limit applied water (Chalmers et al. 1981). Studies on citrus showed that regulated deficit irrigation does not significantly reduce yield in lemon (Domingo et al. 1996) and that deficit intervals do not lead to reduced 'Valencia' orange fruit size at harvest (Hilgeman and Sharp 1970). In eastern Kern Co., CA, a 25% reduction in applied water (i.e., 75% of ET_c) in mid-May to mid-July did not reduce orange fruit yield and quality compared with the ET_c control (Goldhamer and Salinas 2000). That early summer period corresponds to the time when grapevines are most susceptible to damage from Pierce's disease transmission (Feil et al. 2003, Hill 2006) and to a peak of sharpshooter recruitment into the mobile adult stage in citrus (Castle et al. 2005). A buffer consisting of rows or blocks of citrus under regulated deficit irrigation along grape–citrus interfaces throughout the early summer months has the potential to reduce vector populations there without detriment to the citrus crop. Deficit irrigation in vineyards is another alternative. Daane and Williams (2003) showed that deficit irrigation can be used to control variegated leafhopper, *Erythroneura variabilis* Beamer, in vineyards without loss of vine vigor or fruit yield. Management of *H. vitripennis* populations through regulation of xylem tension and chemistry was proposed earlier by Redak et al. (2004).

Understanding if *H. vitripennis* orients toward adequately irrigated hosts from a distance is still unknown. Determining how fertilizers and deficit irrigation affect *H. vitripennis* may ultimately provide management options that benefit producers of both citrus and *X. fastidiosa*-susceptible crops like grapes. Looking ahead, although the *X. fastidiosa* strains currently in California are asymptomatic in citrus, a virulent citrus strain (citrus variegated chlorosis) that can be vectored by *H. vitripennis* (Damsteegt et al. 2006) and related sharpshooters (Brlansky et al. 2002) exists in South America. If introduced, it may have serious implications for the California citrus industry. Understanding *H. vitripennis* movement and management is therefore potentially beneficial to both the citrus industry and to producers of currently susceptible crops.

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