Behavioral Responses of *Homalodisca vitripennis* (Hemiptera: Auchenorrhyncha: Cicadellidae) on Four *Vitis* Genotypes

FELIX B. FRITSCHI,[1] JUAN C. CABRERA-LA ROSA,[2] HONG LIN,[4] MARSHALL W. JOHNSON,[2] AND RUSSELL L. GROVES[3]

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ABSTRACT Pierce's disease is a major threat to the California grape industry. The disease-causing bacterium *Xylella fastidiosa* is vectored by a number of leafhoppers including *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae). Experiments were conducted to study *H. vitripennis* preference, feeding, and survivorship in response to four *Vitis* genotypes. Plants of *V. vinifera* ('Chardonnay'), *V. girdiana*, *V. candicans*, and a *V. rupestris* × *V. arizonica*/*candicans* hybrid (D8909-17) were grown in pots in the greenhouse and transferred to laboratory conditions for experiments with field-collected *H. vitripennis*. A choice test without prior insect acclimation on grapes revealed that *H. vitripennis* selected Chardonnay over *V. candicans* throughout the duration of the experiment, whereas a shift in preference between D8909-17 and *V. girdiana* was observed over time. In a second set of choice tests, which were preceded by an acclimation on one of the four grape genotypes, significant genotype, time, and acclimation × genotype effects were observed. Chardonnay was preferred over *V. candicans* independent of acclimation genotype. Although *H. vitripennis* confined on D8909-17 excreted 1.8-fold (dry-weight corrected) the amount of insects feeding on *V. candicans*, differences in the rate of excreta production per insect or insect dry weight were not significant among grape genotypes. Adult mortality was greatest on *V. candicans* when *H. vitripennis* were confined in parafilm sachets for excreta collection as well as in a no-choice test. Grape genotype affected the behavior of adult *H. vitripennis* under controlled conditions, which may influence Pierce's disease epidemiology under field conditions.

KEY WORDS glassy-winged sharpshooter, xylem sap, preference, Pierce's disease, grape

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Takiya et al. 2006), is a vector of the gram-negative bacterium *Xylella fastidiosa* (Wells et al. 1987), which causes disease in many crops including Pierce's disease in sensitive grapevine genotypes (Kaloostian et al. 1962, Davis et al. 1978, Hopkins 1989, Hopkins and Purcell 2002). The glassy-winged sharpshooter is a xylem feeder that is indigenous to the southeastern United States and northeastern Mexico (Young 1958, Turner and Pollard 1959, Triapitsyn and Phillips 2000). Sorensen and Gill (1996) initially reported its establishment in southern California, with observations as early as 1990. They surmised that it was introduced through egg masses on nursery stock foliage. In the 1990s, glassy-winged sharpshooters spread throughout southern California and into the southern San Joaquin Valley (Blua et al. 1999, 2001), with further spread hypothesized to be likely (Hoddle 2004). Spread and establishment of glassy-winged sharpshooters in southern California have been associated with a Pierce's disease epidemic in the Temecula, CA, area, followed by the spread of Pierce's disease, oleander leaf scorch, and almond leaf scorch in recent years (Blua et al. 1999, Purcell and Saunders 1999, Purcell et al. 1999, Perring et al. 2001, Almeida and Purcell 2003a). Economic losses caused by glassy-winged sharpshooter-vectored *X. fastidiosa* in the Temecula Valley showed the potentially devastating impact that glassy-winged sharpshooter spread and establishment may have on California's agriculture (e.g., viticulture, stone fruit, almonds, and ornamentals) (Siebert 2001). In the absence of effective treatments for *X. fastidiosa*–caused diseases, glassy-winged sharpshooters jeopardize California agriculture (Purcell and Saunders 1999, Blua et al. 1999, Almeida and Purcell 2003a).

Glassy-winged sharpshooters are extremely mobile and highly polyphagous xylem feeders (Turner and Pollard 1959, Hoddle et al. 2003, Blua and Morgan 2003). Its host range exceeds 100 plant species, ranging from grasses to woody dicotyledons and conifers (Turner and Pollard 1959, Hoddle et al. 2003). In contrast to *X. fastidiosa* vectors native to California (e.g., *Graphocephala atropunctata* Signoret, *Draeculacephala minerva* Ball, *Xyphon fulgida* Nottingham),

[1] Division of Plant Sciences, University of Missouri-Columbia, Columbia, MO 65211.
[2] Department of Entomology, University of California, Riverside, CA 92521.
[3] Department of Entomology, University of Wisconsin, Madison, WI 53706.
[4] Corresponding author: USDA–ARS, Crop Diseases, Pests & Genetics Research Unit, 9611 S. Riverbend Ave., Parlier, CA 93648 (e-mail: hlin@fresno.ars.usda.gov).

glassy-winged sharpshooters seem to move further into the vineyards and feed on grapevine woody tissues, facilitating vine-to-vine spread (Varela et al. 2001, Blua et al. 2001, Blua and Morgan 2003, Tubajika et al. 2004). However, Blackmer et al. (2004) reported that *H. liturata* Ball, a sharpshooter native to California, has the ability to disperse farther and/or faster than the glassy-winged sharpshooter and suggested that factors such as host range, population density, and tendency for short-distance movement may be more important than dispersal capacity in explaining greater Pierce's disease incidence associated with glassy-winged sharpshooters.

The economic importance of bacterial pathogens is influenced by a number of factors that include vector host preference (Rosenberger 1982). Vector preference in turn is influenced by various host plant characteristics. It seems that xylem sap nutrient content is a major factor determining host preferences of xylem-feeding sharpshooters including the glassy-winged sharpshooter (Brodbeck et al. 1990, 1993, Andersen et al. 1992, 2005). Other factors influencing sharpshooter host selection behavior, including plant nutrient status and *X. fastidiosa* infection may, at least in part, be explained by differences in xylem sap nutrient concentration and/or xylem tension (Andersen et al. 1992, 2005, Brodbeck et al. 1993, Marucci et al. 2005). However, other aspects (e.g., pubescence and leaf coloration) have also been shown to affect preference and performance of sharpshooters (Brodbeck et al. 2004, Marucci et al. 2005). Regardless of the underlying factors, vector preference is an important component of disease epidemiology because it affects insect density and residence time, and ultimately, Pierce's disease progress (Purcell 1981, Mizell and French 1987, Marucci et al. 2005). Although *X. fastidiosa* acquisition by glassy-winged sharpshooters from inoculated *V. vinifera* was extremely rapid and no association of increased transmission efficiency with increased acquisition access period was documented by Almeida and Purcell (2003b), they showed a significant relationship between transmission rate and inoculation access period. Thus, vector preference manifested as residence time and associated probing and feeding behaviors can be critical to disease epidemiology. Whether a result of xylem sap composition, plant pubescence, leaf coloration, or other plant traits alone or in combination, insect vectors exhibit host preferences that may have consequences in terms of Pierce's disease epidemiology. Vector preferences may be manipulated by a number of management decisions including irrigation, pruning, fertilization, and rootstock and genotype selection (Mizell and French 1987, Brodbeck et al. 1990, 1999, 2004, Andersen and Brodbeck 1991, Andersen et al. 1992, Daane et al. 1995, Marucci et al. 2004).

In this study, we investigated aspects of glassy-winged sharpshooter preference and feeding behavior with respect to four *Vitis* genotypes. The objectives of this study were to (1) investigate glassy-winged sharpshooter preference among four grape genotypes; (2) determine whether acclimation affects preference behavior; (3) quantify glassy-winged sharpshooter excreta production on the four grape genotypes examined; (4) examine how insect mortality is affected by grape genotype, and (5) examine xylem sap amino acid composition of the four grape genotypes with respect to glassy-winged sharpshooter host preference behavior.

Materials and Methods

Plant Material. Four grape genotypes with differential sensitivity to Pierce's disease were evaluated. 'Chardonnay' is a highly susceptible *V. vinifera* genotype (Purcell 1981, Krivanek and Walker 2005, Krivanek et al. 2005) as determined under both field and greenhouse conditions. Genotypes *V. girdiana*, *V. candicans*, and a *V. rupestris x arizonica/candicans* hybrid (D8909-17) are considered tolerant to Pierce's disease either based on *X. fastidiosa* populations in stem tissue or xylem sap bioassays conducted using greenhouse grown plants (unpublished data). All plants were propagated from green cuttings collected from *X. fastidiosa*-free grapevines in the University of California, Davis, vineyards. Cuttings were rooted in cellulose sponges in styrofoam trays that were placed in tubs situated on heating mats maintaining a bottom heat of 26.7 ± 2°C in a controlled environment chamber programmed for an ambient temperature of 15.6 ± 1°C. Light was provided by high output fluorescent lamps (F54W/T5/840/HO; General Electric Company, Fairfield, CT) programmed for a 16/8 (L/D) h cycle. Rooted cuttings were planted into 2.1-liter pots containing Sunshine Mix 3 (Sun Gro Horticulture Canada, Seba Beach, Canada), transferred to the greenhouse, and maintained at ≈24 ± 6°C. Natural light was supplemented by high-pressure sodium lights (Sun System III, HPS400; Sunlight Supply, Vancouver, WA) to extend the day/night cycle to 16/8 (L/D) h as daylength shortened. To ensure uniform shoot growth, plants for all experiments were cut back at the same time to two or three buds and fertilized with 0.15 g of a 20-20-20 (N-P-K) Peters Professional water soluble fertilizer (Scotts-Sierra Horticulture Products, Marysville, OH) per plant at a 2-wk interval.

Experiments 1, 2, 3, and 4 were initiated 50, 62, 79, and 94 d, respectively, after cut-back. All experiments were carried out under laboratory conditions with the photoperiod set to a 16/8 (L/D) h regimen and natural light supplemented by a combination of fluorescent lamps and high-pressure sodium lights (experiments 1 and 2) or high-pressure sodium lights only (experiments 3 and 4). Plants were well-watered throughout the duration of each experiment by manual watering. Temperature sensors (WatchDog Data Logger model 100; Spectrum Technologies, East Plainfield, IL) were used to monitor temperature conditions in 30-min intervals. For experiments 1 and 2, daytime average temperature was maintained at 26.5°C and generally varied between 23 and 30°C, with night-time minimum temperatures ≥15°C. For experiments 3 and 4, mean daytime temperature varied between 25 and 27°C; night time temperatures were ≥21°C.

Insects. Adult glassy-winged sharpshooters used in all experiments were collected by beat-net sweeping from citrus trees on the Citrus Experiment Station at the University of California, Riverside. Adults were maintained on plants of cowpea (*Vigna unguiculata* L.), sorghum (*Sorghum bicolor* L.), and *Euonymus* spp. in cages for 1 d before establishment of experiment 1. Insects collected for experiment 2 were held in cages on cowpea for 2 d before the acclimation treatments. For experiments 3 and 4, adult glassy-winged sharpshooters were held for 1 d on oleander (*Nerium oleander* L.) before a 3-d acclimation on cowpea.

Experiment 1: Free-Choice Experiment without Specific Acclimation. A free-choice experiment was carried out in insect rearing cages (Bug Dorm-2; MegaView Science Education Services, Taiwan) with mesh screening and transparent panels for easy observation from all cage sides. Ten cages were used in this experiment, and each cage contained one plant of every grape genotype with plants randomly arranged within cages. Twenty-five nonsexed insects collected from the holding cage were released in a central position among the plants in each cage. The experiment was assessed at 1, 2, 6, 30, 54, 78, 102, 126, 150, and 174 h after insect release, which corresponded to 1100, 1200, and 1600 hours Pacific Standard Time (PST) the first day and 1600 hours PST every day afterward. At each sample interval, plants were inspected, and the number of insects on the stem, petioles, and leaves was recorded. In addition, the number of dead insects and those remaining on inert surfaces were assessed.

All remaining glassy-winged sharpshooters were killed 1 d after the last assessment and before xylem sap collection, which was conducted between 1100 and 1530 hours. To that end, stems were cut two to three nodes above the base of the shoot and tissue external to the xylem was peeled away at the cut end. After insertion of the stem into a pressure chamber apparatus (PMS Instrument, Albany, OR) (Scholander et al. 1965), the cut end was rinsed with ddH_2O and wiped off with a paper tissue. Xylem sap was expressed by gradually raising the pressure in the chamber to 2 MPa and was collected in tubes resting on ice. Xylem sap was stored at −20°C until analysis. Amino acid analyses of xylem sap samples were conducted at the UC Davis Molecular Structure Facility with standard protocols using a Beckman 6300 (Li-citrate based) amino acid analyzer.

Experiment 2: Free-Choice Experiment with Acclimation on Each Grape Genotype. Experiment 2 was designed to test if acclimation on a specific grape genotype affected insect behavior in a free-choice test. Experimental procedures were similar to the first choice experiment, with the following exceptions. One hundred adult insects were transferred from the holding cages to one of four insect-rearing cages. The four rearing cages each contained four plants of a single grape genotype alone, resulting in a single acclimation cage for each grape genotype. After 3 d of acclimation, 30 nonsexed insects were released in the center of insect rearing cages containing one plant of each grape genotype. For each set of insects acclimated on one particular grape genotype, three cages containing each of the four genotypes were established. Thus, a total of 12 cages (i.e., three replications for each of the four acclimation treatments) were setup in a completely randomized design. The experiment was evaluated in the same manner as experiment 1 with the exception that neither the 1-h and 174-h assessments nor the xylem sap collection was undertaken.

Experiment 3: Excreta Collection. Field-collected adult glassy-winged sharpshooters were transferred after 1 d in a holding cage on oleander to an acclimation cage with cowpea. Adult insects were maintained on cowpea for 3 d before confining them individually for excreta collection. Grape plants were arranged in a randomized complete block design consisting of four genotypes and five replications (one plant per replication). On each plant, six female insects were confined individually in excreta collection sachets similar to those described by Pathak et al. (1982). Briefly, the sachets constructed from Parafilm were ≈8 by 13 cm in dimension. At the open end of the sachets, the Parafilm was cut into "wings" that were used to attach the sachets to the grape stems using small binder clips. After adding one insect to each sachet, the wings were folded around the stem, thereby exposing ≈5–7 cm of stem for insect feeding. Excreta were collected at 1600 hours every day for the first 5 d and on day 7 using fine-tip transfer pipettes. After weighing, the samples were frozen and stored at −20°C. To minimize variation caused by insect age and vigor, only insects that produced measurable amounts of excreta between 120 and 168 h (38% of glassy-winged sharpshooters initially confined in the sachets) were considered for data analysis. From that set of insects, only excreta collected over the course of the first five 24-h periods were considered for analysis, whereas excreta collection for the remaining 48 h of the experiment was used to ensure that all the data analyzed originated from adult insects that survived the entire experimental period.

Experiment 4: No-Choice Experiment. The experiment was designed as a randomized complete block experiment with four genotypes and five replications per genotype with one plant representing one replication. Individual plants were enclosed in cylindrical enclosures that fit the round pots securely. The 75-cm-high cylinders were constructed of a 0.5-mm-thick PETG Vivak sheet (AIN Plastics, Madison-Heights, MI) that measured 15 cm in diameter and included two round (25 mm diameter) mesh-covered ventilation openings that were located opposite each other, ≈25 cm from the bottom of the enclosure. The top of the enclosure consisted of an access sleeve made of fine mesh screen, whereas the open bottom end was fit over the plant. After 3 d of acclimation on cowpea, 10 nonsexed insects were released on each plant. Insects on stems, petioles, leaves, and on the chamber walls, as well as dead insects, were counted daily for the first 7 d and then four additional times at 2-d intervals.

Statistical Analyses. The SAS software package (version 9.1; SAS Institute, Cary, NC) was used to analyze the data. The June 2006 release of PROC GLIMMIX was used to analyze the data using a generalized,

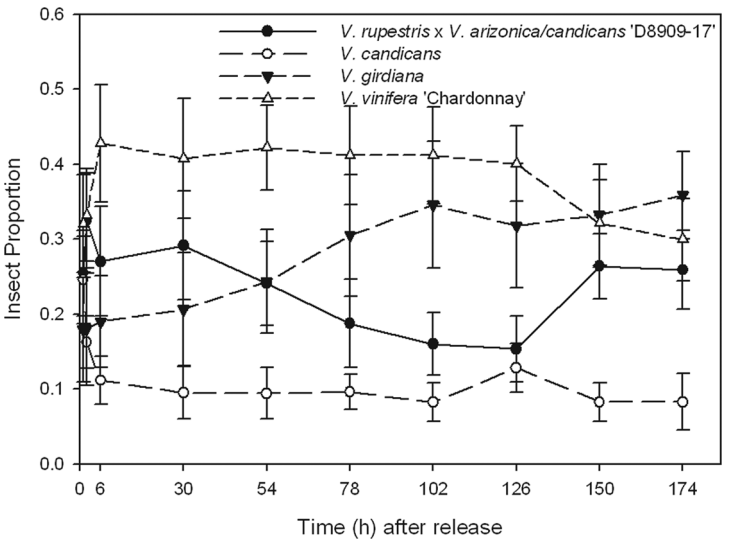

Fig. 1. Mean proportion (±SEM) of glassy-winged sharpshooters on four *Vitis* genotypes in a choice test without specific acclimation.

linear, mixed model approach using Gaussian or Poisson distribution. The Bonferroni adjustment was used for multiple comparisons to achieve a 5% experimentwise error rate. Results from xylem sap amino acid determinations were analyzed by analysis of variance (ANOVA) using PROC GLM, and mean separation tests were conducted using the Tukey-Kramer method ($P < 0.05$). Regression analyses for amino acid concentrations and insect preference were conducted using PROC REG.

Results

Experiment 1: Free-Choice Experiment without Specific Acclimation. Individual insects moved onto plants within minutes of release without apparent preference for any of the four genotypes. However, within the first 2 h of release, the insects started redistributing in a manner that was consistent with the observations made at 6 and 30 h postrelease (Fig. 1). Namely, more glassy-winged sharpshooters were observed on 'Chardonnay' and D8909-17 compared with *V. girdiana* and *V. candicans.* Statistical analysis across all time-points revealed a highly significant genotype main-effect ($F = 6.23$; df = 3,38.49; $P = 0.0015$) and time × genotype interaction ($F = 1.85$; df = 27,288.2; $P = 0.0074$) for the total number insects found on a plant (sum of stem, leaf, petiole, and tendril). However, the time main effect was not significant ($F = 1.74$; df = 9,267.4; $P = 0.0805$). Clear differences were obvious and consistent throughout the experiment between the numbers of insects that chose 'Chardonnay' versus those that chose *V. candicans* plants. In fact, statistical comparisons indicated significant differences ($P < 0.05$) between 'Chardonnay' and *V. candicans* for the observations in the time span from 8 to 104 h after release of the insects. When pooled across samples from 8 to 174 h, 9.7% of all insects found on plants were observed on *V. candicans*, whereas 38.8% were found on 'Chardonnay', and no significant changes were observed for either genotype with respect to experimental duration. Interestingly, the percentage of insects observed on D8909-17 decreased steadily from a maximum of 32.5% at 2 h to 15.3% at 126 h, but increased again to ≈26% at 150 and 174 h after release. In contrast, the number of insects present on *V. girdiana* increased from 18% at 2 h to 34.6% at 102 h and remained between 31 and 36% for the remainder of the experiment.

Across all genotypes, the majority of insects were observed on stem tissue. After the initial redistribution period within the first 30 h after release, insect presence averaged 89 ± 1.7% (SEM) on stems, 7.3 ± 1.4% on petioles, and 3.6 ± 1.2% on leaves. Within a genotype, the percentage of glassy-winged sharpshooters present on petiole and leaf tissues combined never accounted for >20% and averaged 10.7% (30–174 h) across all genotypes. Analysis of the number of insects observed on stems among the different genotypes revealed highly significant genotype ($F = 7.84$; df = 3,37.93; $P = 0.0003$) and time ($F = 3.46$; df = 9,265.6; $P = 0.0005$) effects. Significant time ($F = 7.00$; df = 9,281.8; $P = <0.0001$; $F = 3.42$; df = 9,275.4; $P = 0.0005$) and time × genotype ($F = 1.79$; df = 27,296.5; $P = 0.0111$; $F = 1.67$; df = 27,293.8; $P = 0.0222$) effects were found for the number of insects on leaves and petioles, respectively. During the first 6 h of the experiment, many insects that had initially settled on petioles and leaves moved to stems. On average across genotypes and the first two observations, the proportion of insects counted on petioles and leaves was 36.1% of all insects found on the plants, but averaged only 10.7% across all observations afterward. Insect presence on tendrils was only observed on rare occasions. The mean number of insects observed on inert surfaces was 1.7 individuals per cage (7% of the total number

Table 1. Mean amino acid concentrations (±SEM; μM) in the xylem sap collected from the four grape genotypes at the end of experiment 1 (THR and SER: df = 3,31; all other: df = 3,39)

Amino acid	'Chardonnay'	*V. girdiana*	D8909-17	*V. candicans*	*F*-values	*P* values
ASP	20.3 ± 1.6	26.0 ± 2.3	13.8 ± 2.3	21.3 ± 2.7	4.67	0.0094
THR	14.1 ± 2.0	11.8 ± 1.8	13.6 ± 2.8	8.9 ± 2.0	1.94	NS
SER	23.9 ± 3.8	13.8 ± 1.3	11.1 ± 2.0	9.2 ± 2.8	6.89	0.0025
ASN	31.5 ± 6.9	18.4 ± 4.8	19.2 ± 6.4	13.5 ± 4.9	2.09	NS
GLU	16.6 ± 1.9	20.6 ± 2.6	9.9 ± 1.9	14.8 ± 2.7	4.55	0.0105
GLN	201.1 ± 37.5	227.3 ± 19.2	214.4 ± 56.0	175.5 ± 24.8	0.57	NS
GLY	6.0 ± 0.6	6.6 ± 0.7	4.7 ± 0.9	6.4 ± 1.0	1.44	NS
ALA	5.6 ± 0.5	6.2 ± 0.7	4.6 ± 0.5	4.2 ± 0.7	2.46	NS
VAL	13.2 ± 1.5	12.8 ± 1.2	10.5 ± 2.1	7.0 ± 1.5	4.01	0.0175
MET	1.1 ± 0.5	0.6 ± 0.3	0.8 ± 0.4	0.0 ± 0.0	2.64	NS
ILE	5.3 ± 0.6	6.2 ± 0.6	2.8 ± 0.9	2.4 ± 0.7	7.70	0.0007
LEU	3.2 ± 0.6	4.4 ± 0.3	1.6 ± 0.6	0.6 ± 0.3	10.92	<0.0001
TYR	2.7 ± 0.6	3.6 ± 0.3	2.0 ± 0.7	2.5 ± 0.6	1.56	NS
PHE	5.2 ± 0.8	1.1 ± 0.5	2.9 ± 0.8	0.6 ± 0.4	9.22	0.0002
LYS	1.7 ± 0.5	2.4 ± 0.4	0.8 ± 0.4	2.2 ± 0.6	2.69	NS
HIS	5.4 ± 0.6	5.9 ± 0.4	4.1 ± 0.9	3.0 ± 0.5	6.30	0.0022
ARG	22.7 ± 3.1	39.4 ± 5.9	26.4 ± 7.2	51.1 ± 10.4	3.82	0.0211
PRO	2.4 ± 1.4	0.6 ± 0.6	0.0 ± 0.0	2.7 ± 1.4	2.41	NS
GABA	8.9 ± 1.0	8.3 ± 0.8	5.2 ± 1.8	8.4 ± 1.3	1.83	NS
Total	390.7 ± 39.8	416.0 ± 32.5	348.2 ± 73.9	334.2 ± 43.9	0.66	NS

NS, not significant.

of insects added to each cage), whereas the number of dead insects increased to an average of 6.3 (25.3%) individuals per cage by the last observation at 174 h.

Significant differences among genotypes were observed for nine amino acids (ASP, SER, GLU, VAL, ILE, LEU, PHE, HIS, and ARG), but the patterns among the genotypes were not consistent (Table 1). However, pairwise comparisons of the sum of GLU, VAL, ILE, LEU, PHE, and HIS was greater in 'Chardonnay' and *V. girdiana* than in D8909-17 and *V. candicans* ($P < 0.05$). Regression analyses of individual amino acids, sums of amino acids, or ratios of amino acids with the proportion (log-transformed) of glassy-winged sharpshooters observed on the different genotypes at the sampling before xylem sap collection did not reveal significant relationships (data not shown).

Experiment 2: Free-Choice Experiment with Acclimation on Each Grape Genotype. To test whether acclimation on each of the four genotypes used in

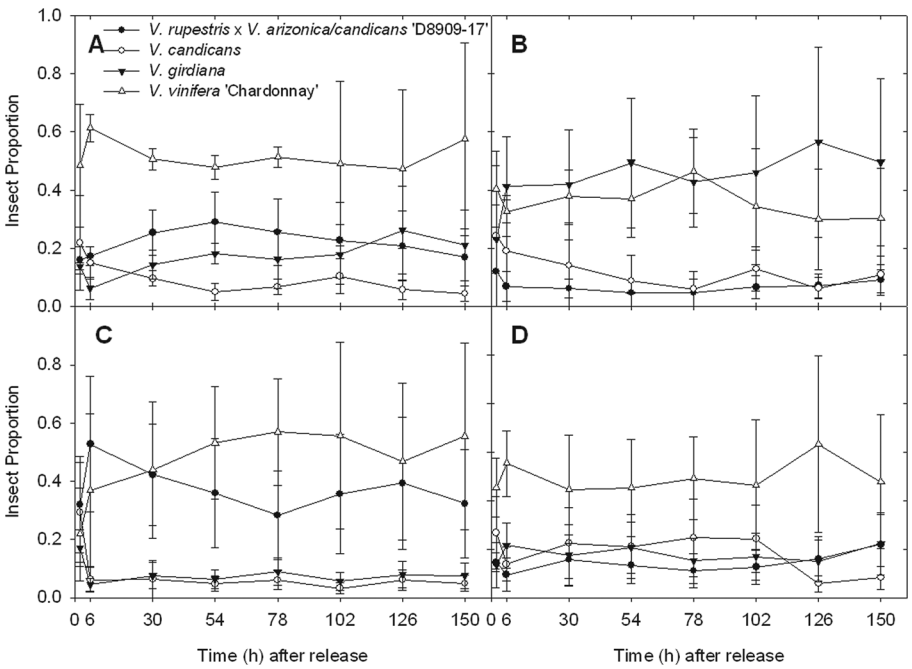

Fig. 2. Mean proportion (±SEM) of glassy-winged sharpshooters on four *Vitis* genotypes in a choice test with acclimation on (A) *V. candicans*, (B) D8909-17, (C) Chardonnay, and (D) *V. girdiana*.

Table 2. Comparison of mean percent *H. vitripennis* found on each grape genotype for the four acclimation treatments (averages across all observations)

Choice genotype	Acclimation genotype			
	D8909-17	'Chardonnay'	*V. candicans*	*V. girdiana*
D8909-17	6.7B	29.8A	19.2B	12.8B
'Chardonnay'	30.2A	35.9A	41.2A	38.9A
V. candicans	10.7B	7.4B	9.0C	15.6B
V. girdiana	34.7A	7.6B	15.0BC	15.6B

Values are percent insects.

Different letters within a column indicate significant differences among genotypes based on mean comparison by Tukey-Kramer ($P < 0.05$).

experiment 1 affected host selection in a free-choice experiment, *H. vitripennis* were exposed separately to each genotype for 3 d before release in cages containing all four genotypes. As observed for experiment 1, insects settled on the plants within minutes of release, and the distribution pattern observed throughout the duration of the experiment was established within the first 2–6 h after release (Fig. 2A–D). Statistical analysis for the total number of insects on the plants indicated significant effects for genotype ($F = 11.23$; df = 3,63.34; $P < 0.0001$), acclimation by genotype interaction ($F = 2.28$; df = 9,62.27; $P = 0.0276$), and time ($F = 2.95$; df = 7,207.3; $P = 0.0057$). When analyzed separately by plant tissue, acclimation and interactions with acclimation were not significant. However, significant effects of genotype were observed for stem ($F = 9.81$; df = 3,32.72; $P < 0.0001$) and petiole ($F = 5.49$; df = 3,36.83; $P = 0.0032$) tissues. The effect of time was significant for stem ($F = 5.02$; df = 7,184.8; $P < 0.0001$) and leaf ($F = 2.56$; df = 7,185.6; $P = 0.0152$) tissues. Across all acclimation treatments and genotypes, the proportion of the total number of insects found on a plant averaged 66.4% on stems, 9.4% on petioles, and 24.2% on leaves. Independent of acclimation treatment, 'Chardonnay' was always in the group of genotypes with the highest number of insects observed per plant, and three of four times, it was the genotype with the numerically greatest percentage of insects (Table 2). Conversely, *V. candicans* was always in the genotype group with the lowest number of insects per plant. In fact, except for the first time-point, differences between 'Chardonnay' and *V. candicans* were always significant ($P < 0.05$).

Experiment 3: Excreta Collection. The mortality of glassy-winged sharpshooter individuals confined on specific hosts for excreta collection increased slowly over time on D8909-17, *V. girdiana*, and 'Chardonnay' from ≈20% at 24 h to ≈45% at 160 h. In contrast, 75% of the insects confined on *V. candicans* died within the first 24 h. However, the insects that lived through the first 24 h remained alive throughout the experiment duration. This resulted in a significant time ($F = 4.10$; df = 5,74.42; $P = 0.0024$) and time × genotype effect ($F = 1.81$; df = 15,74.18; $P = 0.0491$) and a nearly significant genotype effect ($F = 3.36$; df = 3,11.78; $P = 0.0559$). Neither mortality after 160 h ($F = 1.44$; df = 3,11; $P = 0.2851$) nor the percentages of insects producing measurable amounts of excreta ($F = 1.74$; df = 3,11.2; $P = 0.2463$) differed among genotypes (Fig. 3). On average across all sampling dates, 77.5 ± 3.8% of insects produced measurable amounts of excreta. Although the average rate of excreta production was 4.54 gd^{-1} for insects confined on D8909-17 and only 2.96, 2.19, and 2.07 gd^{-1} on 'Chardonnay', *V. girdiana*, and *V. candicans*, respectively, excreta production did not differ significantly ($F = 1.59$; df = 3,8.018; $P = 0.2664$) among insects confined on the four genotypes (Fig. 4). Normalization of excreta production for insect dry weight did not result in significant

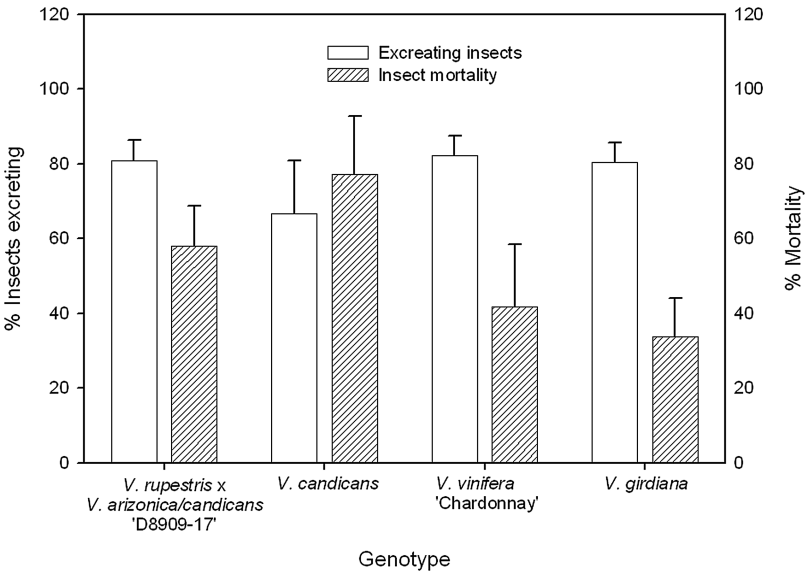

Fig. 3. Mean mortality and mean percentage (±SEM) of glassy-winged sharpshooters producing excreta on four *Vitis* genotypes averaged over all sample intervals (24 h through 160 h).

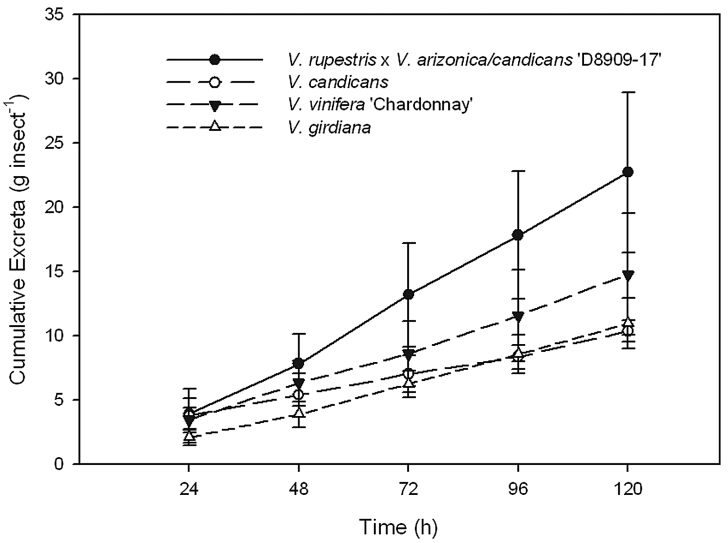

Fig. 4. Mean cumulative excreta production (±SEM) per glassy-winged sharpshooter on four *Vitis* genotypes over time.

differences among insects confined on the four genotypes ($F = 1.16$; df = 3,13.14; $P = 0.3636$). On average, the amount of excreta produced by insects confined on D8909-17, 'Chardonnay', *V. candicans*, and *V. girdiana* corresponded to 422-, 316-, 306-, and 236-fold the insect dry weights, respectively.

Experiment 4: No-Choice Experiment. Adult glassy-winged sharpshooters confined on individual plants were observed over a 15-d period. Mortality and position of the insects on test plants were recorded. Significant time ($F = 23.00$; df = 10,150; $P < 0.0001$) and genotype ($F = 4.68$; df = 3,17.9; $P < 0.0139$) effects were observed for insect mortality (Fig. 5). On 'Chardonnay' plants, the percentage of dead insects increased linearly (≈4.1%/d) throughout the duration of the experiment. In contrast, quadratic functions described insect mortality on D8909-17 ($R^2 = 0.99$ versus 0.96), *V. girdiana* (0.97 versus 0.90), and *V. candicans* (0.99 versus 0.89) better than linear functions. Differences in mortality were particularly pronounced between *V. candicans* and 'Chardonnay,' with insects on *V. candicans* dying at a rate almost three-fold that of insects confined on 'Chardonnay' over the first 6 d of the experiment (Fig. 5). The mortality rate of insects on *V. girdiana* and D8909-17 were similar (7.6 versus 6.6%, respectively) throughout the first 7 d, after which mortality rate started to differ mainly because of a reduction in mortality in the *V. girdiana* treatment.

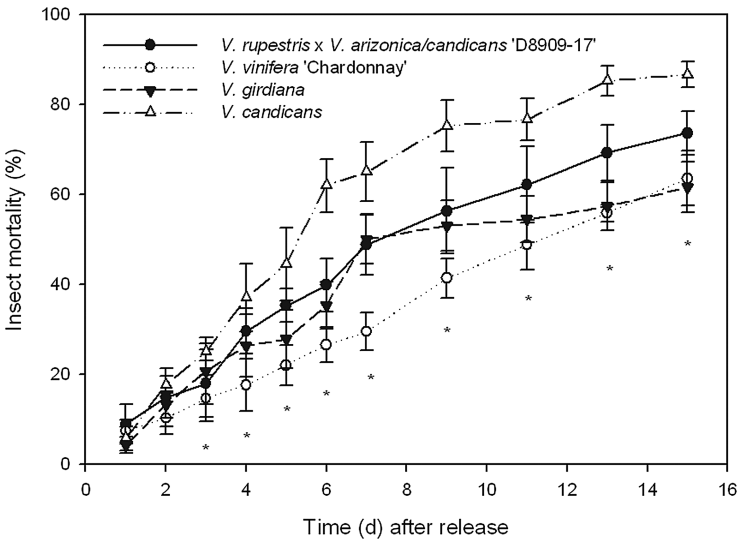

Fig. 5. Mean mortality (±SEM) of glassy-winged sharpshooters on four *Vitis* genotypes in a no choice experiment. *Significant differences among genotypes at $P < 0.01$ (data were sqrt-transformed for analysis; untransformed data shown).

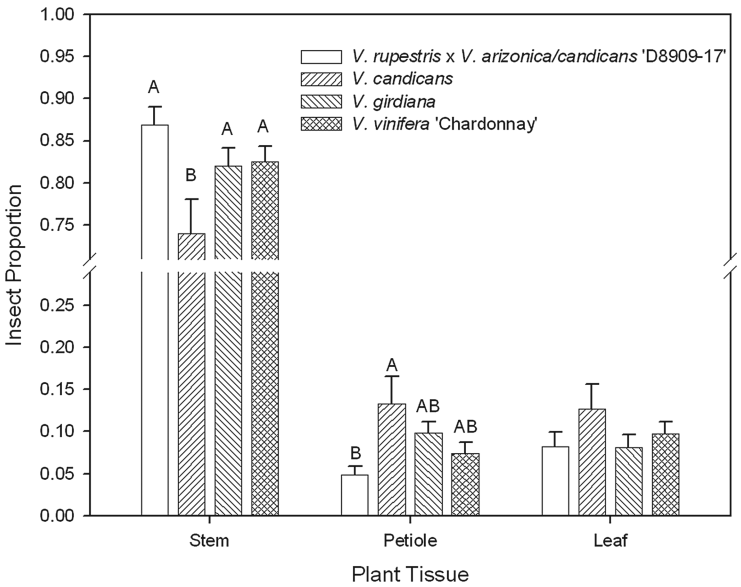

Fig. 6. Mean proportion (±SEM) of glassy-winged sharpshooters observed on different plant parts of four *Vitis* genotypes in a no-choice experiment.

In all treatments, the vast majority of insects were found on the plant stems throughout the experiment (Figs. 6 and 7). Significant time ($F = 10.93$; df = 10,135.5; $P < 0.0001$) and genotype ($F = 18.94$; df = 3,15.36; $P < 0.0001$) effects were documented for insects observed on stem tissue. Trends toward increasing proportions of insects on stems over time observed in all treatments were consistent with significant time effects for leaf ($F = 12.27$; df = 10,136.3; $P < 0.0001$) and petiole ($F = 10.87$; df = 10,134.5; $P < 0.0001$) tissues. The number of insects observed on stems was smallest on *V. candicans* ($P < 0.05$) but did not differ among the remaining genotypes when averaged across all time-points. In contrast, no significant differences were found among genotypes for insects observed on petioles and leaves.

Discussion

Choice experiments with and without specific acclimation resulted in significant grape genotype effects on glassy-winged sharpshooter distribution. In all choice treatments, distribution patterns were evident within the first few hours after insect release (Figs. 1 and 2). Overall, 'Chardonnay' was the most preferred host, whereas *V. candicans* was least preferred. On

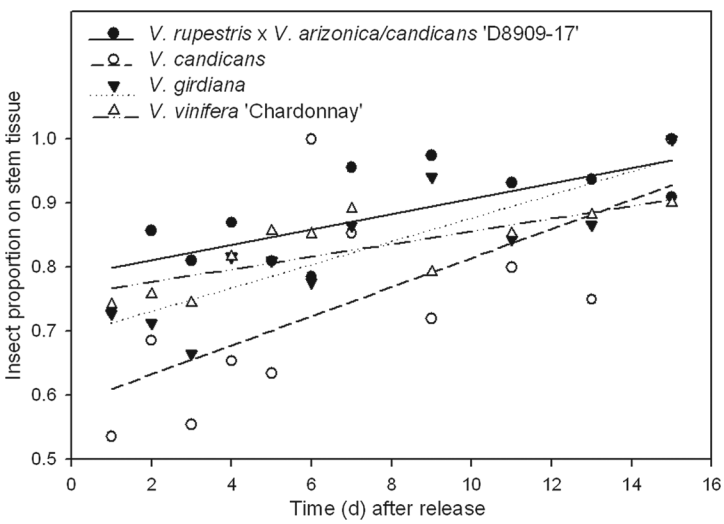

Fig. 7. Proportion of glassy-winged sharpshooters observed on stem tissue of four *Vitis* genotypes over the duration of a no-choice experiment.

average across both choice experiments, 42% of the insects observed on plants were found on 'Chardonnay' compared with 12% on *V. candicans.* Insect selection of *V. girdiana* and D8909-17 hosts was not as consistent as for 'Chardonnay' and *V. candicans.* Glassy-winged sharpshooters acclimated on D8909-17 preferred *V. girdiana* over D8909-17, whereas those acclimated on 'Chardonnay' preferred D8909-17 over *V. girdiana* (Fig. 2). In addition, glassy-winged sharpshooters released into the choice experiment without specific acclimation initially chose D8909-17 over *V. girdiana,* but as time progressed, more insects were observed on *V. girdiana* than on D8909-17 (Fig. 1).

These observations suggest that xylem sap composition may be an important component in glassy-winged sharpshooter host selection. Although other factors such as plant morphology, color, and physiology can affect insect host selection, the results of choice experiments conducted after specific acclimation on the four grape genotypes are consistent with other studies that indicate the importance of gustatory signals for host plant selection by leafhoppers in general (Backus and McLean 1985, Backus 1988) and glassy-winged sharpshooters in particular (Brodbeck et al. 1990, Andersen et al. 2005). Andersen et al. (2005) recently studied glassy-winged sharpshooter abundance and feeding on field-grown plants of numerous grape cultivars from five different species. They reported that insect abundance was positively correlated with total amino acid concentration and percent glutamine in the xylem sap and that glassy-winged sharpshooter consumption rate was positively correlated with insect abundance. Among the 19 amino acids, 7 organic acids, and 3 sugars determined in the xylem sap collected, the glutamine:proline ratio was most consistently associated with glassy-winged sharpshooter abundance and consumption rate in their study (Andersen et al. 2005). The importance of glutamine as well as asparagine has been suggested (Brodbeck et al. 1990). They reported positive correlations between glassy-winged sharpshooter host plant selection and the levels of these particular amides. Brodbeck et al. (1990) and Bi et al. (2005) recently observed seasonal glassy-winged sharpshooter population shifts between orange (*Citrus sinensis* L.) and lemon (*C. lemon* L.) trees that coincided with changes in xylem sap amino acid compositions, further suggesting that amino acids may influence adult glassy-winged sharpshooter host selection. In light of these studies implicating amino acids as important cues for host plant selection, the absence of significant relationships between amino acid composition and glassy-winged sharpshooter host selection in our study was unexpected and suggests that other factors may be involved. Potential reasons for the absence of a correlation between amino acid composition and host plant selection in this study may include factors such as semiochemical compounds, which may influence host plant selection, differences in amino acid composition influenced by the unique experimental setup (low light environment and high soil moisture), the timing of xylem sap collection (at the end of experiment 1, ≈22 h after the last insect count), or the low concentrations of amino acids in the xylem sap compared with those reported by Andersen et al. (2005). Although plants can buffer xylem sap composition substantially in response to soil moisture changes, light is an important factor influencing xylem chemistry (Andersen and Brodbeck 1989, Andersen et al. 1992, 1995.

Overall, results of the two choice experiments support the hypothesis that chemical signals may play a critical role in glassy-winged sharpshooter host plant selection. Interestingly, as indicated by the significant time by genotype interaction observed for experiment 1, host plant preference changed over time between D8909-17 and *V. girdiana* (Fig. 1). The decrease in number of insects observed on D8909-17 between the 2- and 126-h count could indicate the induction of a deterrent in response to glassy-winged sharpshooter feeding. Production of, as well as changes in, the activity of defensive compounds by plants has been shown to affect insect performance (Fritz and Simms 1992, Zangerl and Berenbaum 1993, Karban and Adler 1996, Karban and Baldwin 1997, Agrawal 1998, Agrawal et al. 1999). Alternatively, shifting glassy-winged sharpshooter preference for D8909-17 could have also been caused by a disconnect between insect requirements and xylem sap composition of D8909-17, thus inducing insects to find a new host that would complement or more completely satisfy their nutritional requirements. In fact, results from the 3-d acclimation of glassy-winged sharpshooters on D8909-17 indicate strong selection against the D8909-17 genotype (Fig. 2), suggesting that the response observed in experiment 1 may be the result of insect requirements rather than induction of a plant defense compound. Except for acclimation on 'Chardonnay', the acclimation genotypes were always among the least preferred genotypes. The observed preference pattern may be a consequence of dietary self-selection to obtain a favorable nutrient balance (Waldbauer and Friedman 1991).

In general, the vast majority of glassy-winged sharpshooters were observed on stem tissue. In the choice experiments, no consistent differences were observed in insect proportions within plant among genotypes. Averaged across both choice experiments and all treatments, 78% of insects were found on stems, 8% on petioles, and 14% on leaves (includes all time-points after the first 24 h). In the no-choice experiment, the proportion of insects found on stems was significantly smaller for *V. candicans* than for the other three genotypes, but was greatest, although not significantly different from *V. girdiana* and 'Chardonnay', on petioles (Fig. 6). In the no-choice experiment, the proportion of insects observed on stem tissue increased consistently across all genotypes over time (Fig. 7). On the whole, these results indicate that stem tissue is likely the best feeding site for glassy-winged sharpshooters independent of grape genotype.

Glassy-winged sharpshooter consumption rates, as measured by excreta production per insect and per insect dry weight, were not significantly affected by grape genotype in this study. Even though average excreta production per unit dry weight tended to be greater (1.8-fold) for insects feeding on D8909-17 than those feeding on *V. candicans*, the genotype effect was not significant because of large variation. Because xylem sap composition was not analyzed in parallel with excreta collection, it is unknown how observed consumption rates relate to the nutrient content of xylem sap. However, Andersen et al. (2005) found that consumption rates were positively correlated with xylem sap amino acid concentration.

Although the average percentage of excreta-producing insects was not significantly influenced by grape genotype, mortality was greatest on *V. candicans.* This is consistent with insect mortality dynamics observed in the no-choice experiment. Insect mortality was significantly affected by time, and mortality trends over the duration of the experiment were modulated by grape genotype. Five days into the no-choice experiment, insect mortality on *V. candicans* was nearly 50%, whereas >75% of insects were still alive on 'Chardonnay' for which a mortality level of 50% was reached only after ≈6 d (Fig. 5). Mortality trends recorded on *V. girdiana* and D8909-17 were generally between those of *V. candicans* and 'Chardonnay.'

Overall, the data presented in this study show that glassy-winged sharpshooters show preference among grape genotypes and that acclimation influences the selection. Additionally, grape genotype influenced glassy-winged sharpshooter mortality but did not have a significant effect on excreta production in this study. Generally, *V. candicans* was the genotype least preferred by glassy-winged sharpshooters and had the largest mortality rates. In contrast, 'Chardonnay' was usually preferred over other genotypes and induced the lowest mortality rates. It is important to remember that the plants used for this study were young and grown in pots under greenhouse conditions and that the experiments were conducted under low-light conditions with the soil maintained fully saturated throughout all experiments. Therefore, glassy-winged sharpshooter host selection behavior, with respect to the four grape genotypes examined in this study, may be different for older plants grown under field conditions. In addition, aspects of reproductive success and nymphal behavioral characteristics were not examined, but would certainly be of consequence to pathogen transmission and thus disease epidemiology. Nonetheless, the results presented here indicate that grape genotype characteristics influence glassy-winged sharpshooter behavior, which may have implications in terms of *X. fastidiosa* transmission and Pierce's disease epidemiology. Although the reasons for the preference dynamics observed in this study need further study, the observed results show that grape genotype characteristics influence vector behavior and that breeding efforts and vineyard management options could be explored to exploit glassy-winged sharpshooter host selection within a vineyard. Future research to pinpoint the traits resulting in particular host selection behavior of the vector hold further promise for targeted breeding and would likely open new avenues in vineyard management to control Pierce's disease.

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