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Seasonal Transmission of *Xylella fastidiosa* by GWSS from Grapevines Infected for Various Lengths of Time

Project Investigator:

Thomas M. Perring Department of Entomology University of California Riverside, CA 92521 thomas.perring@ucr.edu

Cooperators:

Jung Joon Park	Tracy R. Pinckard	Charles A. Farrar
Department of Entomology	Department of Entomology	Agricultural Operations
University of California	University of California	University of California
Riverside, CA 92521	Riverside, CA 92521	Riverside, CA 92521
Russell L. Groves Department of Entomology University of Wisconsin Madison, WI 53706	Mark Sisterson USDA-ARS Agricultural Sciences Stn. 9611 S. Riverbend Ave.	

Parlier, CA 93648

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Introduction:

Pierce's disease (PD), a disease of grapes caused by the bacteria, *Xylella fastidiosa* Wells et al., was described in California in the 1880s during an epidemic in Orange County (Pierce 1882). A second epidemic occurred in Tulare County in the 1930s (Hewitt et al. 1949), and until the mid-1990s, it was considered only a minor problem in vineyards close to riparian areas. In the early 1990s a new vector, the glassy-winged sharpshooter (GWSS), *Homalodisca vitripennis* (Germar) (formerly *Homalodisca coagulata* Say), was introduced into the state (Sorenson and Gill 1996), and became associated with a devastating epidemic of PD in the Temecula Valley. Since 1994, at least 1,500 acres of vineyards have been lost to the disease in California; in the Temecula Valley alone, losses have been estimated at \$13 million (Wine Institute 2002).

The GWSS has different feeding and dispersal capabilities than native insect sharpshooter vectors and these attributes are thought to have contributed to the increased number of PD-infected grapevines in California (Almeida et al. 2005a, Blua et al. 1999, Redak et al. 2004). Like other insect-borne plant pathogen systems, there are two potential types of pathogen spread: primary or secondary spread. Primary spread occurs when the pathogen is obtained by the vector from sources outside the crop and transported and inoculated into the crop. Secondary spread occurs when the vector acquires the pathogen from infected vines in the vineyard, and

subsequently inoculates healthy vines within the same vineyard (i.e. vine to vine spread). It is thought that *X. fastidiosa* spread with native California vectors was the result of primary spread, but that rapid spread by GWSS may be the consequence of primary and secondary spread (Almeida et al. 2005a, Hill 2006). GWSS landing and feeding behavior and tissue feeding capacity combine with grapevine phenology, and within-vine *X. fastidiosa* distribution and phenology to make vine to vine spread possible. Our overall goal is to provide information on these various components to enhance our understanding of vine to vine spread so that strategies can be defined to reduce widespread epidemics in other regions.

Objectives, Activities, Progress and Findings:

The objectives of this project were:

- 1. Document GWSS feeding preference, through the growing season, on established Cabernet Sauvignon and Chardonnay grapevines that either are healthy or have been infected with *X*. *fastidiosa* for 2, 3, or 4 years.
- 2. Evaluate the acquisition by GWSS, through the growing season, from established Cabernet Sauvignon and Chardonnay grapevines that either are healthy or have been infected with *X*. *fastidiosa* for 2, 3, or 4 years and determine the subsequent transmission from these acquisitions.
- 3. Determine the relationship between *X. fastidiosa* inoculation by GWSS at different times of the year and the development of the vine as a source for further acquisition by GWSS.

Grapevine Inoculation

All experiments in this project were conducted at the Agricultural Operations Research Farm on the University of California Riverside campus. Cabernet Sauvignon and Chardonnay grapes on 3309 rootstocks were planted in early 2003, with 6ft. between the vines and 8ft. between the rows of the varieties. In order to exclude potential GWSS vectors from feeding on the vines, large screen cages, covered with 60% shade-cloth, were built around the vines, with 6 vines of each variety per cage. Twelve cages were established, but we used 11 of them for our studies. Vines were randomly chosen for inoculation and one vine of each variety per cage was mechanically (needle) inoculated at 3 locations on the vine (at least 6 inches from the main cordon) with 20ul of X. fastidiosa, Temecula PD strain. Inoculations were done in May of 2003, 2004, and 2005. Xylella fastidiosa infection was verified with ELISA one year after inoculation, and this process was done in 2004 (for the 2003 inoculations), and 2005 (for the 2004 inoculations). However, infection was not verified in 2006 (for the 2005 inoculations). An evaluation of all the vines in August 2007 showed almost no vines infected with X. fastidiosa. It is unclear why the inoculations did not become systemic, but the fact that we had no multi-year infections dictated a revision of our original objectives. We re-inoculated the set of vines that had been inoculated in 2003 by scraping the bark on the cordons to expose green tissue for needle inoculation. This procedure was done on November 5, 2007 and September 8, 2008 and vielded severe infections.

While waiting on vines to become infected, we focused our efforts on objective 1; this consisted of choice tests and no-choice tests.

Choice Tests for Grapevine Tissue Selection

Individual GWSS adults were placed in observation cages fabricated from acetate cylinders (25cm x 17cm diameter) with organdy sleeves attached to the ends (Figure 1). The cages were placed over the base of a single Cabernet Sauvignon or Chardonnay grapevine cane with the cane terminal looped back into the cage. The ends of the observation cage were sealed giving a single GWSS in each cage access to old and young stems, petioles, and leaves inside the cage. We made hourly observations during daylight hours over three consecutive days to determine the location of each GWSS. Studies were conducted in the Fall 2007 (29 August and 11 September 2007), Winter 2008 (16 January and 6 February 2008) and Summer 2008 (1 July 2008).

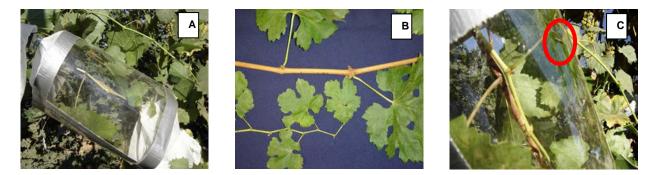


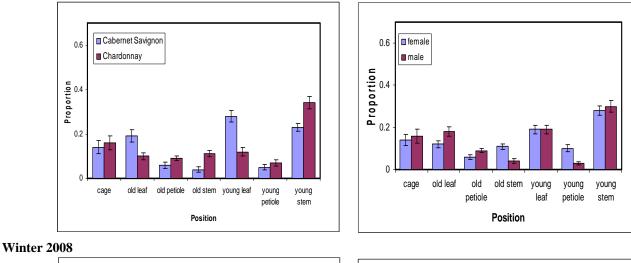
Figure 1. A. Cage enclosing cane base and growing tip for GWSS observation. B. Cane, petiole, and leaf blade tissue of base of cane (top) and cane growing tip. C. Close-up of old and young cane tissue and GWSS adult feeding on leaf blade (circle).

Results of the two fall trials were pooled, as were the results of the two winter trials. In the fall, GWSS were found on the cage in 14% and 16% of our observations on Cabernet Sauvignon and Chardonnay vines, respectively (Figure 2). We also found that a high proportion (35%) of GWSS, averaged across variety and gender, switched from one tissue to another each hour (data not shown). Clearly, GWSS moved frequently among the vegetation, important for the spread of bacteria within and among vines. When GWSS were present on the canes, they utilized all tissues with no consistent preference for any type. However, over the course of the trial and averaged across both varieties, GWSS were found more frequently on young tissue (18.2%) than on old tissue (10.7%). Looking further at the data, GWSS were found more frequently on young stems, petioles and leaves (28.5%, 6%, and 20%, respectively) than on old stems, petioles and leaves (7.5%, 7.5%, and 14.5%, respectively). Interestingly, the insects spent the least amount of time on petiole tissue of any age than on any other tissue type. There also were some interesting results with respect to variety. GWSS were found more frequently on leaves (old and young) of Cabernet Sauvignon compared to the leaves of Chardonnay while the reverse was seen for petioles and stems (old and young). These results suggest that the two grapevine varieties vary in the xylem components that are important for GWSS feeding, a result that could impact the location where X. fastidiosa cells are introduced into healthy grapevines. To finish the discussion of this trial, there appeared to be little difference between sexes in their selection of feeding sites (Figure 2).

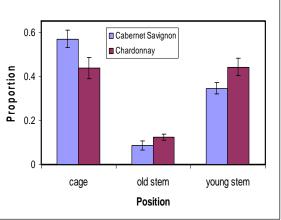
In the winter trial, GWSS were found on the cage walls in 49% of our observations. At this time of year, neither leaves nor petioles were available to the sharpshooters, and GWSS were found on old stems and young stems in 11% and 40% of the observations, respectively. Those tissue preferences differed somewhat among the two varieties and the two sexes (Figure 2). The major departure from these numbers was the preference for the old stem among sexes; females and males were on the old stem in 20% and 1% of the observations, respectively. The general preference for the young stem over the old stem was consistent among varieties and among sexes. Changes in GWSS position occurred in 14% of the observations, considerably less than the 35% exhibited in the fall 2007 trials. There was little difference in the tendency of GWSS to change positions among variety or sexes.

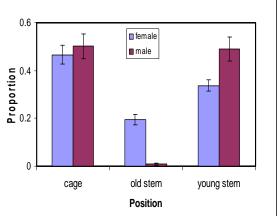
The summer trial again offered GWSS young and old leaf and petiole tissue in addition to young and old stems. GWSS were found on the cage wall 12% of the time (Figure 2). The general preference for young tissue that was found in the fall and winter also occurred in the summer. GWSS chose young leaves, petioles, or stems in 67% of the observations compared to 21% for the older tissues. The young stem was the preferred tissue, both among varietals and among sexes. However, there were some differences in tissue selection among varietals and among sexes. The old stem was selected 24% of the time on Cabernet Sauvignon but only 5% of the time on Chardonnay. The young leaf and young petiole each were selected in 1% of the observations on Cabernet Sauvignon, while they were selected 8% and 7% of the time on Chardonnay. Among sexes, females chose the old stem in 22% of the observations, but males chose that tissue in only 7% of the observations. Among tissue types of any age, leaves, petioles, and stems were chosen in 12%, 5%, and 83% of the observations, respectively. Changes in GWSS position occurred in 21% of the observations, and that rate of change was consistent among the varietals and among the sexes.

Figure 2. GWSS preference on field-grown Cabernet Sauvignon and Chardonnay grapevines in choice experiments initiated on 29 August and 11 September 2007 (Fall 2007), 16 January and 6 February 2008 (Winter 2008) and 1 July 2008 (Summer 2008). Bars represent average proportions of GWSS (\pm SE) observed on various tissue types for the two varieties and for the two GWSS genders.

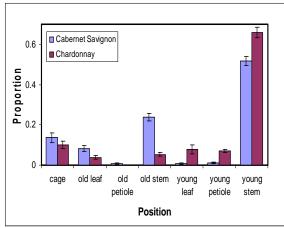


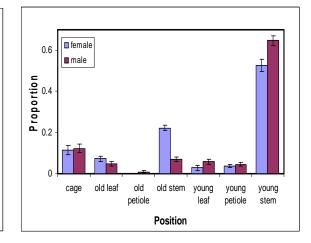












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No-choice Tests Quantifying Feeding on Grapevine Tissues

No-choice studies were conducted in the Winter 2008 (26 February, 4 March), Summer 2008 (15 July), and Fall 2008 (19 September). Individual GWSS were caged on selected grapevine tissue in 50 ml polypropylene centrifuge tubes (Thermo Fisher Scientific Inc., Waltham, MA) by one of two methods. The first method, modified from Andersen et al. (1992), was for use on cordons, stems, and petioles. The cages were made by melting a transverse hole in the side of the tube using hot metal cylinders of diameters similar to the grape tissues. The tube was pressed onto the plant tissue, so the GWSS had access to about 2.5 cm length of the plant through the hole (Figure 3). The cage was affixed and sealed to the tissue by wrapping the tube and tissue with ca. 2 cm wide strips of Parafilm (Pechiney Plastic Packaging, Menasha, WI). The screw cap was tightened, and the cage rested vertically so that excreta collected in the bottom of the tube. The second cage design was for use on leaf tissue. The mouth of an intact 50 ml tube was pressed to the abaxial leaf surface with a piece of coiled spring steel in a clothes-pin like fashion (Blua and Perring 1992). One end of the spring held the 50 ml tube. The other end of the spring had a plastic ring on which was glued a foam pad 1 cm thick by 3 cm in diameter which gently held the leaf against the polypropylene tube, giving the insect access to leaf tissue of ca. 5.7 cm². This cage, too, was oriented vertically, so excreta drained to the bottom of the cage. Each cage type was loosely covered with aluminum foil in order to shade it from direct sunlight.

The day before the start of each test, GWSS adults were collected from citrus trees at Agricultural Operations, UCR, and placed in a cage with a potted rough lemon plant. The following morning, adults were isolated and sexed and then placed individually into the tube cages. Cages were inspected daily and the presence of excreta noted. Cages with dead GWSS were removed, and the amount of excreta was weighed. At the end of the trial, all remaining cages were collected, GWSS mortality was noted, and excreta was weighed.







Figure 3. Cages used on cordons (A), stems and petioles (B), and leaf blades (C) in no-choice studies.

During the winter trials, GWSS were placed on cordons, old stems, and young stems; leaves and petioles were not available. The overall GWSS feeding rate was 0.37 g of excreta per day, but there was considerable variation among sharpshooters (Figure 4). In no case did discernible feeding occur on cordons, tissue several years old with thick dry bark. The old stems were covered with dry, but much thinner bark. Feeding on the old stem averaged 0.92 g of excreta per day and on the young stem, 0.57 g, however those amounts were not significantly different at p=0.05. There were no significant differences in feeding among varietals or among the sexes. Survivorship in the winter trials averaged 2.04 days, and there were no significant differences in survivorship among varietals or sexes. There were significant differences in survivorship among GWSS on different tissues (Figure 4). Of 29 GWSS on cordons, only 6 lived into the second day for an average survivorship of 1.2 days, significantly less than on the other tissues. Among all

insects, only one insect that produced no excreta survived as long as 3 days, and only one insect that produced excreta died before the end of the trial.

Sharpshooters fed on all tissues except cordons in the summer trial (Figure 4), averaging 0.51 g of excreta per day. Feeding on non-cordon tissues was highly variable, but there were some significant differences. Sharpshooters produced significantly more excreta on young stems than on young petioles, old leaves, and cordons. There were no significant differences among varietals, sexes, or tissue age (i.e. old leaves, petioles, and stems vrs. young leaves, petioles, and stems). Among tissue types there were significant differences in feeding. Significantly more excreta was produced on stems (0.92 g) than on petioles (0.45 g), leaves (0.41 g), and cordons (0 g), and the amount of excreta from the petioles and leaves was significantly greater than from the cordons. Average GWSS survivorship in the July trial was 4.06 days. As in the winter, only survivorship on cordons was significantly less than that on other tissues (Figure 4). Other than cordons, there were no significant differences among leaves, petioles, and stems. In addition, survivorship among varietals and among sexes was not significantly different.

In the fall trial, GWSS again fed on all tissues except cordons (Figure 4), averaging 0.229g of excreta per day (range 0-1.18g). This was less excreta than that produced by sharpshooters feeding in the winter (0.37g) and summer (0.51g) trials. While we are not sure why this reduction in feeding might have occurred, it may signal a natural decline in feeding as the sharpshooters enter the winter months. There was substantial variation among GWSS feeding in this trial (Figure 2). While it appears that GWSS feeding on old stems and young stems were nearly the same as the other non-cordon tissue, the means in this case are misleading. For the old stem, there were only 2 GWSS that survived longer than 1 day and of these 2 only 1 produced any measurable excreta (0.168g). On the young stems, only 5/20 GWSS survived longer than 1 day, and these insects produced an average of 0.24g of excreta per day (range 0.014-0.779g). This is a contrast to the summer trials, during which the insects survived well on the young stems. We noticed that in the fall trial, the young stem tissue had become hardened and woody, and while GWSS were able to feed on this tissue in the summer, they were not able to do so in the fall. It also is interesting that survival on old stem tissue seemed much better in the winter than in the fall. This may be due to the adaptability of GWSS that were field collected for our trials. In the winter months, GWSS may be better adapted for feeding on woody tissue than populations in the fall. Survival was consistently high on the leaves and petioles and production of excreta was consistent with this survival. The tissue yielding the most excreta was the young petiole (0.311g/day), followed by young leaves (0.233g/day), and old leaves (0.208g/day).

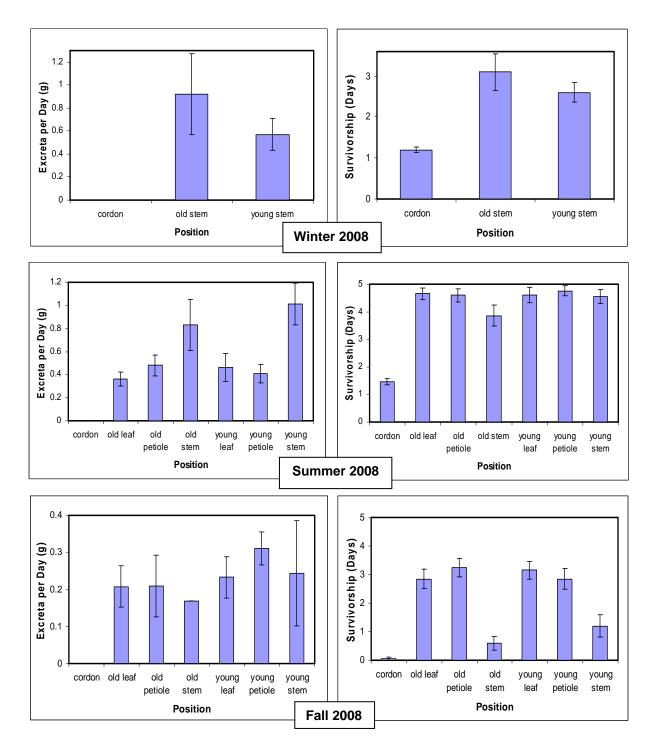


Figure 4. GWSS feeding on field-grown Cabernet Sauvignon and Chardonnay grapevines in no-choice experiments conducted in Winter 2008, Summer 2008 and Fall 2008. Bars represent average amount of excreta/day (\pm SE) and average GWSS survivorship (\pm SE) measured from various tissues.

With the unfortunate lack of Pierce's disease in our caged grapevines, we were forced to modify the original objectives 2 and 3. Using the infected vines that we inoculated on November 5, 2007 and September 8, 2008, we initiated research to determine sharpshooter preference for infected grapevine tissue. We selected canes from putative infected and non-infected Cabernet Sauvignon and Chardonnay grapevines to study GWSS choice for infected or non-infected tissue. Trials were conducted with GWSS on 19-21 February and 25-27 February 2009. Because of the

time of year, there were no leaves or petioles on the canes. All tissue had a brown hardened outward appearance, but we confirmed that the internal tissue was green, so GWSS would be able to feed. We placed GWSS adults individually in observation cages, which were placed over a section of cane from an infected vine and a section of cane from a non-infected vine (Figure 5). The infected cane was marked with a small wire label. All sharpshooters were placed on the cage, not on plant tissue, so they were forced to make a choice of where to feed. The ends of the observation cage were sealed giving a single GWSS in each cage access to infected or non-infected cane tissue. Twenty cages were used for each trial. We made hourly observations from 8am to 5pm over three consecutive days to document the cane (infected or non-infected) on which the GWSS fed.



Figure 5. Acetate cage uses to evaluate GWSS feeding preference for infected (marked with yellow wire label (in circle) and non-infected grapevine tissue. Notice GWSS feeding in center of infected cane (arrow).

At the conclusion of the studies, we determined the infection status of the canes used in the experiment and discarded the cages in which we were unable to make a confident determination. Cages in which the GWSS died also were discarded, because this indicated the inability of the insect to successfully feed on either cane. This filtering resulted in 9 total cages for the 19-21 February trial (4 Cabernet Sauvignon, 5 Chardonnay, 4 females and 5 males) and a total of 11 cages for the 25-27 February trial (4 Cabernet Sauvignon, 7 Chardonnay, 6 females, and 5 males). Because of the small numbers present in each variety and gender, the data are presented as totals for each trial.

Results from both trials showed that GWSS was found more often on the infected vines (Figure 6). For the 19-21 February test, GWSS were present on the infected tissue 71% of observed times, while they were on non-infected tissue just 22% of the time. They were found on the cage only 7% of the time. In the second trial (25-27 February), they again were found more often on the infected cane (71%) compared to the non-infected cane (22%) or the cage (7%). We were surprised that the proportions for each of these trials were the same, and have no explanation for this similarity. This is particularly remarkable, given that there was a total of 215 observation times in the first trial and 303 observation times in the second trial (Table 1) and the two trials were conducted with different insects on different canes, often from different vines, and at two distinct times.

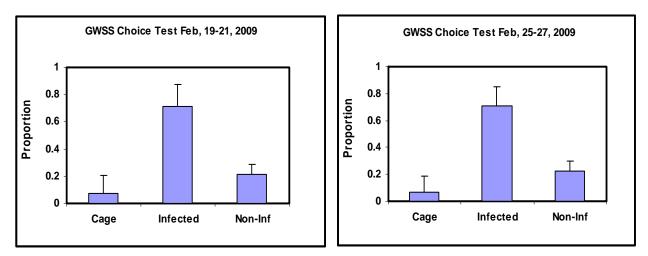


Figure 6. GWSS preference on field-grown Cabernet Sauvignon and Chardonnay grapevines in choice experiments initiated on 19 February (left) and 25 February (right), 2009. Bars represent average proportions of GWSS (\pm SE) observed on the cage, on the infected canes, and on the non-infected canes.

Also interesting were the movements that sharpshooters made throughout the studies. More GWSS moved to infected canes and stayed for 3 or more hours than to non-infected canes (Table 1). Additionally, there were more sharpshooters that fed on infected canes, left these canes and returned to the infected canes, than those on non-infected canes. Clearly there was something unique about the infected canes that the sharpshooters preferred. It also is apparent that sharpshooters in this study moved about the cages often (17 of a possible 215 observations in trial 1 (8%) and 36 of a possible 303 observations (12%) in trial 2).

Parameter	Trial 1 (Feb 19-21)	Trial 2 (Feb 25-27)
Chose Infected and stayed 3h or more	12	13
Chose Non-Infected and stayed 3h or more	3	3
Chose Inf. for 3h, left, returned for 3h or more	3	4
Chose Non-I for 3h, left, returned for 3h or more	0	0
Moved from Cage to Inf.	7	12
Moved from Cage to Non-I	1	7
Moved from Inf. to Cage	5	5
Moved from Non-I to Cage	1	4
Moved from Inf. to Non-I	1	4
Moved from Non-I to Inf.	2	4
Total number of Times insect moved	17	36
Total number of Observed Times	215	303

Table 1. Actions taken by GWSS in two trials (February 19-21 and February 25-27, 2009). Sharpshooters were given a choice between infected and non-infected cane tissue over the 3 day period and observations were made hourly during the daylight hours.

A second set of choice experiments was conducted in September, 2009. These studies, which had the same design as those conducted in February, utilized infected canes that were severely diseased. A healthy, asymptomatic cane was paired with each diseased cane and the canes were stripped of all but 1 leaf within the experimental cage. Twenty cages were established on Chardonnay vines on September 17, and into each cage we introduced a single GWSS female. Observations were made hourly from 8am to 6pm for 3 days. Utilizing the same 20 cages on the same canes, a second trial was initiated on September 20 with 20 female smoketree sharspshooters (STSS). Observations again were made each hour from 8am to 6pm for a period of three days.

Sharpshooter responses from these trials were distinctly different from the studies conducted in February. In the September 17-19 trial, a slightly higher proportion of GWSS were observed on the non-infected cane (56%) than on the infected canes (40%), with just 4% of the observations on the cage (Figure 7). Interestingly, similar results were found for the STSS. This species showed a slight preference for the non-infected canes (51%) rather than the infected canes (40%), with 9% of the observations on the cage (Figure 7).

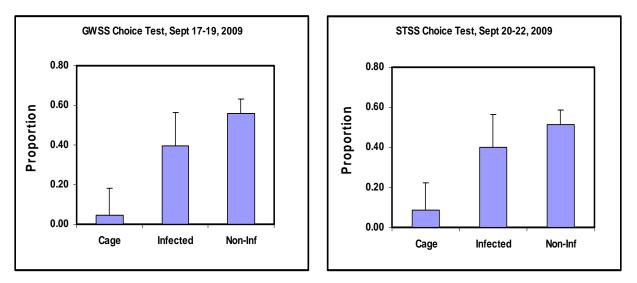


Figure 7. Female GWSS preference (left graph) and STSS preference (right graph) on field-grown Chardonnay grapevines in choice experiments initiated on September 17 (STSS) and September 20 (STSS). Bars represent average proportions of sharpshooters (\pm SE) observed on the cage, on the infected canes, and on the non-infected canes.

Sharpshooters moved slightly more often in this set of experiments than in the February study. In the GWSS trial, insects moved 62 out of a possible 485 observations (13%) and 102 out of 633 observations (16%) (Table 2). There were more GWSS that settled and had prolonged feeding (at least 3 hr.) on non-infected canes than on infected canes. There was only a slightly higher number of STSS that had prolonged feeding on the non-infected canes than the infected canes.

Parameter	GWSS (Sept. 17-19)	STSS (Sept. 25-27)
Chose Infected and stayed 3h or more	11	21
Chose Non-Infected and stayed 3h or more	19	25
Chose Inf. for 3h, left, returned for 3h or more	3	9
Chose Non-I for 3h, left, returned for 3h or more	10	5
Moved from Cage to Inf.	15	23
Moved from Cage to Non-I	14	26
Moved from Inf. to Cage	3	17
Moved from Non-I to Cage	10	14
Moved from Inf. to Non-I	12	10
Moved from Non-I to Inf.	8	12
Total number of Time insect moved	62	102
Total number of Observed Times	485	633

Table 2. Actions chosen by GWSS (September 17-19) and STSS (September 25-27) in choice studies between infected and non-infected cane tissue over the 3 day period. Observations were made between 8am and 6pm.

Intellectual Property:

No intellectual property has been produced as a result of this research project.

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Contribution to Solving the PD Problem in California:

This study contributes to our overall knowledge about feeding biology of the glassy-winged sharpshooter (GWSS) as it relates to acquisition and transmission of *Xylella fastidiosa*. Over the course of this two year project we have determined that GWSS males and females choose to feed on young leaf, petiole, and stem tissue compared to the same tissues on older parts of the grapevine cane, regardless of the time of year. However, they will feed on old stem tissue, which logically would result in more rapid chronic infection than feeding on young tissue. A significant finding is that GWSS moved frequently throughout the days of our studies, changing position in 35%, 14%, and 21% of the observations in the fall, winter and spring, respectively.

This has serious consequence for moving *X. fastidiosa* around the vineyard at various times of the year. We have determined that GWSS adults do not feed on cordon tissue, regardless of the time of year. While others have observed GWSS feeding in this tissue (Almeida et al. 2005b), we were not able to demonstrate it in our trials on mature vines. In winter studies, we found that GWSS prefer to feed on grapevine tissue that is infected with *X. fastidiosa* over tissue that is not infected. This has tremendous implication for bacterial acquisition during the dormant periods of the year, and since GWSS adults retain *X. fastidiosa* for life, this represents another interesting feature of this invasive vector that may contribute to PD spread. If we can determine the cause of this preference, we may be able to design methods to reduce it. In fall studies when vines were in full flush, the preference for infected tissue was not present. We found that GWSS and STSS move readily between infected and non-infected tissue, again a behavior that would contribute to *X. fastidiosa* in the field. Studying these detailed behaviors contributes to our understanding of the epidemiology of PD vectored by GWSS and STSS.