

Design of a candidate vibrational signal for mating disruption against the glassy-winged sharpshooter, *Homalodisca vitripennis*

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Abstract

BACKGROUND: The glassy-winged sharpshooter (GWSS), *Homalodisca vitripennis*, is an important pest of grapevines due to its ability to transmit *Xylella fastidiosa*, the causal agent of Pierce's disease. GWSS mating communication is based on vibrational signals; therefore, vibrational mating disruption could be an alternative to insecticides for suppression of the GWSS population. Our objectives were to identify spectral features of the female signal that elicit male signaling, design disruptive signals able to alter male perception and acceptance of a female, and determine the signal intensity required for future field applications.

RESULTS: Male responses to playback of modified female signals were significantly reduced by 60–75% when part of the female signal spectral components above or below 400 Hz were deleted. Playback bioassays showed that transmission of an 80 Hz pure frequency tone to plants completely suppressed male signaling to female signal playback, even if the disruptive signal amplitude was 10 dB lower than the female signal playback.

CONCLUSION: Although the mechanism underlying cessation of male signaling activity in the presence of disruption is not yet understood, results suggest that an 80 Hz vibrational signal should be tested in laboratory and field experiments to assess its efficacy in disrupting mating of GWSS.

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Keywords: *Xylella fastidiosa*; Pierce's disease; insect vector control; mating disruption; vibrational communication

1 INTRODUCTION

In the last few years, general interest in the use of vibrational signals to manipulate insect pest behaviors has shown a constant increase.^{1,2} For species that communicate or obtain information through substrate-borne vibrational signals, the application of mechanical principles that result in little to no negative environmental impact may constitute a valuable alternative and/or complement to pesticide applications.^{3,4} Current approaches to exploiting vibrational signals include techniques to prevent insect pests from colonizing host plants,⁵ mass trapping (Mazzoni *et al.*, unpublished), and mating disruption^{6–8} to reduce population densities. The choice of approach depends on detailed knowledge of the composition of landscape vibrational signals, noise associated with the target species, and vibrations that elicit specific insect behavioral responses.

Insects that communicate via exchange of substrate-borne vibrations during mate selection behavior use specific signals to identify, locate, attract, and court a potential mate.⁹ To disrupt behaviors that lead to copula, specific transducers attached to the substrate can be used to transmit vibrational signals that confuse and/or mislead individuals.² For example, one approach to interfere with mate location behaviors could be artificial transmission of female vibrational signals that attract males to a trap (i.e., attract and kill) (Mazzoni *et al.*, unpublished). Another approach is the

use of vibrational signals to induce release of alarm pheromones, which elicit dispersal behavior in individuals on the host plant (i.e., repellency).⁵ The vibrational mating disruption method is based on the concept that transmission of a disruptive signal (DS) prevents or alters signal perception by the receiver located on the treated substrate. One approach is to over-power the frequency range of natural vibrational signals with emission of broadband signals (e.g., white noise) of an amplitude equal to or greater than natural pest signals.⁷ However, to reduce or prevent non-target

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effects on natural enemies and other beneficial arthropods, which ordinarily use substrate vibrations as a communication channel for different purposes,¹⁰ it is crucial to design a DS with a frequency band that selectively disrupts pest behaviors while minimizing impact on non-target species. Therefore, in-depth knowledge of the signaling behavior of the target species, spectral and temporal characteristics of natural disruptive signals, and intrinsic portions of a signal that trigger insect responses are necessary to develop environmentally friendly pest management programs.

The overall objective of the present study was to identify candidate disturbance signals for future field implementation of a mating disruption program against the glassy-winged sharpshooter (GWSS), *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae). GWSS is a vector of the bacterium *Xylella fastidiosa*, which causes several economically important plant diseases. GWSS mating behavior includes the exchange of sex-specific vibrational signals that allows reciprocal identification, mate localization, and courtship.¹¹ Because the male searches for a stationary female after the onset of signaling by the female, different DS specifically aimed at interfering with the male search behavior were tested. The objectives of the study were: (1) to identify intrinsic spectral features of female signal that elicit male signaling response; (2) to design DS candidates that alter male perception and acceptance of a female signal; and (3) to determine the minimum threshold of signal intensity (i.e., amplitude) required for an effective DS application.

2 MATERIALS AND METHODS

2.1 Insects

GWSS were collected as eggs in Bakersfield, CA during spring 2015. Insects were reared on cowpea (*Vigna unguiculata* L. Walp. cv. 'Blackeye') and okra (*Abelmoschus esculentus* (L.) Moench) (both from Vermont Bean Seed Co., Randolph, WI, USA), basil (*Ocimum basilicum* L. cv. 'Genovese') and sunflower (*Helianthus annuus* L. cv. 'American Giant Hybrid') (both from Ferry-Morse Seed Co., Fulton, KY, USA). Nymphs were separated by sex as late instar stages (4th to 5th) to ensure a virgin status in the adult stage. Adult females were used after deposition of an initial (non-fertilized) egg mass, as previous work suggests these insects are more likely to emit mating communication signals than insects that had not yet laid eggs (Krugner, pers. obs.). Adult males used in the tests described below were of the same age as reproductively active females. Each individual insect was tested only once.

2.2 Experimental setup

In all tests, insects were randomly positioned on a 30–40-cm tall potted okra plant with two apical leaves, which was placed inside a cage (60 cm length × 60 cm width × 80 cm height) made of 1-cm thick acrylic walls, centered inside a chamber formed by 86 × 86 × 98-cm high blackout fabric and sound isolating walls. The cage and chamber assemblage were placed on an active vibration isolation table (Model 20-561, Technical Manufacturing Corp., Peabody, MA, USA) and enlightened with LEDs affixed to the top of the chamber. A laser Doppler vibrometer (PDV 100, Polytec, Inc., Irvine, CA, USA) was used to record vibrational signals produced by individuals. Recordings were digitized with Adobe Audition® C26 (Adobe Systems, Inc., San Jose, CA, USA) at a 44.1 kHz sample rate and 32 bits resolution. During recordings, the laser vibrometer was focused on a small piece of reflective tape glued to the stem at approximately mid-vertical length. Playback

signals were synthesized with Adobe Audition using a 1024 FFT window (type Hann), 75% of overlapping, and were transmitted into the plants through the conical tip of an electrodynamic mini-shaker (Type 4810, Brüel & Kjær, Inc., Norcross, GA, USA) placed in contact with the plant stem on the opposite position of the reflective tape.

2.3 Selection of the natural female signal (i.e., reference signal)

Identification of the positive reference female signal used in experiments described below was accomplished by randomly selecting 10 female signals (FS1)¹¹ from a signal library, each recorded from 10 different females. A male ($n = 5$) was placed individually on the plant and allowed a 2-min silent (i.e., playback off) adjustment period. After the adjustment period, a randomly selected female signal was transmitted into the plant using the method described above. Males were stimulated twice with each female signal at a 10-s interval. We reported whether males replied (or not) with their own vibrational signals to the stimulation. The female signal selected for the experiments below was the one (i.e., FS1_0, fundamental frequency (ff) = 80 Hz, Fig. 1a) that all tested males replied to at least once.

2.4 Test 1: Identification of intrinsic spectral features of female signal that elicit male signaling response

The frequency pattern of FS1_0 was modified to create four different versions of FS1. Signal modification was conducted using the FTT filter function of Adobe Audition to reduce intensity of signal components above (FS_1) and below (FS_3) 400 Hz by 20 dB, and remove signal components above (FS_2) and below (FS_4) 400 Hz (Fig. 1b–d). A male ($n = 40$) was placed individually on the plant and given 2 min to become familiar with the new conditions. After the adjustment period, the five female signals (i.e., FS1_0 to FS1_4) were transmitted into the plant in a randomized order. Each signal was transmitted into the plant twice at a 10-s interval between the same signal and a 30-s interval between signal types. Again, we reported whether a male replied with his own vibrational signals to the stimulation. After each trial the order of signals within the signal sequence was modified to ensure that all signals occupied every position (first to fifth) within the sequence. FS1_0 was used as a control. Each trial lasted 800 s.

2.5 Test 2: Design of disruptive signals that alter male perception and selection of a female signal

Information obtained from test 1 above (see Results section) was used to assist the design of three candidate disruptive signals. The following candidate disruptive signals were synthesized using Adobe Audition: a signal with a single pure frequency band at 80 Hz (DS1) or 240 Hz (DS2) and a signal with frequency bands at 80 and 240 Hz (DS3). A frequency of 80 Hz was chosen because it was the value of FS1_0 fundamental and dominant frequency; 240 Hz was randomly chosen to represent another harmonic. Prior to the tests, virgin males obtained from rearing cages were stimulated with FS1_0, as described above, to identify individuals that were responsive (i.e., that replied with their own vibrational signals in a time window within 5 s from either of the playback female signals) to playback of female signals. A total of 40 individuals were selected and then used in following trials at least 24 h after the prescreening tests. Males then were maintained together in a separate rearing cage. A male was released on the plant and

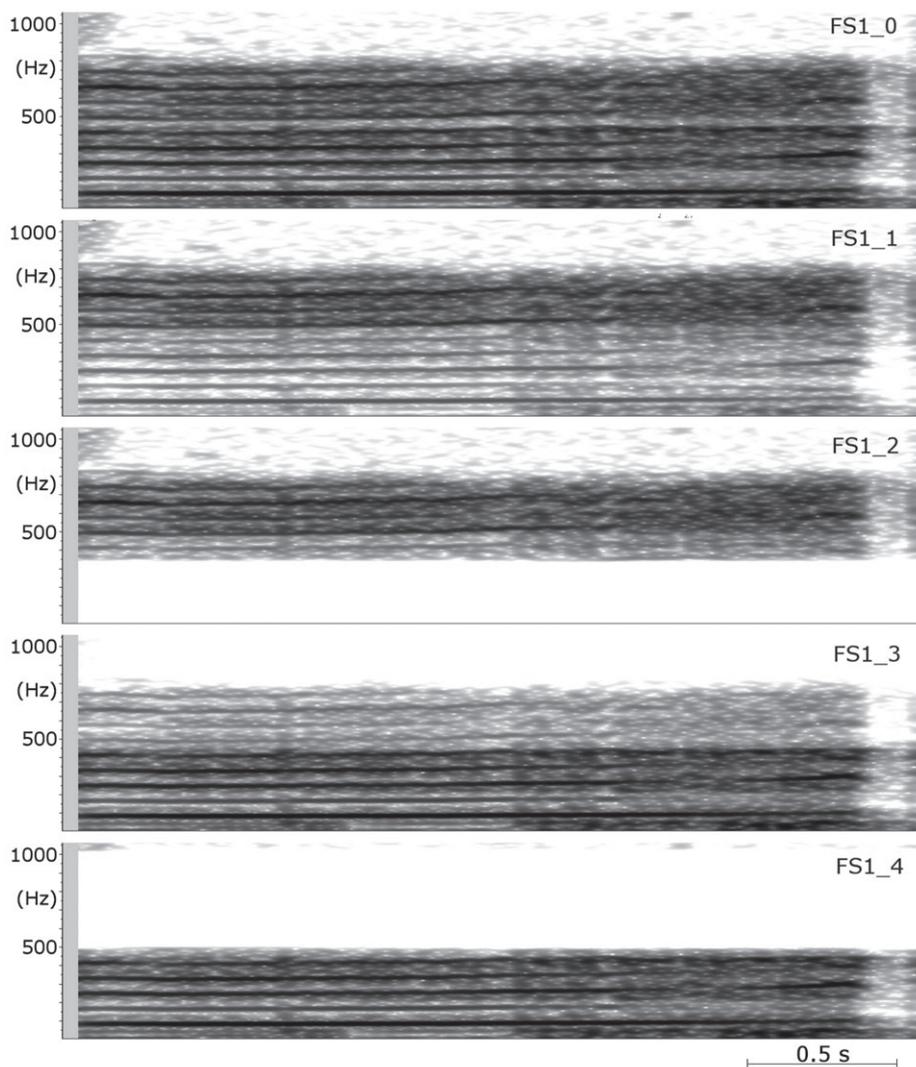


Figure 1. Spectrogram of the playback signals used in test 1: FS1_0, as positive reference in test 1; FS1_1 and FS1_3, whose frequency pattern was reduced by 20 dB under and over 400 Hz, respectively; FS1_2 and FS1_4, whose frequency pattern was deleted under and over 400 Hz, respectively.

allowed a 1-min silent adjustment period. After the adjustment period, playback of a randomly selected DS was activated. The playback file consisted of 2 min of DS only, followed by two FS1_0 repeated in a 10-s interval simultaneously with DS, then both DS and FS1_0 were turned off for 30 s before replaying FS1_0 in the absence of DS. Amplitude of DS and FS1_0 was the same in all trials. The number of males that replied to FS1_0 playback at least once in the presence or absence of DS emission was recorded. As a control, insects were tested using the protocol described in test 1 above.

2.6 Test 3: Defining effective DS intensity for suppression of male signaling

The DS (i.e., DS1, see Results) that most effectively disrupted the male response in test 2 above was modified to create three versions at different amplitudes: -10 dB (DS1-10), -20 dB (DS1-20), and -30 dB (DS1-30) than the amplitude of FS1. To determine whether males were responsive to playback of female signals in the presence of modified DS, 50 individuals were selected and tested as described in test 2, except that males were not re-stimulated after the DS cessation. The respective non-modified DS was used

as positive control, while the negative control was conducted as described in test 1 above.

2.7 Data analysis

In test 1, male responsiveness to the different FS1 was measured as (1) the number of individuals that responded at least once to the playback and (2) the total number of male replies to the playback. A male response was defined as emission of Male Signal 1 or 2.¹¹ Male responsiveness that did not statistically differ from the positive control (FS1_0) was used to characterize 'good' signals; signals that elicited significantly lower responses were characterized as 'bad' signals. Then, data were separated in two categories according to the position of the signal within the playback sequence: P1–P2 and P3–P5. Male responsiveness to each signal within each category was compared. To assess the possible effect of precedence, meaning the influence of the previous signal on the following signal in the sequence, the number of male replies to the first FS1 coming after any 'good' or 'bad' signal was compared, with the hypothesis being that previous perception of a 'good' signal increases male responsiveness to 'bad' signals. Data were analyzed using χ^2 test in contingency table (2 × 5) after

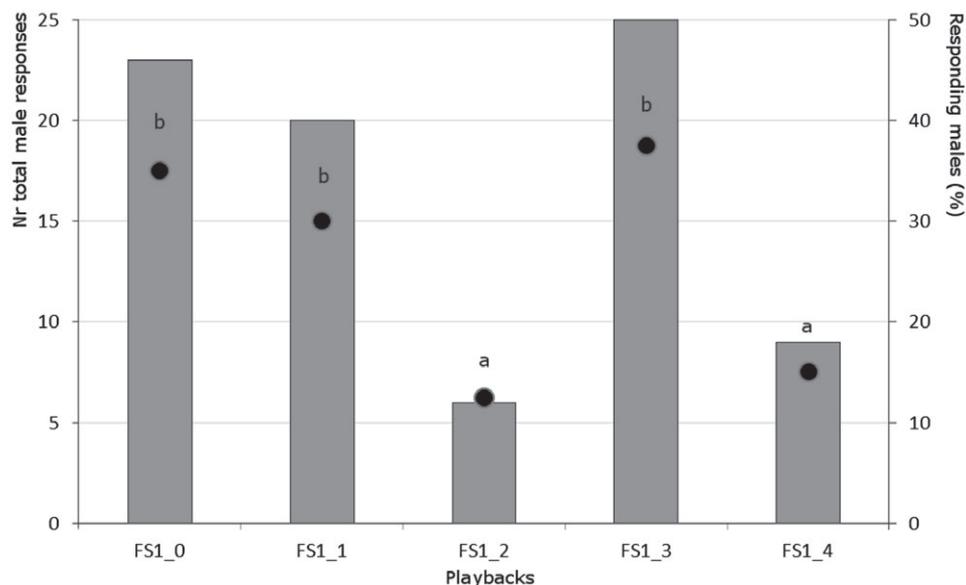


Figure 2. Number of total male responses (columns, primary y-axis) and percentage of responding males (dots, secondary y-axis) to FS1 playbacks in test 1. Different letters indicate significant differences for both parameters ($P < 0.05$).

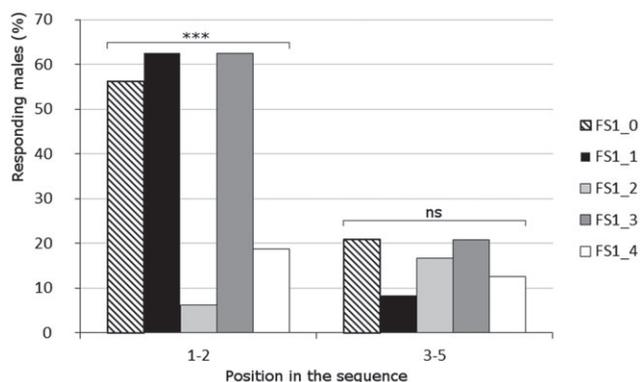


Figure 3. Percentage of responding males to each FS1 playback according to its position (P1–P2 vs P3–P5) in the stimulation sequence. ***Significant difference ($P < 0.001$) after chi-squared test.

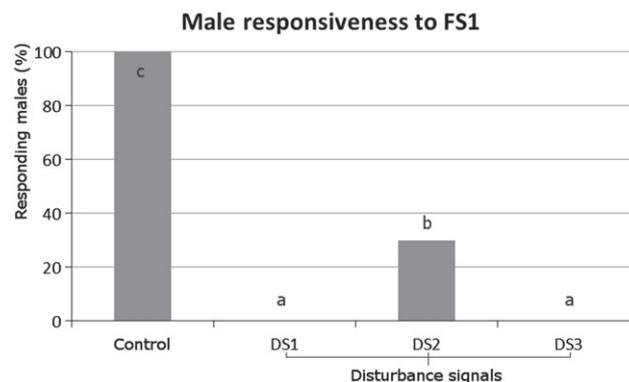


Figure 4. Percentage of males that responded to the FS1 stimulation in the absence (control) or presence of any of the three disturbance signal (DS1, DS2 and DS3) playbacks. Different letters indicate significant differences ($P < 0.05$) in the percentages of responding males.

Yates' correction followed by Ryan's test for multiple comparisons of proportions.¹²

In tests 2 and 3, χ^2 test in contingency table was used, followed by Ryan's test to assess statistical differences among percentages of successful disruption due to the different DSs. In test 2, χ^2 test in contingency table (2 × 2) was also used to assess differences between male responsiveness during and after emission of the DS.

3 RESULTS

3.1 Test 1: Deletion of frequency components of GWSS female signal alters male response

Two of the four modified FS1, those with amplitude reduction in sections of the signal spectrum (FS1_1 and FS1_3), elicited a male response rate not different from the control (FS1_0) but significantly higher than the others with full deletion of signal components above or below 400 Hz (FS1_2 and FS1_4), both in number of male responses ($\chi^2 = 17.7$, $df = 4$, $P = 0.001$) and percentage of responding males ($\chi^2 = 10.7$, $df = 4$, $P = 0.03$) (Fig. 2). Moreover, male responsiveness to FS1_0, FS1_1, and FS1_3 was

higher than the others when played either as first or second signal of the sequence ($\chi^2 = 18.9$, $df = 4$, $P < 0.001$), but male responsiveness to these signals was the same when played as third or later in the sequence ($\chi^2 = 2.1$, $df = 4$, $P = 0.71$) (Fig. 3). On average, male responses to a signal after playback of a 'good' signal was 20% vs 22% of responses after a 'bad' signal ($\chi^2 = 0.06$, $df = 1$, $P = 0.81$), which indicates that signal precedence did not affect male response.

3.2 Test 2: Playback of an 80 Hz frequency band to plants disrupts male response to female signals

The percentage of males that replied to the FS1 playback was significantly higher ($\chi^2 = 30.4$, $df = 3$, $P = 0.002$; Fig. 4) in the absence than in the presence of any DS. None of the males responded to playback of FS1 in the presence of an 80 Hz frequency band (DS1 and DS3), whereas only three of 10 males responded to playback of FS1 in the presence of a 240 Hz frequency band (DS2). On the whole, male responsiveness to FS1 significantly increased ($\chi^2 = 11.4$, $df = 1$, $P = 0.002$) after a DS playback was turned off.

Fifteen males that were silent during emission of DS replied to the FS1 playback with the emission of Male Signal 1.

3.3 Test 3: Defining the working intensity

The number of males that replied to FS1 stimulation in the presence of DS1, DS1-10, DS1-20, or DS-30 was significantly lower ($X^2 = 29.7$, $df = 4$, $P < 0.001$) than those in the absence of disturbance signals. Specifically, 0, 0, 1, and 3 males replied to FS1 in the presence of DS1, DS1-10, DS1-20, or DS-30, respectively, whereas 9 replied to FS1 in the absence of DSs (silent control).

4 DISCUSSION

Results of the experiments determined that an 80 Hz pure frequency tone, namely DS1, is a candidate disturbance signal to be tested in field trials of vibrational mating disruption against GWSS. In laboratory trials, simultaneous transmission of natural female signals and DS1 into plant tissues effectively prevented the male reply, which suggests that continuous playback at an amplitude similar that of a natural female signal may prevent establishment of a vibrational duet between a male and a female under field conditions. Although the mechanism underlying cessation of male signaling activity in the presence of DS1 is not yet understood, results suggest that DS1 negatively interferes with male perception of a female signal. For instance, in the absence of DS1 GWSS males responded to female vibrational signals significantly more often when the full signal frequency spectrum was presented, regardless of whether part of the signal components (low or high frequency harmonics) was reduced in intensity. That is, not even an amplitude reduction of the most intense harmonics of the signal (which means to shift the dominant frequency to another, higher, harmonic) significantly compromised male responsiveness. On the contrary, complete deletion of part of the frequency spectrum of the female signal was sufficient to significantly reduce male responsiveness. Therefore, further research is needed to determine whether males perceive female signals deprived of part of the frequency spectrum as a non-GWSS signal or as a GWSS signal emitted by a low-quality mate.

All playbacks used in trials had identical temporal features (i.e., signal duration and repetition time) and differed only in the frequency pattern. This signal design was chosen to minimize any potential effects independent of frequency because the temporal features of GWSS, and leafhoppers more generally, vibrational mating signals are strongly associated with partner identification.^{9,11} However, the results of test 1 indicate that the signal temporal pattern alone was not sufficient to elicit high responsiveness. Therefore, the frequency pattern of the modified female signal mediated male choice to reply to a vibrational stimulation. It must be noted that ~20% of tested males also replied to 'bad' female signals (deprived of part of the harmonics), which suggests that some individuals, perhaps those who were particularly well motivated, still accepted the modified signals and attempted to establish communication. Again, lack of evidence prevents the assumption that the majority of males did not reply to the playback stimulation simply because it was perceived as a non-GWSS signal or a signal emitted by a low-quality mate. In a treehopper species, the frequency pattern of female signals is known to be used by males to assess mate qualities related to physiological or physical characteristics.^{13,14} A possible role of the signal frequency in determining male behavioral responses to female calls was suggested also for mating communication of the planthopper, *Hyalesthes obsoletus*, where even minor changes in the frequency pattern

strongly reduced the individual responsiveness to female calls with identical temporal pattern.¹⁵ This subject would be certainly worthy of more specific investigation in GWSS, but it overshoots the objectives of the present research of identifying features that make a female signal more or less attractive to males.

Whereas the results of test 1 suggested that altering the female signal frequency spectrum disrupts GWSS mating communication, the results of test 2 provided evidence to support this hypothesis and also showed that, when the first (and dominant) FS1 harmonic (80 Hz) was overpowered by disturbance noises DS1 and DS3, the result was complete suppression of male signaling. An important methodological difference between tests 1 and 2 was that female signal harmonics were deleted in test 1 and overpowered by DS in test 2. Compared with male signaling rate in test 1, in test 2 there was a prolonged reduction in male responsiveness occurring after interruption of DS playback, which suggests induction of a signaling refractory period. In practice, males may have been able to perceive a female signal in the presence of DS, but presumably recognized the DS as a potential threat and therefore adopted a defensive strategy by hiding their presence for a period that goes further than the noise cessation.^{16,17}

On the other hand, it must be considered that the reduction in male responsiveness was only partial in the case of DS2 (240 Hz pure frequency tones) when 30% of males replied to FS stimulation, a percentage similar to that from test 1 when individuals were stimulated with 'bad' signals. Similarly, in test 3 some males still responded to the playback in presence of DS reduced by -20 and -30 dB. In this case, however, males could perceive the FS1 playback, because the DS was not sufficient to mask it. This observation would reinforce the hypothesis of a hiding behavior adopted by GWSS males in the presence of abiotic noise, rather than misidentification of the FS1. This would imply that prolonged exposure to the DS under an intensity threshold would determine an habituation effect that eventually will lead to restoration of the calling activity.¹⁸ By contrast, the release of sufficient volumes of DS into the target substrates would guarantee adequate masking that can be translated as efficacy of vibrational mating disruption. A masking approach was proved to be efficient against the grapevine leafhopper, *Scaphoideus titanus*. In this case, continuous emission of a disturbance noise at around 187.5 Hz caused complete interruption of ongoing male-female duets in laboratory trials¹⁹ and the prevention of >70% of mating under semi-field conditions.^{6,7} Such results were possible when the disturbance noise was above an intensity threshold of $15 \mu\text{m s}^{-1}$ (as substrate velocity), under which the success rate dropped and did not differ from the non-treated control.⁷ Therefore, amplitude of continuous DS is likely critical to maintain efficacy of DS in interfering with GWSS communication.

In conclusion, GWSS is potentially susceptible to vibrational mating disruption using signals with a sufficiently intense 80 Hz spectral band. In general, noise stressors induce substantial fitness deficit^{16,20} and multiyear repetition of mating disruption methods eventually leads to substantial reductions in pest populations.²¹ Because GWSS is a grapevine pest, initial efforts in developing a mating disruption strategy should target reproductive populations in vineyards. However, GWSS is polyphagous and highly mobile, which suggest that a strategy focused exclusively on disrupting communication in vineyards would presumably affect the densities of resident populations only. Therefore, targeting the pest in adjacent habitats (e.g., other crops) is critical to suppress area-wide populations. Although the transmission of disruptive signals to grapevines is facilitated by wires used in trellis

systems, further research is needed to identify and design devices that fit the requirements (e.g., plant structure, plant physiology, and human management) for best signal transmission in different crops.² Many technological issues and insect behavioral constraints remain to be elucidated prior to implementation of vibrational mating disruption methods, but these can be solved through solid interaction between research and industry. Finally, this type of approach could be extended to other *Xylella fastidiosa* vectors (e.g., *Graphocephala atropunctata*). Therefore, to have an all-embracing strategy that deals with the general hopper populations, further investigations on the mating behavior and vibrational communication of other pest species are needed in the near future.

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