Applied Entomology and Zoology
https://doi.org/10.1007/s13355-020-00711-9

SPECIAL FEATURE: ORIGINAL RESEARCH PAPER

Behavioral Control and Pest Management Using Vibrations

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Substrate-borne vibrations reduced the density of tobacco whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) infestations on tomato, *Solanum lycopersicum*: an experimental assessment

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Received: 11 September 2020 / Accepted: 9 November 2020
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Abstract

Managing pests with insecticides is probably the most conventional available control method. However, insecticide overuse often results in resistance and subsequent pest resurgence, and often adversely affects the ecosystem. The physical management of insect pests by utilizing substrate-borne vibrations, sounds, or both is increasingly attracting attention as an alternative, as it has modest ecosystem impacts. This method exploits vibroacoustic insect communication used for mating and the perception of approaching enemies, provoking behavioral responses in an ingenious manner. We aimed to examine whether substrate-borne vibrations effectively drive away tobacco whiteflies [*Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae)], which are serious agricultural pests. To do so, *B. tabaci* individuals were artificially introduced into greenhouses where tomato (*Solanum lycopersicum* L.) plants were reared. A substantial reduction in the average density of *B. tabaci* nymphs and adults was achieved by transmitting vibrational stimuli to the plants. At the same time, no obvious reduction was found in the number of tomato plant flowers. Although the performance of the vibrational device and transmission procedures requires further improvement, the present results shed light on the potential of substrate-borne vibrations as a promising alternative for pest management.

Keywords Pest management · Tobacco whiteflies · Behavioral disruption · Vibrational communication · Mechanical control

Introduction

The tobacco whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) is a significant global agricultural pest that causes serious damage to vegetable and ornamental crops: directly by consuming phloem tissue and indirectly by causing sooty molds due to honeydew secretion (Mound and Halsey 1978). Whiteflies act as a vector for disease through the transmission of plant pathogenic viruses such as those in the genera *Begomovirus*, *Crinivirus*, *Ipomovirus*, *Carlavirus*, and *Torradovirus* (Jones 2003; Navas-Castillo et al. 2011). In particular, *B. tabaci* serves as a vector for the tomato yellow leaf curl virus (TYLCV; *Begomovirus* in Geminiviridae). This virus has a wide host range and causes serious symptoms such as leaf curling and yellowing, which subsequently lead to yield reduction (Kil et al. 2014). Moreover, *B. tabaci* comprises more than 40 cryptic species or "biotypes" among which the most invasive are

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13355-020-00711-9) contains supplementary material, which is available to authorized users.

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the Middle East-Asia Minor 1 (MEAM1 or B biotype) and Mediterranean (MED or Q biotype) (De Barro et al. 2011; Vyskočilová et al. 2018). In addition to the habit of infesting a wide range of plant species (Bradshaw et al. 2019), *B. tabaci* resistance against pesticides is a serious problem because it may allow the rapid spread of invasive biotypes that express strong resistance to a variety of insecticides (Luo et al. 2010; Wang et al. 2020). To overcome the problem of resistance, it is necessary to combine approaches to prevent the spread of potentially harmful *B. tabaci* biotypes (Horowitz et al. 2011; Riley and Srinivasan 2019).

Intra- and interspecific insect communication, mediated by mechano-receptive information such as substrate-borne vibrations, airborne sounds, or both, has recently attracted considerable attention for pest management (Mankin et al. 2013; Polajnar et al. 2015; Takanashi et al. 2019; Uechi and Takanashi in press). Vibrations or sounds similar to those produced by insects can be used to provoke disturbances in communication between individuals and behaviors in various ways, leading to fitness reduction (Eriksson et al. 2012; Lee et al. 2012; Lujo et al. 2016; Takanashi et al. 2019). Unlike chemical pesticides, the exploitation of vibrations or sounds does not release harmful compounds into the environment, although a lowered sensitivity to temporary successive stimuli, habituation, should be taken into account (Kishi and Takanashi 2019; Loxdale 2018; Rohde et al. 2019; Takanashi et al. 2019).

Here, for the first time, we aimed to test whether substrate-borne vibrations resulted in significant overall disturbance to the reproduction and settlement of *B. tabaci* on tomato leaves, using the observed number of individuals as an index. We additionally examined whether the reproduction of tomato plants was affected by vibrational stimuli, using the number of flowers as a fitness indicator.

Materials and methods

Bemisia tabaci cultures

Bemisia tabaci (B biotype) individuals were collected from green peppers (*Capsicum annuum* L.) grown in Yaese, Okinawa, Japan on June 2, 2017. Prior to the experiment, they were reared for six generations on kidney beans (*Phaseolus vulgaris* L.) in an acrylic case [0.3 m (height, H) × 0.29 m (width, W) × 0.24 m (length, L)] at 25 ± 2 °C with a photoperiod of 14:10 (L:D) h.

Experimental design

This study was conducted in a greenhouse [5 m (H) × 9 m (W) × 19 m (L)] at the experimental farm of the University of the Ryukyus, Okinawa, Japan. Two vinyl houses [2 m (H) × 1.8 m (W) × 8 m (L)] were constructed parallel to each other and 2 m apart in the greenhouse. The northernmost structure is referred to as ‘house 1’ and the other as ‘house 2’ (Fig. 1b). A steel rack [1.72 m (H) × 0.96 m (W) × 0.45 m (L)] was placed in the center of each house. A control driver (SMT-KN-DR-001; Shonan Metaltec, Kanagawa, Japan) of a vibrational exciter, made using giant magnetostrictive materials (L: 0.203 m, diameter: 46 mm; SIP-100/10-MB-wp; Shonan Metaltec; Fig. 1a), was placed on the rack. The vibrational exciter was controlled by an outlet timer (534–02; Sogo Laboratory Glass Work, Kyoto, Japan).

To grow 12 tomato plants in each house, props (L: 2.1 m, diameter: 11 mm) were buried at depths of 0.3–0.4 m, 0.5 m apart (Fig. 1c). A tomato seedling (Momotaro®; Takii Seedlings, Kyoto, Japan) was planted in a pot that was filled with mixed soil (depth: 0.26 m, diameter: 260 mm) on October 30, 2017. The stem of each plant was tied to a prop using

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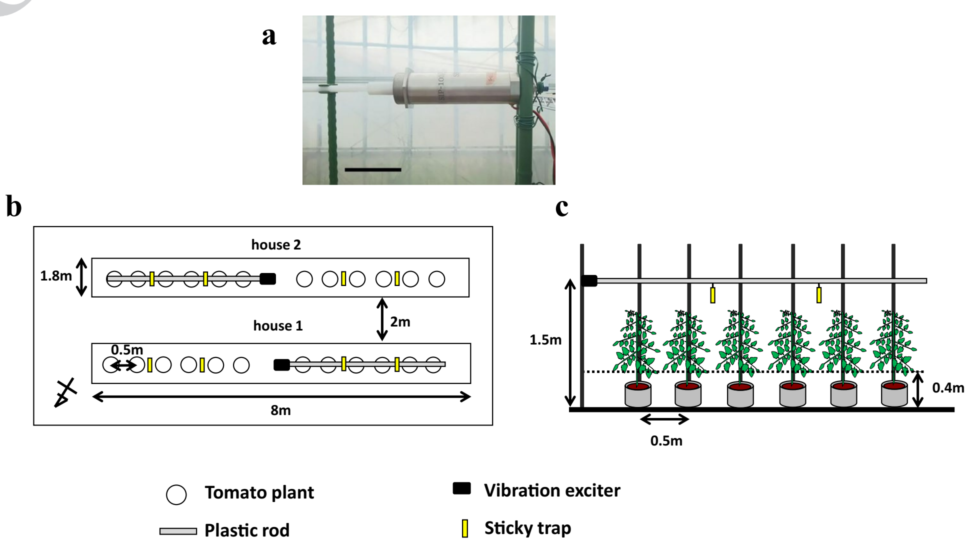

Fig. 1 Schematic diagram of tomato plant positions and associated equipment for providing vibrations: **a** vibrational exciter (scale bar: 0.10 m), **b** horizontal view of experimental setting, **c** vertical view

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a soft wire (#4907052726697; Takagi Co. Ltd., Niigata, Japan). In total, 24 seedlings that had been cultivated in liquid fertilizer (Ohtsuka House 1 + 2®, "A" prescription; OAT Agrio, Tokyo, Japan) were planted in the 2 houses. In the vibration-treatment area, the vibrational exciter was fixed between props at a height of 1.5 m above the ground (Fig. 1c). Three pieces of plastic rod (L: 1 m, diameter: 11 mm) that transferred vibrational stimuli to the props were connected serially to the exciter and were attached to the props using supporting clips (props joint clip, 11 × 11 mm; Takagi Co. Ltd., Niigata, Japan; Fig. 1). We did not set the vibrational exciter or plastic rods in the non-vibration-treatment area (Fig. 1b).

The vibrational exciter was operated for 1 min (a cycle of 1 s pulse and 9 s pause) every 30 min between 7:00 and 18:00, under the control of the outlet timer described above. The output vibrational frequency was 100 Hz. The vibrational frequency was determined based on the findings of our previous studies on other insects (Kishi and Takanashi 2019; Takanashi et al. 2016) that reported startle responses (see "Discussion" for further details) and the number of abdominal movements of *B. tabaci* counted in courtship behavior (Yanagisawa, unpublished data). The stimulation cycle and timing were configured to moderate habituation against continuous stimuli and were based on preliminary experiments and a previous study (Kishi and Takanashi 2019).

Vibrational intensity was measured using an accelerometer (Type 3052-A-030; Brüel & Kjær, Nærum, Denmark) connected to an input module (Type 4519-003; Brüel & Kjær), that was controlled by a laptop computer (CF-S9; Panasonic, Osaka, Japan) on December 26, 2017. The accelerometer was fixed to the target position using plastic tape. We measured vibrations at the intersections of props and plastic rods, and on plant stems at a height of 0.4 m above the ground. Vibrations were recorded using the PULSE Data Time Recorder software (Type7708; Brüel & Kjær); zero-to-peak values were used for acceleration measurements. Measurement of acceleration was conducted five times at each position on the same day. The output frequency (100 Hz) was detected in the harmonic series of the detected signals based on spectral analysis (fast Fourier transform: type Hamming, window size = 512).

Field surveys

Two days before starting the experiment (on November 15, 2017), 30 adult (1- to 9-day-old) *B. tabaci* were released on each tomato plant. These individuals were not sexed before the release. Field surveys started on November 17, 2017, and ended on January 1, 2018, and were conducted every 5 days (ten surveys were conducted in total). Prior to conducting the surveys, we randomly selected three compound leaves from each tomato plant. Three leaflets were then randomly selected from the compound leaves, and the number of *B. tabaci* adults and nymphs on leaflets was counted by visual observation. The number of flowers was also recorded for each flower cluster in each tomato plant. Yellow sticky traps (New Insect Bang Bang®; Daikyo Giken Kogyo, Kanagawa, Japan) were suspended from plastic rods using polyethylene strings so that the traps were placed at almost equal intervals at a height of 1.5 m (Fig. 1b, c). Each trap was replaced every 5 days, and the number of *B. tabaci* adults trapped was recorded.

Statistical analysis

Prior to conducting our statistical analysis for insects and plants, we compared the acceleration between the measurement positions. We first used a generalized linear mixed model (GLMM) to examine how the acceleration decreased in proportion to the increase in the distance from the vibrational exciter. The intensity of the vibration varied depending on the height of the measurement position and the horizontal distance from the vibrational exciter, therefore, the effects of these variables were included as explanatory (fixed) variables. A Gaussian error distribution with an identity link function was applied to the error distribution. The order of repeated measurements and greenhouses (houses 1 and 2) were included as random effects.

We then examined whether the periodical vibrational stimuli generated by the vibrational exciter effectively decreased the population density of *B. tabaci* adults and nymphs on leaves. In the GLMM, the number of *B. tabaci* adults or nymphs was included as the response variable, with treatment type being included as an explanatory (fixed) effect. Plant location, nested within greenhouses, and the date of the survey were included in the models as random effects. In both cases, we first postulated Poisson errors, but detected greater overdispersion than expected based on the dispersion estimator $\hat{\phi} = D/(n\text{-}p)$ proposed by Wedderburn (1974), where D is the deviance of the model, n is sample size, and p is the number of parameters for the model (adults: $\hat{\phi} = 2.046$, nymphs: $\hat{\phi} = 14.017$). Therefore, we adopted the negative binomial GLMM with a log-link function for the above comparisons.

Additionally, we compared the average and total number of tomato plant flowers between the treatment and control groups. Because we detected overdispersion (average number: $\hat{\phi} = 1.877$, total number: $\hat{\phi} = 8.919$), a negative binomial GLMM with a log-link was used. The average number of flowers was included as the response variable, with the treatment type included as an explanatory variable. Plant location, nested within greenhouses, and the date of the survey were included in the model as random effects. Similarly, the total number of flowers per tomato plant was included as the response variable, the treatment

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type was included as an explanatory variable, and greenhouse location was included as a random effect.

Finally, we examined the number of *B. tabaci* adults caught on yellow sticky traps set in the houses (Fig. 1). A negative binomial GLMM with a log-link was adopted because overdispersion was detected ($\hat{\phi} = 6.477$). The number of *B. tabaci* was included as the response variable, and the vibrational condition (with or without vibrations) of the installation site was included as an explanatory variable. Traps, greenhouses, and survey dates were included as random effects.

All statistical analyses were conducted using the R statistical software ver. 4.0.0 (R Core Team 2020).

Table 1 Averaged acceleration at measuring positions

Horizontal distance (m) from vibration actuator	Mean ± SD (m/s^2)	
	1.5 m High from the ground	0.4 m High from the ground
House 1		
0.5	67.1 ± 0.7	11.9 ± 0.2
1	48.5 ± 0.3	21.2 ± 0.6
1.5	48.6 ± 0.8	7.0 ± 0.4
2	73.2 ± 0.5	18.2 ± 0.8
2.5	21.3 ± 0.2	13.2 ± 1.5
3	46.6 ± 0.3	16.8 ± 0.8
House 2		
0.5	76.8 ± 0.3	20.2 ± 0.3
1	53.9 ± 1.0	23.4 ± 1.0
1.5	38.8 ± 0.2	13.3 ± 0.2
2	29.4 ± 0.4	7.2 ± 0.3
2.5	57.7 ± 0.2	19.8 ± 0.3
3	53.8 ± 0.3	28.3 ± 0.1

Measurements were repeated five times at each position

Results

Significantly smaller values for vibrational accelerations were detected at the lower height (0.4 m) positions compared with higher (1.5 m) positions (GLMM: $\beta = 34.02$, $t = 16.56$, $p < 0.001$). As such, in the comparison, we examined how the acceleration decreased as the horizontal distance between the vibrational exciter and measurement positions increased (Table 1). At the higher positions, the acceleration tended to decrease as the distance increased (GLMM: $\beta = -0.16$, $t = -3.33$, $p = 0.002$); however, such a relationship was not detected at the lower positions (GLMM: $\beta = 0.02$, $t = 1.00$, $p = 0.322$).

On average, the number of *B. tabaci* nymphs was significantly lower in the vibrational treatment than in the control treatment (GLMM: $\beta = -0.62$, $z = -2.271$, $p = 0.023$; Table 2; Fig. S1, S2). Similarly, the average number of *B. tabaci* adults on the tomato leaves was significantly lower in the vibrational treatment than in the control treatment (GLMM: $\beta = -0.33$, $z = -2.147$, $p = 0.032$; Table 2).

However, neither the average nor the total number of tomato plant flowers differed significantly between the control and treatment groups (GLMM: $\beta = 0.266$, $z = 0.551$, $p = 0.582$ and $\beta = 0.162$, $z = 0.357$, $p = 0.721$, respectively; Table 2).

The number of *B. tabaci* adults caught on the yellow sticky traps was compared between installation sites (the area treated with vibrations versus the area without vibrations), but no significant differences were detected (GLMM: $\beta = 0.217$, $z = 1.038$, $p = 0.299$; Table 2).

Discussion

The present study revealed that the application of vibrations to tomato plants using a vibrational exciter reduced the overall number of *B. tabaci* on these plants. It is notable that approximately 40% fewer nymphs were observed on the plants that were subjected to vibrational treatment compared to the control. Additionally, we conducted a secondary

Table 2 Numbers of larval and adult whiteflies and flowers on plants

Variable	Mean ± SD	
	With excitation	Without excitation
Insects		
Nymphs (/observation/plant)	5.9 ± 11.5	10.5 ± 16.9
Adults (/observation/plant)	0.5 ± 0.9	0.6 ± 1.0
Adults trapped (/trap)	8.9 ± 6.2	7.6 ± 6.8
Plants		
Flowers (/observation/plant)	0.6 ± 0.9	0.5 ± 0.9
Accumulated number of flowers (/plant)	5.6 ± 4.9	4.8 ± 5.5

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experiment under different conditions and confirmed a significant decrease in the number of *B. tabaci* nymphs and adults on tomato leaves that were subjected to vibration (Yanagisawa et al. unpublished data). The significant reduction in the nymphal density of *B. tabaci* implies that the reproduction and settlement of *B. tabaci* on the plants is disturbed by vibrations.

Male and female whiteflies, including *B. tabaci*, communicate via substrate-borne vibrations (Kanmiya 2006). Notably, the male vibrational signals and the subsequent female responses vary, even among closely related species (Kanmiya 2011). During the courtship stage, males emit calling and courtship sounds consisting of a burst separated by long irregular intervals. Females subsequently respond to males by emitting sounds comprising short and simple bursts (Kanmiya 2006). The temporal and spectral domain characteristics of male sounds differ even among closely related species, and females do not respond to the sounds emitted by males of different species (Kanmiya 2011). This results in strict premating reproductive isolation (Perring et al. 1993). Based on these facts, male vibrational signals should be critical for species discrimination by females, and for the decisions by females to accept or refuse mating. It is therefore possible that the vibrational signals generated by the exciter interrupt the courtship sequences between the sexes, consequently hindering mating opportunities as a disturbance effect. Substrate-borne vibrations could also cause "startle responses" in *B. tabaci*, such as fast jerky movements, freezing, and escaping (Bullock 1984; Friedel 1999). Startle responses are considered to have evolved for evasion from predation, and can be found in various insect species (e.g., Kishi and Takanashi 2019; Takanashi et al. 2016; Tsubaki et al. 2014; Uechi and Takanashi in press). Marked reduction in nymphs might be due to not only a disturbance effect, but also due to startle responses induced by the signals irrelevant to courtship sounds. Future studies need to be carried out to carefully address how the transmitted vibrational signals manipulate behavior in *B. tabaci*.

In the adult stage, vibrations reduced the number of individuals observed by 26%, which was much smaller than the percentage in the nymphal stage. Moreover, the number of trapped *B. tabaci* did not differ between the vibration-treatment and non-vibration-treatment areas. Unlike the apterous nymphal stages, *B. tabaci* adults can fly for long distances and colonize various plant species (Bar et al. 2019). We did not place any shields between the experimental areas, which allowed *B. tabaci* adults to move freely between them, and some of the emerged *B. tabaci* migrated due to the vibrational stimuli. It is therefore likely that an influx of *B. tabaci* adults emerged in the non-vibration-treatment area simultaneously. Analogous to the 'push–pull' approach to managing pests (Miller and Cowles 1990), vibrations are expected to 'push' *B. tabaci* adults out of the infested plants by exploiting their startle response. To enhance the effect of vibrations, future studies should develop a method to 'pull' escaping and migrating *B. tabaci* adults by utilizing traps attractive to this species.

Together with the assessment of pest management efficacy, we also investigated the impact of substrate-borne vibrations on plants. However, we did not find an overall difference in the blooming of tomato plant flowers between the vibration- and non-vibration-treatment areas. This might indicate that physiological conditions remained almost the same irrespective of the presence or absence of vibrational stimuli. However, attention should be paid to the indirect effect of *B. tabaci*, which is likely to negatively affect plant reproduction as well as the direct effect of vibration. The positive and negative effects exerted by vibration on the plants should be carefully evaluated under more targeted experimental designs in the future.

Our results indicate that the vibrational stimuli decreased with increasing distance from the exciter. The maximum and minimum average accelerations were 76.75 m/s^2 and 6.96 m/s^2, respectively, suggesting more than a tenfold difference between them (Table 1). Such a spatially heterogeneous vibrational transmission might drive whiteflies into areas in a greenhouse with lower accelerations, resulting in an unintended concentration of crop damage. As the size of farming fields managed by the use of vibrations increases, more exciters are required, which consequently increases costs. To optimize the efficiency of exciters, it is necessary to use assembling materials that are suitable for transmitting vibrations while suppressing vibrational attenuation and increasing the accelerations from the exciter.

Acknowledgements We thank all the members of the Laboratory of Entomology at the University of the Ryukyus for their encouragement and thoughtful discussions. The authors also thank Takumi Uesato (Okinawa Prefectural Agricultural Research Center) for providing cultured whiteflies and the Japanese Apricot Laboratory, Wakayama Fruit Tree Experiment Station for providing the vibrational exciter.

Author contributions All authors contributed to the study conception and experimental design. Material preparation and data collection were undertaken by RY. The experimental technique was advised by TT and RS. Data analysis was performed by RY and HT. The first draft of the manuscript was written by HT and RY, and all authors commented on the manuscript. All authors have read and approved the final manuscript.

Funding This work was supported in part by the Grants for Supporting Industry-University-Government Cooperative Research (Nos. 2017-278, 2019-150 to HT and RS) provided by the Bank of Okinawa, Ltd.; Grants-in-Aid for Scientific Research (Nos. 19KT0040 and 18KT0042 to TT, Nos. 17H03722 and 17K20068 to HT) from the Japan Society for the Promotion of Science; and by Grants-in-Aid of the Uruma Fund for the Promotion of Science (No. 2018-14 to RS).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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