



What's shaking for caterpillars? Leaf-borne vibratory stimuli and behavioral responses in the fall armyworm, *Spodoptera frugiperda*

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Abstract

Leaf-borne vibrations are predicted to be significant for caterpillar communication and risk assessment, but the caterpillar's vibratory landscape remains largely unknown. To address this, we used the fall armyworm *Spodoptera frugiperda*, as a model in our study with two main goals: (1) to characterize the vibratory landscape on a leaf in the presence of abiotic (wind and rain) and biotic (conspecifics and invertebrate predator) stimuli; and (2) to assess whether different larval instars detect and respond to those vibrations. Our findings show that abiotic and biotic vibrations were distinct from background noise, except for those produced by 1st instar larvae. Wind-induced leaf movement produced vibrations with a low-frequency and high-amplitude (< 100 Hz and 2.97 mm s⁻¹), in contrast with raindrops (> 174 Hz; 3.25 mm s⁻¹). The 2nd to 5th instar larvae and predatory stinkbugs moving on leaves produced vibrations with dominant frequencies ranging from 140 to 326 Hz and amplitudes from 1.42 to 2.95 mm s⁻¹. Furthermore, the spatial distribution of vibrations across bean leaves revealed that abiotic vibrations were more widely spread across leaves, unlike the more concentrated biotic vibrations. Regarding the caterpillar response to vibratory stimuli, caterpillars exposed to abiotic stimuli behaved differently from undisturbed caterpillars, regardless of instar. By contrast, caterpillars exposed to biotic stimuli do not respond consistently. Our findings contribute insights into a caterpillar's vibroscape and support the hypothesis that armyworms can perceive and respond to both abiotic and biotic vibrations, filling a knowledge gap about this economically important pest species' sensory ecology.

Keywords Caterpillar · Vibratory landscape · Spatial distribution · Biotremology · Vibrational communication

Key message

- Caterpillars are substrate-bound organisms and leaf-borne vibrations are potentially important for their communication and risk assessment.
- Leaf vibrations were mapped in vibroacoustic landscapes and behavioral responses of fall armyworm were assessed.
- Abiotic and biotic vibrations differed in their physical characteristics and leaf distribution.

- Fall armyworm larvae responded differently in the presence of biotic and abiotic vibrations compared to controls where vibrations were absent.

Introduction

Vibratory sensing and communication in insects are widespread and have received significant attention in recent decades. There is a burgeoning body of evidence for the importance of substrate-borne vibrations in a variety of behaviors, ranging from the detection of passive cues to complex communication signals (Virant-Doberlet and Čokl 2004; Cocroft and Rodríguez 2005; Cocroft et al. 2014; Hill et al. 2019). Despite the rapid progress of this field, a research bias remains in favor of adults, leaving a significant knowledge gap on the role of vibration for juveniles (Turchen et al. 2022). Such an observation is intriguing, given that most juveniles reside on the substrate and are less likely to jump or fly. Thus, the ability to detect and

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distinguish plant-borne vibrations is likely to play a crucial role in the sensory ecology and survival of insects, including insect pest species (Cocroft et al. 2014; Yack 2016, 2022; Yack and Yadav 2022).

For insects that live on plants, biotic and abiotic vibratory sources potentially provide a wealth of information that can be used by a multitude of potential receivers within a vibrational communication network (Virant-Doberlet et al. 2019). Caterpillars for example live mostly within or on the substrate and must cope with a complex environment that includes biotic and abiotic noise, as well as interactions with competitors and exploiters. For caterpillars in particular, there is a growing body of literature demonstrating or suggesting that they are capable of detecting and discriminating between vibration sources, including biotic vibrations emitted by conspecific or heterospecific organisms (e.g., predator detection and risk assessment (Bacher et al. 1996, 1997; Castellanos and Barbosa 2006), recruitment and spacing (Fletcher et al. 2006; Yadav et al. 2017), egg-laying decisions (Guedes and Yack 2016), territorial defense (Yack et al. 2001; 2014; Bowen et al. 2008), and maintaining relationships with ants (Casacci et al. 2019) or, vibrations arising from abiotic sources, such as wind or rain (Casas et al. 1998; Guedes et al. 2012). Even so, the natural vibratory landscapes of caterpillars that live on different plant substrates remain poorly understood for most species.

By vibratory landscape, we refer to a collection of biological, geophysical, and anthropogenic vibrations emanating from different sources to create unique vibrational patterns across a variety of spatial and temporal scales (Šturm et al. 2019). The richness and complexity of this vibratory landscape are not attributable only to vibration sources but also to the medium through which the vibrations travel. Plants, for instance, are highly complex structures and exhibit wide variability in traits that might act as a physical constraint on mechanical waves and can affect the transmission and perception of vibratory stimuli (Michelsen et al. 1982; Cocroft et al. 2006; Velilla et al. 2020). This is relevant for organisms living on plants, such as caterpillars, by limiting the area over which they can gather or send vibrational information (i.e., vibratory active space, Mazzoni et al. 2014). Therefore, a comprehensive characterization of the sensory environment is crucial for understanding what vibrations are available to an organism.

In this study, we investigated the vibratory landscape of caterpillars, using the fall armyworm as a model species. The fall armyworm, *Spodoptera frugiperda* (Smith 1797) (Lepidoptera: Noctuidae), originated from the Americas but has become an invasive pest in Africa (in 2016), Asia (in 2018), and recently in Oceania (in 2020) (Deshmukh et al. 2021; Wan et al. 2021). This species is a highly polyphagous pest and is reported to attack over 350 commercial and non-commercial hosts across 76 plant families, including mainly

Poaceae, Asteraceae, and Fabaceae (Montezano et al. 2018). We chose this species because understanding the sensory ecology of a pest species is critical for generally understanding its life history, and for the development of management tactics. Furthermore, although the acoustic sensory ecology of adult fall armyworms has received some research attention (e.g., Tougaard 1998; Nakano et al. 2009; Mora et al. 2014), to the best of our knowledge, the vibrations generated or received by the larvae have not been studied. This study had two primary goals. The first was to characterize the vibroacoustic landscape on a leaf scale in the presence of different abiotic (wind and raindrops) and biotic (caterpillars and predatory stinkbugs) stimuli. The second goal was to test if larvae respond to vibrations from abiotic and biotic sources, and if so, how they respond.

Materials and methods

Insect rearing and plant material

Two insect species were included in these experiments: larvae of the fall armyworm, *S. frugiperda*, and adults of the predatory stinkbug *Podisus nigrispinus* (Dallas 1851) (Hemiptera: Heteroptera: Pentatomidae). Both were obtained from colonies maintained under laboratory conditions at the Department of Entomology of the Federal University of Viçosa. In fall armyworm rearing, moths were maintained in PVC cages (40 cm high × 30 cm in diameter) with sulfite paper on the inner walls for oviposition; cotton soaked in a solution of 10% sugar and 5% ascorbic acid was provided as food. Eggs were collected and stored in plastic bags until hatching. Batches of neonates were transferred to an artificial diet (Kasten et al. 1978) in 500-ml plastic cups until the 2nd instar and then individually until pupation. In stinkbug rearing, the nymphs and adults were kept in cages and fed *Tenebrio molitor* Linnaeus, 1758 (Coleoptera: Tenebrionidae) pupae and leaves of *Eucalyptus grandis* (W. Hill ex. Maiden) ad libitum. All insects were kept at a controlled temperature of $27 \pm 2^\circ\text{C}$, relative humidity of $70 \pm 15\%$, and 14L: 10D photoperiod.

The plant species used in experiments was green bean (*Phaseolus vulgaris* L.), which is listed as a host plant of the fall armyworm (Montezano et al. 2018). Plants were grown in pots (1.7 L) containing a mixture of soil, washed coarse sand, and organic matter, in a ratio of 1:1:1 (v/v/v), and commercial substrate in a ratio of 3:1 (v/v). Plants were housed in a greenhouse (temperature of $28 \pm 8^\circ\text{C}$, relative humidity of $65 \pm 9\%$, and maximum natural irradiance), free from insect infestation, and received the fertilization recommended for the crop (Fancelli 2010). When they reached the phenological stage V₃–V₄ (20–25 cm of height), the plants were used in the trials.

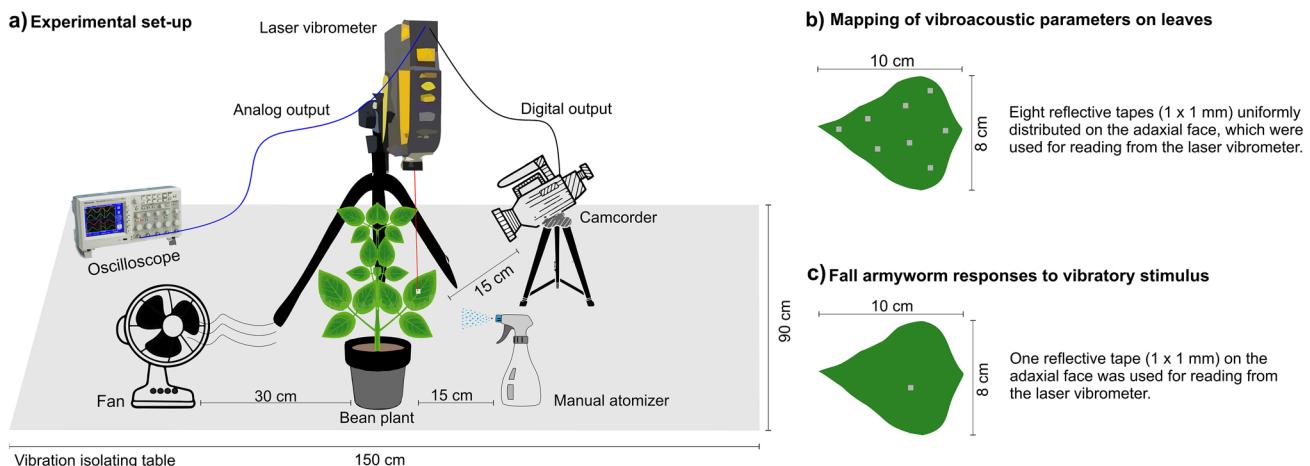


Fig. 1 Schematic illustrations of **a** the experimental set-up, **b** the recording scenarios used for mapping of vibroacoustic parameters on leaves, and **c** the fall armyworm response to vibratory stimulus

Vibration and video recording set up

Leaf vibrations and insect behaviors were recorded simultaneously using a laser-Doppler vibrometer (PVD-100; Polytec, Waldbronn, Germany) and camcorder (HDR-CX455; Sony, Tokyo, Japan) (Fig. 1a). Two different recording scenarios with slightly different recording conditions were performed, as mentioned in the subsections below. Here we describe the general recording set up. Bean plants 20–25 cm tall were transported from the greenhouse to the laboratory and individually placed on top of a vibration isolating table (63–500 Series Micro-g; TMC, Peabody, MA, USA). The plant leaves with a size of ~8 × 10 cm were subsequently tagged by affixing one or more pieces of reflective tape (1 × 1 mm) to the adaxial side of the leaf, depending on the trial (Fig. 1b, c). The laser vibrometer was set with a velocity of 100 mm s⁻¹ (or 25 mm s⁻¹ V), high-pass filter off, and low-pass filter set at 20 kHz. The laser beam was positioned perpendicularly to the reflective tape. The analog output of the laser vibrometer was connected to an oscilloscope (TDS-2012C; Tektronix, Beaverton, OR, USA) to measure instantaneous velocity. Simultaneously, the digital output of the laser vibrometer was connected to the microphone port of a high-resolution camcorder to sync audio-video recordings. The camcorder was set for 1920 × 1080 pixels with 30 frames/second and an audio sampling rate of 48 kHz with 16-bit resolution. All the recordings were performed on top of the vibration isolating table to reduce external interference (see Fig. 1a).

Audio files were extracted from videos (waveform audio, '.wav') using the software Audacity(R) [version 3.0.2] with the FFmpeg library (Audacity Team, 2021). Audio files were analyzed for the characterization of dominant frequency (Hz) and amplitude (mm s⁻¹). The peak frequency

was obtained by the signal after applying a FFT (sampling frequency: 22.050, window type: "Hanning," window size: 1024, overlap: 50) by means of the R packages '*tuner*', '*see-wave*', and '*phonTools*', according to procedures described by Sueur (2018). The amplitude was corrected based on instantaneous velocity obtained from the analog output of the laser vibrometer. The video files (mega tree session, '.mts') of the caterpillar behavioral responses were analyzed using the Behavioral Observation Research Interactive Software (BORIS) (Friard and Gamba 2016). A list containing the brief behavioral descriptions (Table S1) was used as a reference during behavioral annotation.

Mapping of vibroacoustic parameters on leaves

The goal of this experiment was to characterize the vibroacoustic characteristics of bean leaves and to describe how vibrations are spatially distributed in the presence of different abiotic and biotic stimuli. In this bioassay, eight pieces of reflective tape (1 × 1 mm) were uniformly distributed on the adaxial face of a bean leaf for recording with the laser vibrometer (Fig. 1b). Subsequently, the leaf was submitted to one of the following conditions: (1) background noise (i.e., control)—that was recorded in the absence of external vibration provided to plants. (2) Vibration produced by abiotic factors—that consisted of a simulation of light wind or moderate rain. The wind was simulated using a domestic fan (Arno S.A., Brazil) at a velocity of 1.3 m s⁻¹ (measured with a Knup Anemometer, KP-8016) positioned at a distance of 30 cm from a bean plant. The fan was turned on for approximately 30 s at a rate of 1 event per minute (Fig. 1a). Raindrops were simulated using a manual atomizer sprayed from a distance of 15 cm from the bean leaf, delivering multiple and simultaneous water droplets to the leaf surface at a rate

of about two spritzes per minute and a volume of 0.15 mL per spritz (Fig. 1a). (3) Vibration from biotic factors—a larva of *S. frugiperda* (from first to fifth instar) or an adult predatory stinkbug was individually released on the central region of the leaf and the vibrations produced by this insect were recorded (Fig. 1a). Leaf vibrations resulting from each stimulus were recorded with a laser and video simultaneously, as described previously. The recordings were performed on each reflective tape (i.e., sampling point) individually for 120 s, which was replicated three times for each leaf recording point. After each replicate, the leaf and insect (when used) were replaced. The audio and video files were analyzed using BORIS to identify the segments containing a stimulus (i.e., wind, raindrops, caterpillar crawling, and stinkbugs walking). For each sampling point, three recording segments (windows of 30 s per segment) containing the stimulus were used for temporal, spectral, and amplitude characterization of the vibration, totaling 24 segments in each replicate. The average of dominant frequency (Hz) and amplitude (mm s^{-1}) obtained in each sample point were used for the overall characterization of vibration and building of spatial models.

Fall armyworm responses to vibratory stimulus

The goal of this experiment was to assess whether larvae of each instar responded to stimuli from abiotic and biotic sources. In this bioassay, a piece of reflective tape ($1 \times 1 \text{ mm}$) was attached to the central region of the adaxial face of the leaf of a bean plant, which was placed on a vibration isolating table (Fig. 1c). For each replicate, a caterpillar was collected from a cup with diet and placed on a bean leaf. The caterpillar was left undisturbed for at least 2 min on the leaf to allow for acclimatization before starting the recording session. Following acclimatization, leaf vibrations and larval behaviors were recorded while a caterpillar was submitted to one of following trials: (1) background noise (i.e., control) (no-stimulus on leaf) [$n = 10$ replicates/instars]; (2) simulated wind [$n = 10$ replicates/instar]; (3) raindrops [10 replicates/instar]; (4) approaching by conspecific of the same instar [$n = 10$ replicates/instar] or (5) approaching by an adult of a predatory stinkbug [$n = 10$ replicates/instar].

All stimuli were tested separately, and the caterpillar was replaced in each replicate. In the trials where a caterpillar was exposed to background noise (or control), wind, or raindrops, the simulation of abiotic factors occurred under the same conditions described above except that only a single reflective tape was attached to the leaf for recording. In trials where a caterpillar was exposed to a conspecific of the same instar or a predator, the recordings started 1 min prior to introducing the other organism with a paintbrush to the leaf. In trials with predators, the stinkbugs were individually held in a plastic vial and food-deprived for at least 12 h prior

to the trial. In all trials, the interactions between insects were recorded for 10 min or until an organism left the leaf or the predator attacked the caterpillar. In this bioassay, the audio and video files were analyzed using BORIS to assess the behavioral responses of fall armyworms and the frequency of behavioral transitions when exposed to different stimuli. Table S1 summarizes the categories used to classify behaviors in video records. We specifically focused on the behavioral response of the first caterpillar on the leaf (namely, the focal caterpillar) to assess their response to the stimulus provided. The results were represented as simplified ethograms based on first-order behavioral transitions after exposure to each stimulus. Our bioassays did not include playback experiments (i.e., presentation of only vibration stimuli); thus our assessment of the caterpillar's response to vibratory response was not direct, but indirect through correlation between the presence of a vibratory stimulus and behavioral response.

Statistical analyses

All analyses were performed using the R-software [version 4.0.1] run in the RStudio interface [version 1.4.1] (R Core Team 2021; RStudio Team, 2021). The graphical illustrations were produced with Wacom creative table (Intuos S, Tokyo, Japan) using Corel Painter (Essential 7, Ottawa, ON, Canada).

Vibroacoustic parameters

To characterize the vibroacoustic parameters of bean leaves and verify whether they differ from background noise, the data from dominant frequency (Hz) and amplitude (mm s^{-1}) were subjected to analyses of deviance and generalized linear model (GLM) with Gaussian distribution. Subsequently, the assumptions of normality and homoscedasticity of model residuals were checked with Shapiro–Wilk and Bartlett tests, respectively. When required, the overdispersion of models was adjusted and significant treatments were compared by the test of contrasts ($P < 0.05$), using the R package “*stats*”.

Spatial analysis and mapping of vibroacoustic parameters

To assess how vibrations are spatially distributed across the leaf in the presence of different abiotic and biotic stimuli, suitable spatial models were selected and tested based on the distances between the leaf sampling points; the averages of dominant frequency (Hz) and amplitude (mm s^{-1}) were determined for each sampling point with a laser vibrometer. The empirical semivariogram (i.e., the variance of variable differences between two sampling points) was used to adjust the best model to fit the theoretical semivariogram as a function of the spatial location of the determinations. The semivariogram models tested were spherical, exponential,

and Gaussian. The models were selected using cross-validation with the best data adjustment using the R package ‘*performance*’. The semivariogram functions allowed for the estimation of three parameters: range (r), partial sill (C), and nugget (C_0) (Isaaks and Srivastava 1989). The first parameter, range (r), indicates the distance of spatial autocorrelation. The second parameter (namely, partial sill) refers to its respective semivariance value, which increases and then reaches the sill ($C_0 + C$). The third, nugget (C_0), refers to the intercept of the y-axis on the semivariogram and represents variance occurred at scales finer than lag distance. Two further parameters were determined from the basic parameters described above: the sill ($C_0 + C$) and level of spatial dependence (LSD) [$C_0/(C_0 + C)$], where the spatial dependence of the semivariogram is considered strong when LSD ≤ 0.25 , moderate when $0.25 < \text{LSD} < 0.75$ and weak when LSD > 0.75 (Cambardella et al. 1994). The spatial maps depicting the vibroacoustic distribution on leaves were generated using the semivariance data obtained with the selected models, according to procedures described by Brunsdon and Comber (2019) using the R packages “sf,” “stars,” “gstat,” “geoR,” “rgdal.”

Behavioral analysis

The behavioral responses of fall armyworms were represented as simplified ethograms based on first-order behavioral transitions after each stimulus. To test whether the behavioral transitions of the fall armyworm were independent of the vibratory stimulus, the frequencies of the behavioral transitions of caterpillars in the control [without stimulus] were contrasted with the behavioral transition of caterpillars

exposed to each vibratory stimulus using the *G*-test of independence in contingency tables and the measure of association between variables was estimated using Cramer's V, with the R package “*DescTools*.” Cramer's V values range of 0.0–0.3 is considered as weak, 0.3–0.7 as medium, and > 0.7 as strong. The proportion of time spent in each behavior was submitted to the Kruskal–Wallis test by ranks (H-test) when significative post-hoc tests were performed using Fisher's least significant difference (LSD) test ($P < 0.05$) with the R package “*agricolae*.”

Results

Characteristics of leaf vibrations and mapping of vibroacoustic parameters

Leaf vibrations resulting from exposure to abiotic and biotic factors differed in the dominant frequency ($F_{8,207} = 50.10$; $P < 0.01$; Fig. 2a) and amplitude ($F_{8,207} = 33.63$; $P < 0.01$; Fig. 2b). Overall, vibrations from abiotic and biotic stimuli were distinct from background noise, except for those produced by crawling of 1st instar larvae, which exhibited dominant frequency and amplitude similar to background noise (i.e., vibrations were almost undetectable by the laser). By contrast, simulated wind and raindrops, crawling of 2nd to 5th instar larvae, and walking of predatory stinkbugs exhibited dominant frequencies ranging from 100–350 Hz and amplitudes $> 1 \text{ mm s}^{-1}$ (Fig. 2).

Based on “Tobler’s First Law of Geography,” which states that things close together are more similar than things farther apart (Tobler 1970), we used spatial

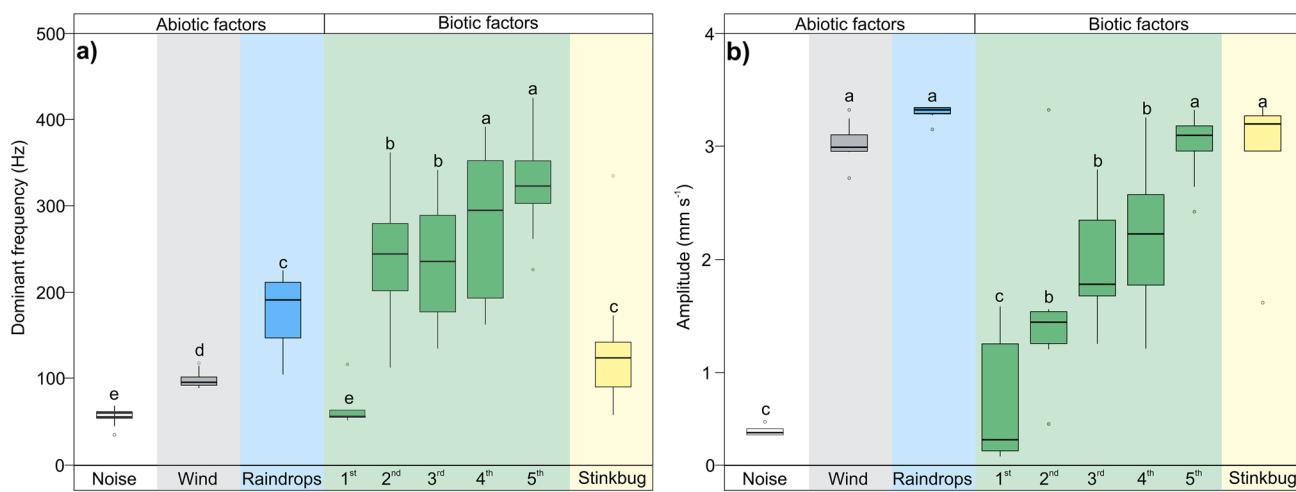


Fig. 2 **a** Dominant frequency and **b** amplitude of leaf vibrations when exposed to background noise—no stimulus (empty boxplot), wind (gray boxplot), raindrops (blue boxplot), crawling of fall armyworm from 1st to 5th instar (green boxplot), and walking of predatory stink-

bug (yellow boxplot). Box plots indicate the median (solid line) and dispersal (lower and upper quartiles and outliers) of the vibroacoustic parameters. Different letters at the top of the box plot indicate significant differences by contrast test ($P < 0.05$)

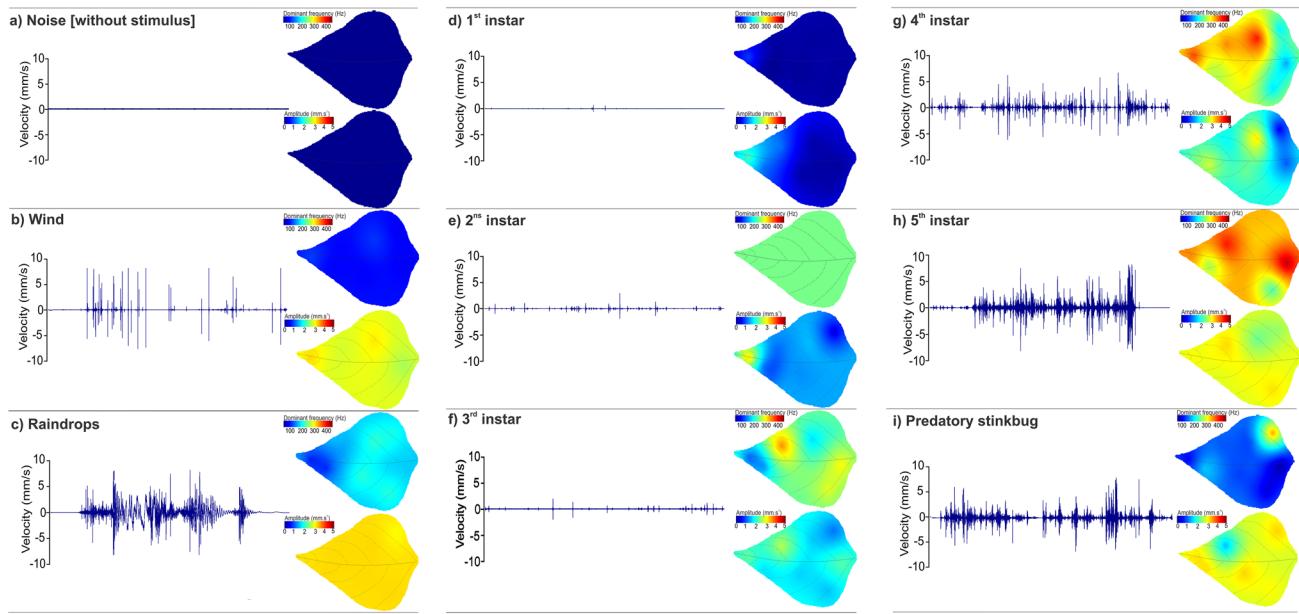


Fig. 3 Waveforms and spatial distribution of dominant frequency [top-right leaf of each section] and amplitude [bottom-right leaf of each section] produced through the bean leaf when exposed to **a** background noise, **b** wind, **c** raindrops, **d** 1st instar fall armyworm

crawling, **e** 2nd instar crawling, **f** 3rd instar crawling, **g** 4th instar crawling, **h** 5th instar crawling, and **i** solitary predatory stinkbug walking

interpolation with the purpose to map the distribution of dominant frequency (Hz) and amplitude (mm s^{-1}) through bean leaves (Fig. 3), while recording these traits at spatially distributed sampling points spread over the leaf surface. Regardless of the stimulus, the semivariogram models showed similar spatial autocorrelation (range = 2.47 cm) and strong spatial dependency (LSD ≤ 0.11), suggesting that vibroacoustic parameters were not randomly distributed on the leaves (Table S2). Indeed, the vibroacoustic parameters were more uniformly distributed through leaves when submitted to background noise (Fig. 3a), wind (Fig. 3b), and raindrops (Fig. 3c), although there is a clear difference in levels of dominant frequency and amplitude when compared between each stimulus (see Fig. 2). By contrast, the vibrations produced by armyworm crawling (Fig. 3d–h) or stinkbug walking on leaves (Fig. 3i) exhibited a less uniform distribution of both vibroacoustic parameters on the leaves. In these cases, vibrations are concentrated in some leaf regions, which relates to the position of organisms. In larvae, the variation was less evident in early instars [1st and 2nd instar, Fig. 3d–e], mainly concerning dominant frequency. On the other hand, it was more pronounced in later instars [3rd until 5th instars, Fig. 3f–h], regardless of vibratory parameters.

Fall armyworm responses to vibratory stimuli on the leaves

To test whether vibrations of abiotic and biotic sources might elicit behavioral responses in the fall armyworm, we subjected 1st to 5th resident instar larvae to each stimulus described above (i.e., wind, rain, conspecific, stink-bug), and assessed their behavioral response and time spent in each behavior. Time and behavioral responses of resident larvae exposed to background noise (i.e., no vibration stimuli present) were used as the control.

Abiotic factors (wind and raindrops)

The behavioral responses of fall armyworm did not differ between instars when caterpillars were subjected to wind (G-test, $\chi^2=63.41$; d.f.=56; $P=0.23$) and raindrops (G-test, $\chi^2=74.34$; d.f.=72; $P=0.40$), suggesting that the behavioral response is independent of caterpillar instar. Thus, we combined the results from all instars to assess the overall response of caterpillars. Nonetheless, it is noteworthy that larvae of all instars [1st to 5th instar] exhibited different behavioral responses to wind (Fig. S1b) and raindrops (Fig. S1c) when compared with their control (Fig. S1a). Therefore, we provide supplementary materials with details of behavioral responses of each instar (Fig. S1a–c), as well as the time budget spent on each behavior (Fig. S2a–e).

Regardless of instar, the overall response of fall armyworm when submitted to wind (G -test, $\chi^2 = 98.07$; d.f. = 14; $P < 0.001$, Fig. 4b) and raindrops (G -test, $\chi^2 = 80.08$; d.f. = 18; $P < 0.001$, Fig. 4c) differed from the control condition (Fig. 4a), indicating that larvae can detect and respond to abiotic stimuli (Fig. 4). Remarkable differences in behavioral transitions were observed when wind-exposed caterpillars were compared with control-exposed caterpillars, mainly in the transition between crawling to touching around, whose frequency was much higher in wind-exposed caterpillars. Caterpillars exposed to raindrops exhibited a similar transition between crawling to touching around (Fig. 4c) when compared to control. However, there was an increase in transition between crawling to resting (Fig. 4c). In both cases, behaviors not reported in the control were incorporated into the caterpillar behavioral repertoire (e.g., wind [mandible scrape, and dropping off (Fig. 4b)]; raindrops [rearing up and jerking, dropping off, and dodging (Fig. 4c)]) ; however, these behaviors were less frequent.

Consistently, we observed that caterpillars subjected to background noise (i.e., control–no stimulus) did not exhibit significant differences in the proportion of time spent among behaviors (Kruskal–Wallis, $\chi^2 = 6.41$; d.f. = 3; $P = 0.09$) with a similar proportion of time spent in crawling, touching around, resting, or feeding (Fig. 5a). In contrast, caterpillars exposed to wind (Kruskal–Wallis, $\chi^2 = 13.89$; d.f. = 4; $P = 0.007$) spent more time crawling and touching around, while caterpillars exposed to raindrops (Kruskal–Wallis, $\chi^2 = 14.54$; d.f. = 5; $P = 0.01$) spent more time touching around, crawling, and resting (Fig. 5a).

Biotic factors (conspecific or a predatory stinkbug)

The behavioral response of fall armyworms differed between instar when focal caterpillars were presented with a conspecific of the same instar (G -test, $\chi^2 = 106.06$; d.f. = 132; $P = 0.04$) or predatory stinkbugs (G -test, $\chi^2 = 215.72$; d.f. = 148; $P = 0.0002$). Therefore, the results from all instars were presented individually (Fig. 6; Fig. 7).

Behavioral responses of 1st instar caterpillars, when exposed to a conspecific of the same instar did not differ from control (G -test, $\chi^2 = 17.89$; d.f. = 10; $P = 0.06$, Fig. 6c). In contrast, the behavioral response of caterpillars of 2nd instar (G -test, $\chi^2 = 48.57$; d.f. = 15; $P < 0.001$, Fig. 6c), 3rd instar (G -test, $\chi^2 = 35.15$; d.f. = 12; $P = 0.004$, Fig. 6c), 4th instar (G -test, $\chi^2 = 39.01$; d.f. = 21; $P = 0.01$, Fig. 6c) and 5th instar (G -test, $\chi^2 = 92.45$; d.f. = 22; $P < 0.001$, Fig. 6c), when exposed to a conspecific of the same instar, differed significantly from control (Fig. 6b). Second and 3rd instar(s) exhibited a higher frequency of transition between crawling to touching around (Fig. 6c). Also, in the presence of a conspecific, caterpillars of the 2nd and 3rd instar did not feed, and eventually showed defensive behaviors (Fig. 6c).

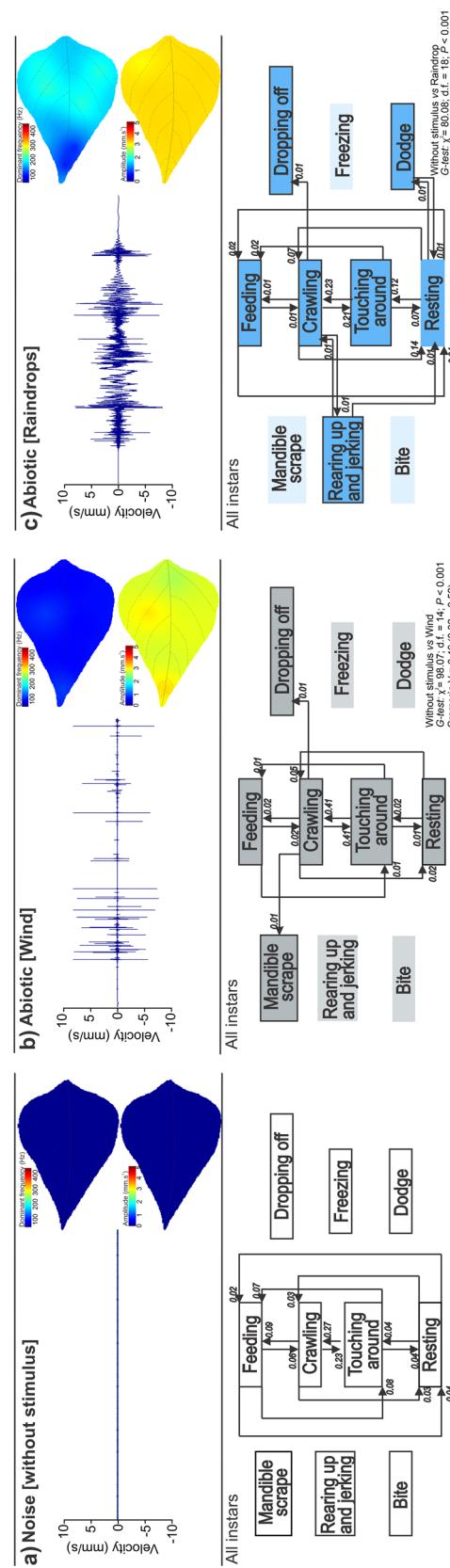


Fig. 4 Top panel shows waveforms and spatial distribution of dominant frequency (Hz) [top-right leaves] and amplitude (mm s^{-1}) [bottom-right leaves] through the bean leaf when exposed to a background noise. **b** wind, and **c** raindrops. Bottom panel presents ethograms for each stimulus for the combined response of 1st to 5th instar larvae to these stimuli (or lack thereof). Ethograms are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark color boxes indicate the observed behaviors, while light color boxes refer to non-observed behaviors. Statistics values refer to the G -test of independence and Cramer's V

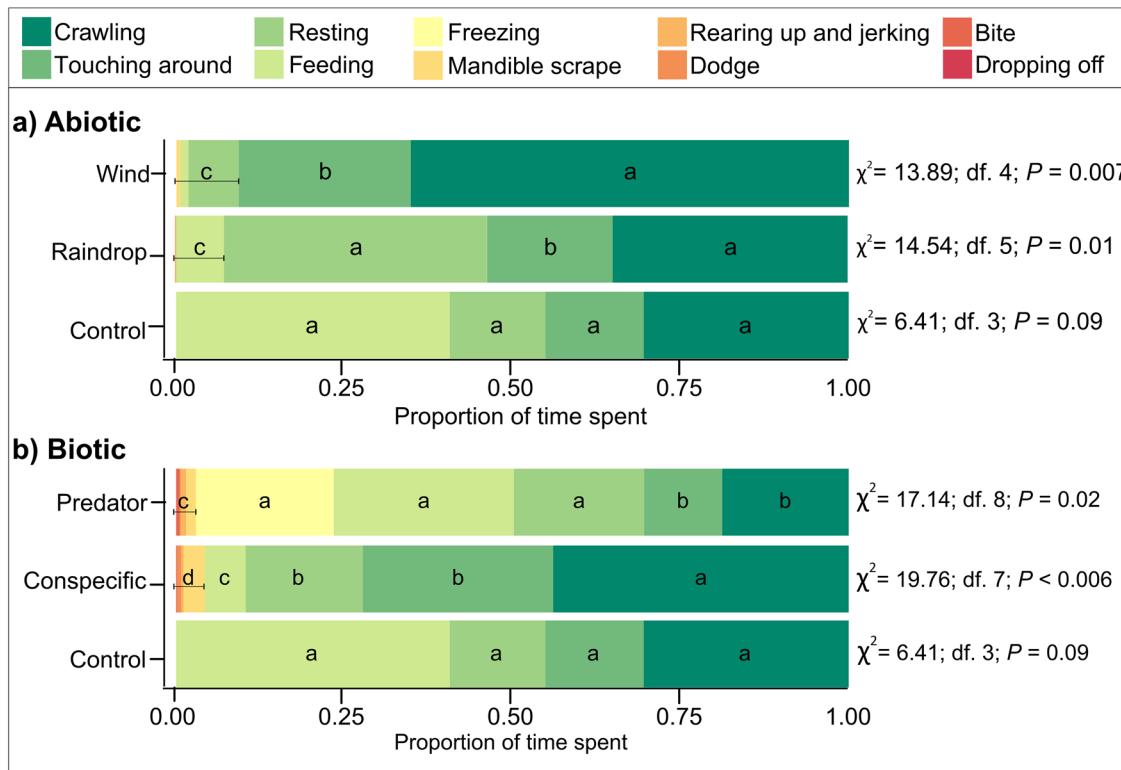


Fig. 5 Time budget spent on each behavior when caterpillars were exposed to **a** abiotic and **b** biotic stimuli. The proportion of time spent within each stimulus was submitted to Kruskal–Wallis test by

ranks. Different letters within the box indicate significant differences by contrast using Fisher's least significant difference ($P < 0.05$)

On the other hand, caterpillars of the 4th and 5th instar exhibited a higher diversity of behaviors (Fig. 6c), including non-aggressive behaviors (e.g., mandible scrape, dodge, and dropping off) and eventually aggressive behaviors (e.g., biting) (Fig. 6c). Regardless of instar, caterpillars exposed to conspecifics (Kruskal–Wallis, $\chi^2 = 19.76$; d.f. = 7; $P < 0.006$) spent more time crawling, touching around, or resting, with only a modest fraction of time used for feeding or defense (Fig. 5). Details of the proportion of time spent in each behavior by instar are provided in the supplementary material (Fig. S3).

Similar to their behavioral response to conspecifics, 1st instar caterpillar responses to a predatory stinkbug did not differ from the control (G -test, $\chi^2 = 10.81$; d.f. = 11; $P = 0.459$, Fig. 7a, b). In contrast, the behavioral response of 2nd instar caterpillars (G -test, $\chi^2 = 44.29$; d.f. = 22; $P = 0.003$, Fig. 7b), 3rd instar (G -test, $\chi^2 = 27.01$; d.f. = 14; $P = 0.02$, Fig. 7b), 4th instar (G -test, $\chi^2 = 36.41$; d.f. = 16; $P = 0.002$, Fig. 7b) and 5th instar (G -test, $\chi^2 = 182.39$; d.f. = 29; $P = 0.001$, Fig. 7b) when exposed to a predator, differed significantly from control (Fig. 7a). The presence of predators on leaves increased the repertoire of behaviors performed by caterpillars of the 2nd to 5th instar(s) (Fig. 7b). Second, 3rd, and 4th instar(s) exhibited a higher frequency

of transition between crawling to touching around (see 2nd to 4th instar(s) in Fig. 7b) and eventually showed defensive behaviors. On the other hand, caterpillars from the 5th instar exhibited a higher frequency of other behaviors (Fig. 7b), including aggressive (e.g., biting, rearing up, and jerking) and non-aggressive (e.g., mandible scraping, freezing, dodging, and dropping off) behaviors. Regardless of instar, caterpillars exposed to predators (Kruskal–Wallis, $\chi^2 = 17.14$; d.f. = 8; $P < 0.02$) spent more time freezing, feeding, and resting, spending only a modest fraction of time used for crawling, touching around, and other behaviors (Fig. 5b). Details of the proportion of time spent in each behavior by instar are provided in the supplementary material (Fig. S3).

Discussion

A leaf's vibrant world

Our perceptions shape our understanding of the world around us. Does this also apply to caterpillars? Although it is assumed that plant-borne vibrations play a crucial role in communication and risk assessment for caterpillars, the subject remains poorly understood (Yack and Yadav 2022).

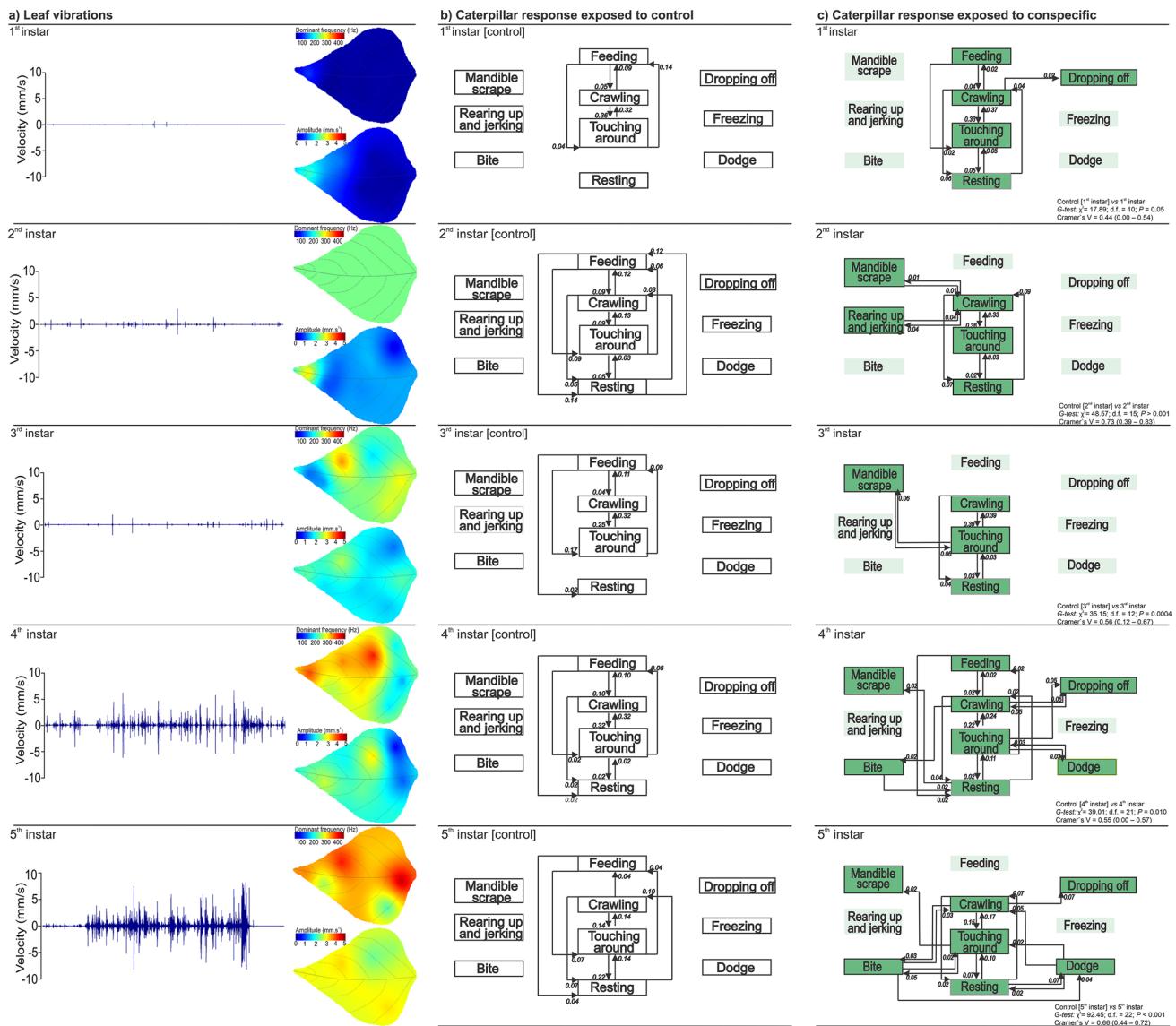


Fig. 6 **a** Waveforms and spatial distribution of dominant frequency (Hz) [top leaf] and amplitude (mm s^{-1}) [bottom leaf] represent the leaf vibrations produced by caterpillars of 1st to 5th instar. **b** Ethograms of the response of 1st to 5th instar when exposed to background noise (control). **c** Ethograms of the response of 1st to 5th instar when exposed to a conspecific of the same instar. Ethograms

are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark colored boxes indicating the observed behaviors, while light colored boxes refer to non-observed behaviors. Statistic values refer to the G -test of independence and Cramer's V

Our findings revealed that even on a small scale, there are complex vibratory environments. The results showed that abiotic (wind and raindrops) and biotic (caterpillar and predatory stinkbug) vibrations were available to resident *S. frugiperda* larvae, and that these vibrations differed in their physical characteristics and distribution on the leaf depending on the source. Our results also supported the hypothesis that *S. frugiperda* larvae respond to vibrations produced by abiotic and biotic sources.

Vibrations induced by wind and raindrops generated a noisy environment on leaves. Wind induced a random

movement of leaves, generating vibrations of low-frequency (< 100 Hz) and high-amplitude ($> 3 \text{ mm s}^{-1}$). Raindrops generated higher frequency ($> 170 \text{ Hz}$) and higher amplitude ($> 3 \text{ mm s}^{-1}$) vibrations due to the impact of the drop on the leaf. Wind and rain are widely recognized as sources of background noise for insects that reside on plants (Cocroft and Rodríguez 2005; Hill 2009; Cocroft et al. 2014). Wind-induced vibrations are described in the literature to have generally low frequencies (< 100 Hz), albeit they may contain energy up to 20 kHz (cf. Casas et al. 1998; Tishechkin 2007; McNett et al. 2010; Guedes

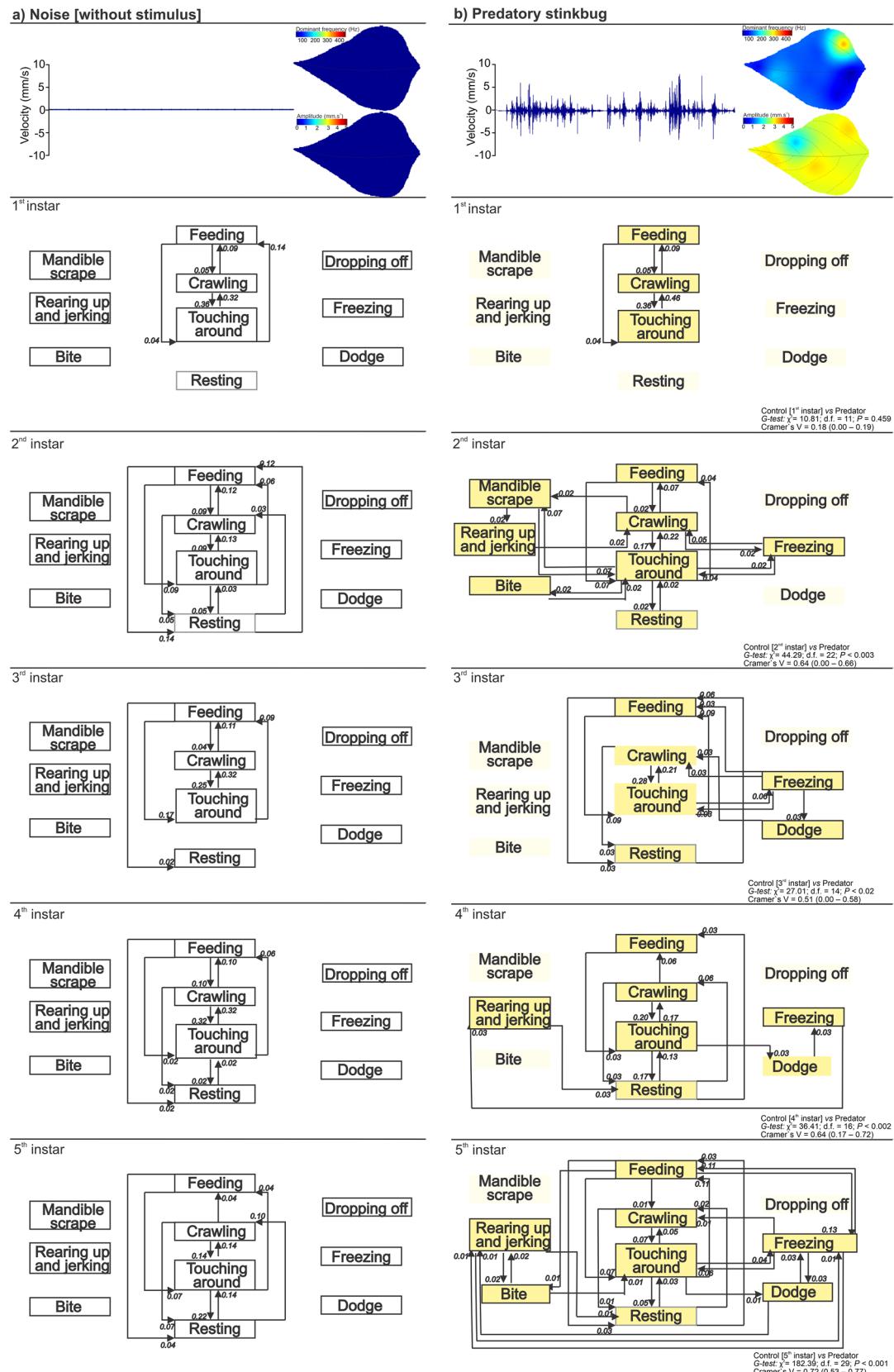


Fig. 7 **a** Top panel shows waveforms and spatial distribution of dominant frequency (Hz) [top leaf of figure] and amplitude (mm s^{-1}) [bottom leaf] through the bean leaf when exposed to background noise (control) and **b** when exposed to predatory stinkbug. Ethograms below refer to the response of 1st to 5th instars when exposed to each stimulus. Ethograms are represented as first-order transition diagrams. Solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark colored boxes indicate the observed behaviors, while light colored boxes refer to non-observed behaviors. Statistic values refer to the *G*-test of independence and Cramer's V

et al. 2012). Raindrops falling on plants were reported to cause intermittent and high-amplitude waveforms with most energy below 1 kHz, which is evidently variable as it correlates to the intensity of simulated rain (Casas et al. 1998; Guedes et al. 2012). In our study, when leaves were exposed to abiotic stimuli, the dominant frequency and amplitude were uniformly distributed on leaves reflecting the standardized method of delivering the stimuli. Widespread abiotic noise may impair a caterpillar's ability to detect or recognize relevant information, as these vibrations may overlap with those produced by conspecifics or predators (Casas et al. 1998; Guedes et al. 2012). Caterpillars may also use vibrations as cues to reduce activity during rainfall or wind gusts, or, they may use episodes of environmental noise (or even the intervals between noisy periods) to move (or rest) to avoid being detected, as occurs in other insects (e.g., Tishechkin 2007; Wignall et al. 2011). In these scenarios, temporal cues may be crucial for a caterpillar, but because they were not quantified, this remains speculative.

Leaf vibrations produced by biotic stimuli (conspecifics and predatory stink bugs) were distinct from the background noise, except those produced by crawling of 1st instar larvae. Vibrations caused by larval crawling on the leaf surface was predicted because the caterpillars employ two or more anchor points at the same time while moving, compressing the substrate for at least part of their crawling action (van Griethuijsen and Trimmer 2014). Vibrations caused by walking stinkbugs are predicted as they use three legs in contact with their substrate to propel their bodies forward (Gullan and Cranston 2014). The crawling of 1st instar larvae did not exhibit a noticeable oscillation on leaves. This is most likely due to the small size (< 1.7 mm) and low body mass (< 30 mg) of 1st instar caterpillars, both of which limit the ability to generate waves with sufficient energy to overcome material resistance (i.e., impedance) (Mortimer 2017). On the other hand, the vibrations produced by the crawling of 2nd to 5th instars exhibited substantial vibration on leaves with a dominant frequency ranging from 243 to 326 Hz and an amplitude ranging from 1.42 to 2.95 mm s^{-1} . Predatory stinkbugs walking on leaves created notable vibrations as well, with a dominating frequency of 140 Hz and an

amplitude of 2.92 mm s^{-1} . Vibrations induced by caterpillar or stinkbug movement are described in the literature to have generally a continuous low amplitude waveform with a bandwidth of 150 Hz at -30 dB, and frequencies extending to around 2 kHz (Guedes et al. 2012). These results were expected due to the greater mass of the caterpillars, as well as the use of adult stinkbugs in the trials that increased the impact generated on the leaf surface when caterpillars crawled, or stinkbugs walked. Such findings are biologically relevant in light of the fact that caterpillars may assess risk and make decisions based on unintended vibrations made by other insects, whether conspecifics or predators.

Our findings indicated that, unlike abiotic stimuli, vibrations arising from biotic stimuli were concentrated in certain leaf areas, resulting in a finer mosaic of vibration and suggesting that vibrational information is only available in a limited area of the leaf. This implies that there is a limit to the area over which the insects can gather or send vibrational information (i.e., active space; Mazzoni et al. 2014) such as detecting prey or hosts, avoiding predators or parasitoids (Pfannenstieler et al. 1995; Meyhöfer et al. 1997; Castellanos and Barbosa 2006; Wignall and Taylor 2011; Guedes et al. 2012), or avoiding conflicts (Yack et al. 2001; 2014; Fletcher et al. 2006; Scott et al. 2010; Kojima et al. 2012). The concentration of vibrations on specific regions of the leaf is most likely related to the organism's position on leaves. Nevertheless, our results also showed that the vibrations generated by caterpillar crawling or stinkbug walking were more conspicuous on the edges than in the central region of leaves or close to the petiole. Previous studies have demonstrated how plant traits, such as the presence of leaf veins (Magal et al. 2000; Casas et al. 2007), leaf area, or leaf thickness (Velilla et al. 2020) affect the propagation of vibrations. This result is important for caterpillars, since they may seek out less resonant leaf areas to rest throughout the day to avoid detection by predators.

Do caterpillars respond to leaf vibrations?

Our findings support the hypothesis that fall armyworm larvae are able to detect and respond to abiotic and biotic vibrations. Caterpillars exposed to abiotic stimuli consistently changed their behavior when exposed to wind and raindrops, regardless of instar. For instance, wind-induced vibrations led caterpillars to crawl more, particularly in the direction of the leaf's border and abaxial portion. In addition, prior to each new crawl, the caterpillar performed a 'touch around' activity in which it lifted its thoracic legs and anterior segments and then touched the leaf along its own axis (Table S1), which likely allows it to inspect the environment. Raindrop-induced vibrations on the other hand caused caterpillars to change from 'crawling' to 'resting', which also resulted in more time spent in both of these behaviors. These

are important responses, as both wind and rain can affect the growth and survival of caterpillars (e.g., Chen et al. 2018; 2019). Thus, it is likely that fall armyworm larvae are gathering information about the environment and changing their behaviors accordingly. We suspected that the caterpillars' movement toward the abaxial portion of the leaves was an act to find refuge and avoid being blown away by a strong wind gust. Similarly, staying still (i.e., resting) during rain may anchor larvae to the substrate to avoid being dislodged.

Our results also support the hypothesis that caterpillars detect and respond to biotic stimuli when approached by a conspecific of the same instar, or a predator. The behavioral responses were not consistent between instars, as first instars did not respond to the approach of a conspecific or predator, whereas caterpillars from second to fifth instars responded. Our findings showed that second to fifth instars displayed different behavioral responses when confronted with conspecifics compared to predators. Caterpillars exposed to conspecifics spend more time crawling, touching around, or resting, and only a small percentage of their time feeding or defending themselves. In contrast, caterpillars exposed to predators spend more time freezing, feeding, and resting, and only a small proportion of time engage in other behaviors. These results suggest that fall armyworm larvae can distinguish between the vibrations produced by the two types of invaders that they would naturally encounter. Neonates of the fall armyworm exhibit a highly aggregated spatial distribution on plants, as females lay eggs in large masses (Santos et al. 2004; Farias et al. 2008). However, in subsequent instars, the caterpillars disperse, assuming a more random spatial distribution (Farias et al. 2008), which occurs to mitigate the possibility of cannibalistic behavior (Sparks 1979; Andow et al. 2015) that can occur under low food availability and high population densities (Elgar and Crespi 1992). As a result, only one or very few larvae per plant are typically found (Sparks 1979). Additionally, the fall armyworm larvae are prey and hosts for a variety of predators and parasitoids (Gross and Pair 1986; Zalucki et al. 2002). Therefore, caterpillars would benefit from detecting and responding to leaf vibrations resulting from these threats. We argue that first instars do not respond to conspecifics or predators because first instars do not generate noticeable vibrations on the leaves while crawling, making it unlikely that other organisms can detect them. Also, early instars do not supply enough food for predatory stinkbugs, which is evidenced by their preference for later instars and pupae of lepidopterans (Vacari et al. 2013).

Overall, these results support the hypothesis that fall armyworm larvae detect and respond to both abiotic and biotic vibrations, as caterpillars responded differently in the presence of leaf-borne vibrations than they did under control conditions where vibrations were absent. However, it is important to note that other sensory modalities (e.g.,

tactile, visual, and chemical) may contribute to behavioral responses. Further studies aimed at decoupling vibrations from other stimuli using playback methods, or isolating vibrations from other stimuli, will expand our understanding of the vibratory sensory ecology of these insects.

Author contribution

All authors contributed to the study conception and design. LMT and LCJr established the experimental protocols, and JEY and RNCG provided analytical tools. LMT and LCJr performed the experiments. LMT analyzed the data. LMT, JEY and RNCG wrote the manuscript, which was read, corrected, and approved by all of the authors.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. The datasets supporting the conclusions of this article are included within the article and its additional files.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were considered in the present investigation.

Informed consent The authors of this manuscript accept that the paper is submitted for publication in the *Journal of Pest Science*, and report that this paper has not been published or accepted for publication in another journal, and it is not under consideration at another journal.

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