

Resonance in herbaceous plant stems as a factor in vibrational communication of pentatomid bugs (Heteroptera: Pentatomidae)

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Pentatomid bugs communicate using substrate-borne vibrational signals that are transmitted along herbaceous plant stems in the form of bending waves with a regular pattern of minimal and maximal amplitude values with distance. We tested the prediction that amplitude variation is caused by resonance, by measuring amplitude profiles of different vibrational pulses transmitted along the stem of a *Cyperus alternifolius* plant, and comparing their patterns with calculated spatial profiles of corresponding eigenfrequencies of a model system. The measured distance between nodes of the amplitude pattern for pulses with different frequencies matches the calculated values, confirming the prediction that resonance is indeed the cause of amplitude variation in the studied system. This confirmation is supported by the resonance profile obtained by a frequency sweep, which matches theoretical predictions of the eigenfrequencies of the studied system. Signal bandwidth influences the amount of amplitude variation. The effect of both parameters on signal propagation is discussed in the context of insect vibrational communication.

Keywords: resonance; herbaceous stems; substrate-borne vibrational communication; Pentatomidae

1. INTRODUCTION

Herbaceous plants are the usual environment of most species of the insect family Pentatomidae [1] and their stems represent the communication channel for short- to medium-distance exchange of vibratory signals produced mainly in the context of mating behaviour [2]. This family comprises some of the best known species that communicate by plant-borne vibration, which is an otherwise understudied communication modality. The work of Michelsen *et al.* [3] is regarded as pioneering in understanding the significance of rod-like herbaceous plant tissues as a channel for propagating insect vibrational signals. It shed light on basic aspects of physics of plant-borne vibrational communication, showing that signals produced by plant-dwelling insects transmit in the form of bending waves, with particle displacement occurring in the plane perpendicular to the surface and propagation of vibration in the plane parallel to the surface [3,4]. The authors also raised the issue of vibration reflecting from endpoints of the plant, which they suggested as the cause of nonlinear spatial variation of amplitude observed in the same study [3]. Since then, spectral characteristics of signals used for

vibrational communication by plant-dwelling species of suborder Heteroptera were shown to be generally tuned with resonance properties of herbaceous host plant stems [2,5] that act as a low-pass filter [6]. As a consequence, transmission of signals along this type of substrate is remarkably efficient, so reflection might indeed be important.

Mechanisms of signal production within the family Pentatomidae include dorsoventral abdomen vibration involving a specific series of muscles attaching to the fused first and second abdominal tergites (previously called ‘tymbal’), percussion (striking the surface with a body part) and tremulation (whole-body oscillations not involving specific anatomical features or striking the substrate) [5,7]. Until now, species of the subfamily Pentatominae have been described as producing signals by abdomen vibration, with the dominant frequency around 100 Hz [2]. However, the recently described repertoire of vibratory songs of the pentatomid subfamily Asopinae has shown that the frequency range of signals produced by other mechanisms may extend down to 10 Hz and to well above 1 kHz [8,9].

The amplitude/distance profile of pentatomid vibratory signals with fundamental frequencies of around 100 Hz exhibits low attenuation and regularly repeated, stationary amplitude peaks on plants [10]. The observed

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variation with distance is assumed to be caused by waves rebounding from endpoints and interfering with forward-travelling vibrations [3]; in other words, it is the consequence of standing waves formed at the plant. However, this assumption has not been systematically tested. Moreover, in research on plant transmission properties, vibrations are usually induced by a vibrating device fixed to the plant [10–12], which constitutes mass loading and may influence boundary conditions of the system. The question as to whether the observed amplitude variation is representative of natural dynamics remains open. Standing waves in finite size systems are a common phenomenon; however, there are certain aspects that need to be checked, most notably (i) the properties of damping that lead to the attenuation of bending waves and (ii) whether the wave pattern is stationary, i.e. given a particular excitation, is the transient of the build-up of the standing waves short enough for a fully developed, stationary standing wave to form. Any of these factors could prove hindering to the formation of standing waves. If the attenuation length is comparable with or shorter than the length of the stem, there is no wave to be reflected from the free end of the stem or it is very weak, and no standing wave will be formed. Furthermore, when the excitation is started, or if it is not stationary (as is certainly true in the case of natural excitation), many eigenmodes are being excited simultaneously, leading to a transient, irregular wave pattern that does not exhibit the stationary amplitude envelope characteristic of the standing wave. A certain time after the beginning of the excitation process is required for these eigenmodes to be damped, and only a few with eigenfrequencies close to the excitation frequency remain, resulting in a standing wave. The characteristic time of this transient again depends on the damping of the eigenmodes: the larger the damping, the shorter the transient and the quicker the formation of stationary standing waves.

To address these questions, we investigated the variation of the amplitude of artificially and naturally induced vibrations relative with distance from the source of vibrations on a model plant species. As a model, we chose the umbrella flat sedge (*Cyperus alterifolius* L., Cyperaceae) because it has a single long, straight and relatively uniform stem without branches, which simplifies the geometry and the boundary conditions. Such a system can be modelled as a long, thin elastic rod, the dynamics of which is well established and described in standard engineering literature [13].

Our attention was focused on the relationship between the dynamics of the studied system and spectral properties of vibratory signals produced by members of the subfamily Pentatominae, as well as the less understood tremulatory signals of *Podisus maculiventris*. Signals of *Nezara viridula* were included since this species' sexual behaviour is the most extensively studied, representing a model for the whole family [14]. The umbrella flat sedge is not typically regarded as the host plant of this species, however, *N. viridula* is an extremely polyphagous herbivore, feeding on herbaceous plants from over 30 families (reviewed by Todd [15]). Hosts

include monocot crops, such as rice, wheat and barley with geometry and structure similar to that of a sedge plant, which also serve as the mating and oviposition sites [15]. It is therefore reasonable to assume that the studied system can be generalized to at least a part of the pentatomid host range. Furthermore, animals from the laboratory colony of *N. viridula* fed readily on the sedge bush we kept for experiments (J. Polajnar 2010, personal observation).

The aims of the present study were (i) to determine the degree of peak amplitude variation of various types of signals during their transmission through a sedge plant stem, (ii) to test the observed amplitude/distance variation against a simplified model of resonance modes, and (iii) to evaluate the applicability of these results to conditions in nature, i.e. the emitter–receiver system of singing bug and listener.

2. MATERIAL AND METHODS

All experiments were conducted at room temperature at the Department of Entomology of the National Institute of Biology in Ljubljana.

2.1. Plants

The sedge plant was grown in a mix of natural soil and vermiculite in a 20 cm high pot of 25 cm diameter. The pot, placed on an antishock iron table, was isolated from its surface by 10 cm thick foam. Environmental noise was reduced below 20 dB SPL for airborne sound and 10^{-4} m s⁻¹ for substrate-borne vibrations. Experiments were conducted on individual stems not in contact with others from the bunch above ground level, with leaf rosettes cleanly cut off. Two stems from the same plant were used, with approximately 4.5 mm diameter and heights of 84 and 89.5 cm. Another stem with comparable diameter was cut for determining material properties—density and elasticity.

Material properties, including the static Young's modulus, were determined using stem sections of 4.36 mm diameter. The cross-section geometric moment of inertia, described by the equation

$$I = \frac{\pi \cdot r^4}{4}, \quad (2.1)$$

was 1.77 m⁴. A cut section was clamped on one side in a horizontal position, with a 17.3 cm long free end. A series of weights were hung on the far side and vertical displacement was measured. Young's modulus of the stem could then be calculated from

$$E = \frac{F \cdot L^3}{3 \cdot \delta \cdot I}, \quad (2.2)$$

where δ is displacement, F is force and L is length.

2.2. Excitation

The plant was vibrated by the tip of a metal cone (base diameter = 15 mm, height = 45 mm), screwed firmly into the head of a mini-shaker (Type 4810 10N, Brüel & Kjær, Denmark) and fixed to the stem with Blu-Tac

putty (50–60 mg weight). Vibrations were introduced directly to the stem 2 cm below the top, perpendicularly to the stem's long axis. The mini-shaker was driven from a computer via a sound card (24-bit, 96 kHz, 100 dB signal-to-noise ratio, Sound Blaster Audigy 4, Creative laboratories Inc., Milpitas, CA, USA).

The signal simulation program consisted of pure-tone sine wave pulses with different temporal and spectral characteristics, and natural vibratory pulses of *P. maculiventris* and *N. viridula* pre-recorded on a non-resonant loudspeaker membrane (10 cm diameter low-midrange loudspeaker, 40–6000 Hz frequency response, 8 Ω impedance, RadioShack Taiwan). The simulation sequence was assembled using the Cool EDIT PRO software (SYNTRILLIUM Software, 2003) that was also used to normalize the pulses to 10^{-3} m s^{-1} peak velocity, measured at the tip of the cone, which is within or just above the range of vibrations produced by the studied species and other pentatomid species in which vibrational communication is described [8–10]. The program included sequences of 10 artificially synthesized pure-tone pulses with 20, 100 and 200 Hz followed by sequences of spectrally different signals produced by abdomen vibration or tremulation. Tremulatory signals of the regularly (MS-Tr) and irregularly (MS-Tirr) repeated pulses were produced by *P. maculiventris*, and male and female calling song (FCS) pulses by *N. viridula*. Pulses were separated by at least 0.5 s long periods of silence. Pulses' temporal and spectral characteristics measured at the point of excitation are shown in table 1.

The resonance profile of plant stems was analysed using a custom software-generated 10–500 Hz frequency sweep that followed the signal sequence. The constant-amplitude sweep was modified to compensate for nonlinear frequency response of the playback equipment, and to produce constant-velocity output at 10^{-3} m s^{-1} .

2.3. Recording

Vibrations were detected with an OFV 5000/505 laser vibrometer (Polytec GmbH, Waldbronn) directed horizontally at a right angle to the stem. Three millimetre-wide bands of reflective tape were glued around the stem, 5 cm apart along the stem, from 2 to 50 cm below the leaves. The bands were not glued more densely in order not to influence wave propagation. The first measurement point, serving as a reference for other measurements, was opposite to and level with the point of vibration by the mini-shaker. After recording the whole pulse and sweep sequence, the laser was lowered to a point 5 cm below and the stimulation by this sequence was repeated. The same computer sound card was used for both playback and recording. Laser output in velocity units was digitized at 16 kB s^{-1} sample rate and stored in an uncompressed format.

2.4. Modelling

Frequencies of measured resonance peaks—the system's eigenfrequencies—were compared with values calculated with the formula for a fixed-free elastic rod [13],

Table 1. Signals used for artificial excitation of the stem. Sin: pure-tone sinusoidal vibration; MS-A: *P. maculiventris* male song, vibratory pulses; MS-T_r: *P. maculiventris* male song, regularly emitted tremulatory pulses; MS-T_{irr}: *P. maculiventris* male song, irregularly emitted tremulatory pulses; Nez-FCS: *N. viridula* female calling song, vibratory pulses; Nez-MCS: *N. viridula* male calling song, vibratory pulses. Bandwidth is measured in the frequency spectrum 20 dB below the dominant frequency peak (figure 3), except for MS-T_r pulses where determination was not possible due to low frequency and wide frequency peaks.

signal type	dominant frequency (Hz)	duration (s)	bandwidth (Hz)
Sin200	200	0.200	26
Sin100	100	0.600	8
Sin20	20	0.600	8
MS-A-hi	145	0.214	61
MS-A-med	127	0.188	44
MS-A-lo	87	0.148	26
MS-T _r -hi	23	0.130	—
MS-T _r -med	13	0.127	—
MS-T _r -lo	5	0.188	—
MS-T _{irr} -hi	90	0.989	75
MS-T _{irr} -med	50	0.847	63
MS-T _{irr} -lo	31	0.766	113
Nez-FCS	89	1.232	7
Nez-MCS	40	0.240	29

which is a reasonable approximation of the studied system, using material parameters of the cut stem.

Bending of a thin elastic rod is described by the dynamic equation

$$EI \frac{\partial^4 u}{\partial x^4} + \rho_1 \frac{\partial^2 u}{\partial t^2} = 0, \quad (2.3)$$

where E is the Young's modulus, I is the cross-section geometric moment of inertia and ρ_1 is the mass density per unit length. For a given vibration frequency, $\nu = \omega/2\pi$, the solution is of the form

$$u(x, t) = (A \sinh kx + B \cosh kx + C \sin kx + D \cos kx)e^{-i\omega t}, \quad (2.4)$$

where

$$k^4 = \frac{\omega^2 \rho_1}{EI}, \quad (2.5)$$

and A , B , C and D are constants, determined by the boundary conditions. A non-trivial solution exists, when

$$\sin kL \cos kL = -1, \quad (2.6)$$

where L is the length of the rod. The first 10 solutions are $\xi_n = k_n L \approx 1.88, 4.69, 7.85, 11.00, 14.14, 17.28, 20.42, 23.56, 26.70, 29.85, 32.99, 36.13, 39.27, 42.41, 45.55$ and 48.69 . The frequencies ν_n of the eigenmodes are thus:

$$\nu_n = \frac{\xi_n^2}{2\pi L^2} \sqrt{\frac{EI}{\rho_1}}. \quad (2.7)$$

A convenient way of verifying equation (2.7) is to shorten the stem in steps and repeat the frequency sweep at lower values of L . By fitting the function

$$y = \frac{a}{L^2}, \quad (2.8)$$

to the measured dependence of a given eigenfrequency, ν_n , on the stem length, L , one can effectively extract the coefficient a , and hence the Young modulus:

$$E = \left(\frac{2\pi a}{\xi_n^2} \right)^2 \frac{\rho_1}{I}. \quad (2.9)$$

The spatial profile of the vibration eigenmode corresponding to the frequency ν_n is

$$u_n(x) = A \left[\sinh k_n x - \sin k_n x - \frac{\sinh k_n L + \sin k_n L}{\cosh k_n L + \cos k_n L} \times (\cosh k_n x - \cos k_n x) \right]. \quad (2.10)$$

In a case where the excitation frequency does not correspond to one of the eigenfrequencies of the system, the amplitude at x , when excited at x' , is obtained by the following response function:

$$G(x, x', k) = \sum_n \frac{u_n(x)u_n(x')}{k_n^2 - k^2}, \quad (2.11)$$

where k is the excitation wavenumber (equation (2.6)). Note that this is the response function for undamped vibration modes and is, as such, only approximate in a realistic scenario. Furthermore, the eigenfunctions u_n entering equation (2.11) must be normalized. It turns out, however, that the norm of all the u_n , except the lowest one, is very close to 1 and hence need not be considered for our purpose. In practice, one typically adds only two adjacent eigenmodes with k_n closest to k ,

$$G(x, x', k) \approx \frac{u_n(x)u_n(x')}{k_n^2 - k^2} + \frac{u_{n+1}(x)u_{n+1}(x')}{k_{n+1}^2 - k^2}. \quad (2.12)$$

Points where this function crosses zero are nodes, while peaks are antinodes. In recordings, we analysed the peak amplitude disregarding its sign, so the absolute value of the eigenfunction has to be plotted for comparison.

2.5. Terminology and data analysis

Time characteristics of pulses or pulse trains are described by their duration (the time between the onset and the end), repetition time (the time between the onsets of two consecutive pulses) and the pause (the time between the end of one pulse and the onset of the next). Frequency characteristics of pulses are described by the dominant frequency peak and bandwidth, where the bandwidth is the frequency range of a pulse measured 20 dB below the maximum in its frequency spectrum. Signal amplitude is expressed as particle velocity on a plane perpendicular to the surface, which is proportional to particle displacement in sinusoidal movement (according to the equation: velocity = $2\pi f \times$ displacement). Note that this slightly

changes the relative amplitudes of eigenmodes with frequencies different from those modelled using the methods described above, which represents displacement rather than velocity. However, this mainly changes the amplitude and leaves the positions of resonance peaks virtually unaltered. Likewise, the sum of the two eigenmodes in equation (2.12) is only weakly modified as their frequencies are close to each other. The peak velocity of the whole pulse envelope is used for determining its amplitude at a given location. Amplitude differences are expressed in relative units (decibels).

Data analysis and calculations were performed by the R programming language v. 2.9.2 (R Development Core Team 2009), with the package SEEWAVE [16] for sound analysis. The amplitude at a given distance, for a given pulse type and frequency, is presented as the average of 3–10 repetitions of the same pulse. Individual repetitions were excluded if their amplitude differed visibly owing to either external (acoustic) or internal (electronic) noise bursts. Frequency spectra were obtained by selecting a whole pulse and performing a fast Fourier transform (FFT) analysis with the package SEEWAVE (Hanning window, window length 512 points). One representative spectrum of the given pulse type at a given point is shown in each figure.

3. RESULTS

3.1. Material properties

A weight of 9 g produced 6 mm displacement in 17.3 cm long cut section of the 4.36 mm wide stem, and other displacements confirmed that the weight/displacement ratio was linear. For the given values of force, displacement, length and second moment of area, Young's modulus was $1.42 \times 10^9 \text{ Nm}^{-2}$. A 10 cm long section of the same stem weighed 0.989 g, which gives $7.49 \times 10^5 \text{ g m}^{-3}$ density and 9.89 g m^{-1} density per unit length.

3.2. Characteristic equilibration time

Even in the case of pure sinusoidal excitation at one frequency, all vibration eigenmodes are excited at the beginning, which can result in rather chaotic transient wave behaviour. During this transient, the excited modes are subject to damping, while only those with frequencies close to the excitation frequency increase in amplitude as energy is pumped in. This transient time, in which a steady vibration at the excitation frequency sets in, forming the standing wave, is inversely proportional to damping: the stronger the damping, the shorter the transient. The steady state is reached within a fraction of a second (figure 1). Such short equilibration time means that, whenever a steady excitation lasts for a fraction of a second or more, a standing wave is formed on the stem.

3.3. Eigenfrequencies and resonance

Frequency sweep was applied to two *C. alternifolius* plants by a mini-shaker attached to the top of the stem. The sweep revealed several resonance frequencies

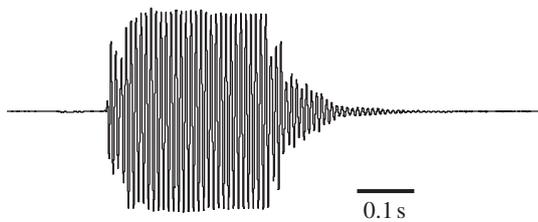


Figure 1. An oscillogram of a sine pulse with rectangular pulse envelope and the frequency corresponding to one of the eigenmodes of a cyperus plant (109 Hz on *Cyperus 1*), recorded 10 cm below the source of vibration. Steady state is reached after a couple of tenths of a second.

between 10 and 500 Hz (figure 2 and table 2). The exact position of peaks differed between the plants, but their ratios were constant.

The calculated and measured resonance characteristics were compared for both sedge plants (table 2). The first two resonance peaks were too low to be detected by a sweep from 10 Hz up, but the values obtained correspond well with the calculated values. The measured frequency of successive eigenmodes increases slightly faster than those of the calculated sequence.

We also tested the resonance properties of an intact stem. All the resonance frequencies of an intact stem are only 4 per cent higher than those of the same stem with the leaf rosette cleanly cut off at the top, which indicates that the change in wave propagation at the stem–rosette junction is large enough for it to act as a free end. Apparently, the presence of a leaf rosette does not significantly influence the resonance properties of the stem.

3.4. Amplitude variation along the stem

The peak transverse velocity of the stem's surface changed with distance for all the frequencies tested with pure-tone signals. We observed a regular pattern of local maxima and minima, consistent with the model of rebound signals interfering with forward-travelling vibration (figure 3). The same phenomenon was apparent when the amplitudes of individual resonance peaks within the frequency sweep were measured down the length of the stem.

The spatial profile of the vibration eigenmodes (equation (2.10)) represents the spatial dependence of the standing wave amplitude. The measured wavelengths of peak amplitude oscillations are in agreement with the calculated values for different points along the stem (figure 4).

Equation (2.7) predicts a reciprocal quadratic dependence of the resonance frequency on the length of the stem; this is clearly seen on the plot of the observed resonance frequencies versus stem length (figure 5). Starting with the second resonance frequency peak (the first one was too low to be detected by a sweep from 10 Hz up), fitting to the function in equation (2.9) yields values of E that increase consistently on going to higher resonances, ranging from $4.81 \times 10^9 \text{ N m}^{-2}$ (using the second resonance peak, roughly three times the originally measured E) to $1.97 \times 10^{11} \text{ N m}^{-2}$ for the

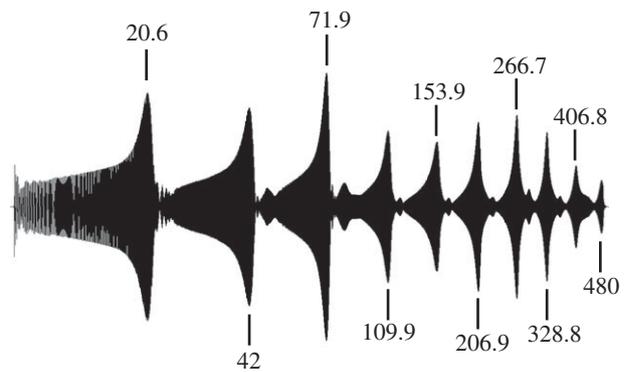


Figure 2. An oscillogram showing the resonance profile of the 89.5 cm tall sedge plant (*Cyperus 2*) with leaf rosette cut off, recorded at 5 cm away from the source of vibration. The frequency sweep starts at 10 Hz on the left and ends at 500 Hz on the right (note that the increase in frequency is not linear). Ten resonance peaks are clearly visible, starting with the third one at 20.62 Hz and ending with the 12th one at 480 Hz (see table 2 for details).

ninth resonance peak which is 100 times the original E (figure 6).

Examples of spatial profiles of vibration at non-resonance frequencies are given in figure 7. The distance between nodes of the measured amplitude pattern at successive points along the stem, of both pure-tone sine wave pulses and animal signals, agrees with theoretical prediction.

The pattern of narrow-band, naturally emitted pulses with pronounced dominant frequencies, such as that of the *N. viridula* FCS, reproduced by a mini-shaker, was comparable with that of pure-tone signals. On the other hand, irregularly repeated tremulatory pulses of *P. maculiventris* (MS-Tirr) and male calling song pulses of *N. viridula* (MCS) generally have broad frequency peaks [17], which is also the case with recordings used in this study (figure 3 and table 1). Different frequency components within a single pulse contributed to smoothing of variation, which became practically unobservable further away from the source.

We analysed amplitude ratios obtained by subtracting relative velocity values of antinodes from relative velocity values of adjacent nodes (in decibels, both relative to the reference) in the spatial profile. The correlation between node–antinode amplitude ratio and bandwidth of dominant frequency peaks was negative, with a correlation coefficient of -0.56 ($p < 0.001$, $n = 105$). The eigenmodes of the plant are still evident within the erratic vibrational motion in Fourier space when the plant is vibrated with pulses that have wide frequency peaks (figure 8), and it is their amplitudes relative to one another that change with distance from the source.

The largest observed amplitude reduction in narrow-band natural signals was -13 dB for a *N. viridula* FCS pulse at a distance of 85 cm from the source on one of the sedge plants, which corresponds to a velocity of 0.22 mm s^{-1} at 1 mm s^{-1} reference. Even with the top of the plant fixed to the mini-shaker, amplitude either increased or decreased immediately next to it, depending on the positions of nodes and antinodes.

Table 2. Comparison between calculated and measured resonance characteristics for the two sedge plants.

plant	Cyperus 1		Cyperus 2		
height	84 cm		89.5 cm		
resonance peaks up to 500 Hz					
no.	K_n	calculated (Hz)	measured (Hz)	calculated (Hz)	measured (Hz)
1.	3.52	1.23	—	1.12	—
2.	22.03	7.94	—	6.99	—
3.	61.70	22.22	20.62	19.58	15.13
4.	120.90	43.55	42.02	38.36	31.06
5.	199.86	71.99	71.94	63.41	68.49
6.	298.56	107.54	109.89	94.73	103.09
7.	416.99	150.20	153.85	132.30	145.45
8.	555.16	199.97	206.90	176.14	190.48
9.	713.08	256.85	266.67	226.25	250
10.	890.73	320.83	328.77	282.61	307.69
11.	1088.12	391.93	406.78	345.24	372.09
12.	1305.25	470.14	480.00	414.14	438.36

In most cases, peak velocity varied around 0 dB relative to the reference along the whole distance tested, gradually attenuating towards the far end. Despite attenuation, amplitude decreased less than the difference between nodes and antinodes in all pulse types except *N. viridula* MCS.

Consequently, such signals detected at the last antinode up to 60 cm away still had higher velocity than the reference. Attenuation is not included in models presented above. To obtain a rough estimate, we therefore measured, where possible, the amplitude at the first and last antinodes. Attenuation of 100 Hz pure-tone pulses amounted to -2.98 dB at 30 cm distance, or 0.1 dB cm^{-1} , and 200 Hz pure tone pulses were attenuated 0.06 dB cm^{-1} . The lowest measured attenuation was 0.02 dB cm^{-1} for *N. viridula* FCS, which has a dominant frequency of 89 Hz, and the largest was 0.1 dB cm^{-1} for both 100 Hz pure tone signals and *P. maculiventris* MS-1, with 145 Hz dominant frequency. Attenuation correlated with neither frequency difference from the nearest resonance peak nor with the bandwidth of pulses used. All attenuation values are approximate, because the actual peaks may be missed by up to 2.5 cm owing to the given measuring resolution.

4. DISCUSSION

Plants, and especially their rod-like structures like stems and stalks, constitute the medium for long-range vibratory communication between insects along the plant. Judging by the propagation velocities and frequency characteristics of their signals, insects produce and use bending waves [3,4]. Regular variation of frequency-dependent peak amplitude with distance from the source, as observed in this study, has been detected along herbaceous stems of various plant species for both artificially [18] and naturally induced stink bug signals [11]. On the other hand, little is known about transmission of vibration along other herbaceous tissues, where research has been limited to

general transmission properties. Experiments indicate low-pass frequency filtering by unstructured leaves [19], whereas in leaf petioles, the situation is more complex: for example, in the biologically relevant range, petioles of *Cercis canadensis* L. appear to impose a high-pass filter, but in *Ptelea trifoliata* L. petioles, the filtering is band-pass type [20].

The measured periodicity of peak amplitude variation in a sedge stem corresponds reasonably well to the mathematical representation of resonance, confirming the hypothesis that this variation has its origin in resonance. It should be noted again at this point that the actual system's structure differed from the model's assumptions—the stem's cross section is not perfectly homogeneous, and the 'free' end was in contact with the vibrating device, all of which influenced node positions. Nevertheless, the measured internode distance of amplitude patterns for pulses with different frequencies matches the calculated values, confirming the prediction that resonance is indeed the cause of amplitude variation in the studied system. This conclusion is further supported by the resonance profile obtained by a frequency sweep, which matches theoretical predictions of the eigenfrequencies of the studied system.

Slight differences are not surprising, due to the non-homogeneous nature of the measured system and the difference between the stem used for determining material properties and the vibrated ones. Most notably, Young's modulus calculated from resonance frequency/stem length curves differs from the directly measured one, especially at higher frequencies.

Likewise, the frequency of higher resonance modes differs from calculated values more than the frequency of lower resonance modes. This could be attributed to the difference between static and dynamic properties of the stem as a viscoelastic object and is an interesting result by itself, but is out of the scope of this study. The directly measured values of Young's modulus are comparable with those obtained by other researchers, for example, 3×10^8 N m^{-2} in the reed *Phragmites communis* Trin. [3].

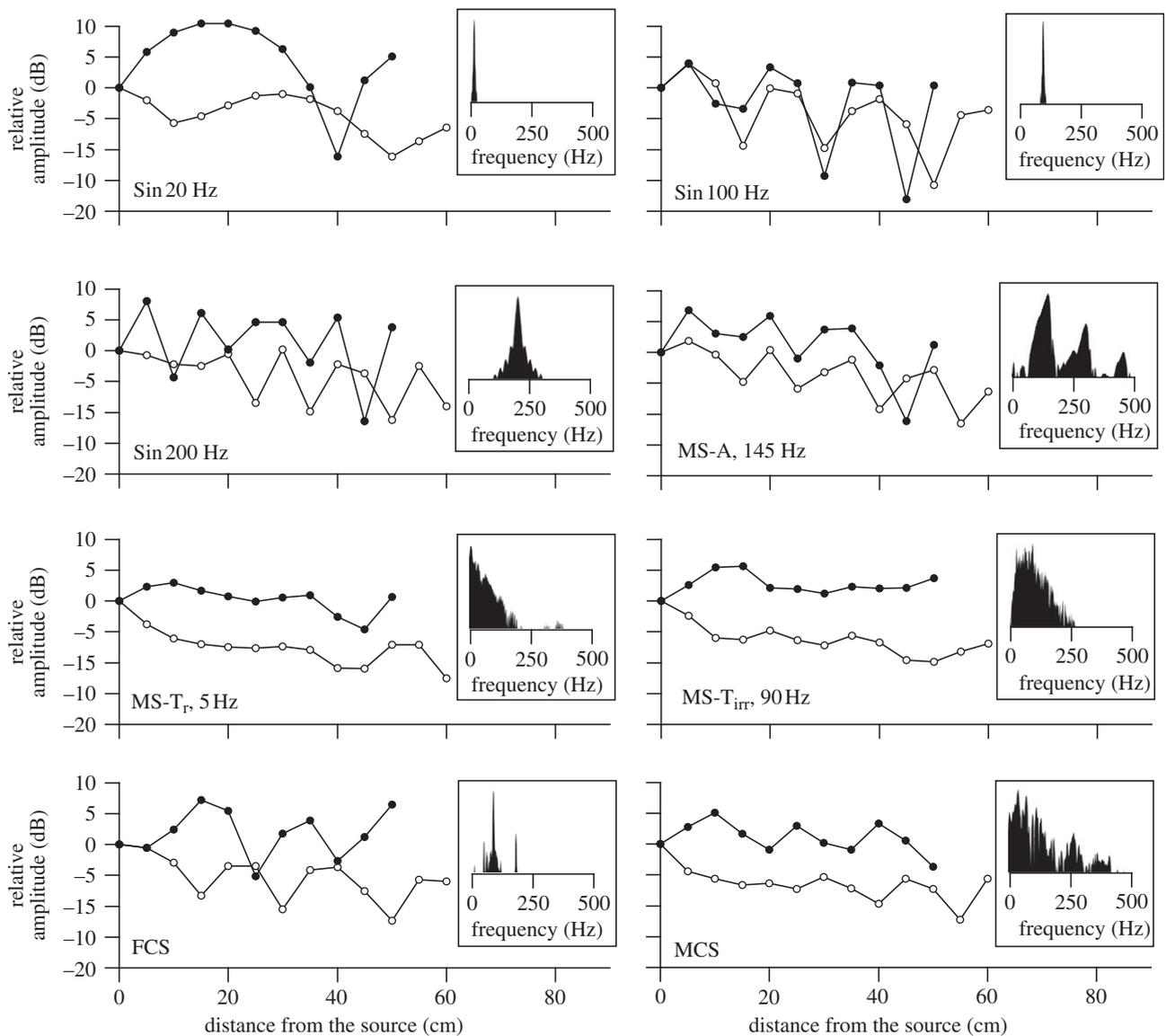


Figure 3. Distance–amplitude profiles of studied signals on the two sedge plants (filled circles: *Cyperus 1*, empty circles: *Cyperus 2*). One frequency variant of each *P. maculiventris* signal type is shown. Amplitudes are given in decibels relative to the amplitude at the source, which is approximately 1 mm s^{-1} peak-to-peak velocity. Each signal's frequency spectrum is shown in the graph's inset. Amplitude scale is in decibels relative to the strongest peak's amplitude (0 dB) and -60 dB at the bottom. Parameters are listed in table 1.

We were not able to record propagation of live animals' signals in the studied system with leaves cut off. Propagation of *N. viridula* female signals has been recorded in a similar study, with animals standing on sedge leaves and with the reference point 0.5 cm below the leaf rosette [10]. The distance–amplitude profile of FCS signals obtained on 50–60 cm long stems matches the one presented here, with 14 cm distance between the nodes and attenuation by approximately 0.14 dB cm^{-1} overall. Therefore, it is reasonable to conclude that results obtained in the present study can be generalized to conditions in nature, despite difference in excitation method. It should also be noted that in principle, neither the nature of waves, nor the existence of resonance itself are critically affected by boundary conditions. The difference from excitation by insects is therefore merely quantitative, in terms of values of the resonance frequencies and the position of nodes.

The observed phenomena have several implications for insect vibrational communication which need to be further tested experimentally. Most notably, a regular pattern of nodes and antinodes is expected to influence signal detection. Even though absolute values at nodes do not fall below the vibrational receptor threshold, as determined for *N. viridula* [21], signals in nature are affected by competitive signalers' output and by ambient noise. Therefore, we predict that the searching animal prefers to listen at or near internodes when approaching the signaller, in order to increase signal-to-noise ratio. If animals are able to detect their own signals, the difference in resonance properties between plants is also expected to influence the choice of signalling position and frequency, but there is no experimental data so far to support these hypotheses. A study on a non-resonant surface revealed that *N. viridula* females are able to adapt the frequency of

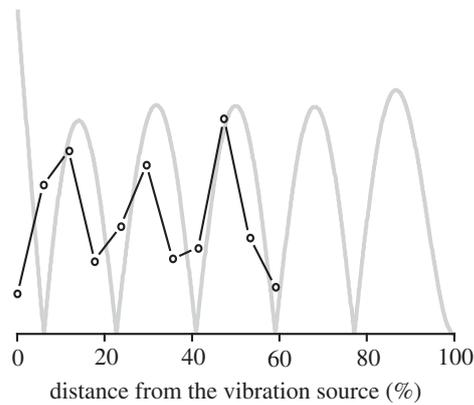


Figure 4. Comparison between peak amplitude variation of the sixth resonant peak with 109.9 Hz frequency at different points along the stem of the 84 cm high cyperus plant (black circles) and values calculated with equation (2.10) (grey line). Values on the y -axis are arbitrary.

their signals within singing bouts to varying conditions in their acoustic environment [22]. Both spectral and temporal characteristics of vibratory signals covary with host use in *Echenopa binotata* species complex of treehoppers (Hemiptera: Membracidae), which is regarded as a potential cause of species divergence [23] with demonstrated consequences of individual substrate variation for insect communication through plants [24]. However, in the case of larger phytophagous pentatomid bugs with strong flight capabilities, which can therefore use a wide range of hosts during their lifetime [1], the main part of variation is expected to occur between individuals rather than between populations.

On the basis of the amplitude profile of signals with different bandwidths (figure 3) and the change in spectral composition of signals with wide frequency peaks (figure 8), we argue that natural signals with complex spectral characteristics behave as the sum of their frequency components, as expected for a linear system. Different frequencies within a signal contribute to smoothing of variation which becomes practically unobservable in tremulatory signals. This may be a reason for the existence of signals with different bandwidths in a single species' repertoire [25]. In theory, signals with significant frequency components covering more than one resonance peak of the medium may convey information about presence which is less influenced by the signaller's position, while the function of signals that resemble sinewave pulses is probably more specific. Bending waves propagate dispersively along plants, meaning that propagation speed is frequency-dependent [26]. Thus, fewer frequency components would mean smaller degradation of the signal's envelope during propagation, preserving information stored in the signal's time domain which is important for mate recognition [27,28].

Finally, energetics of vibrational communication should be considered in connection with the described properties of the system. In principle, it is advantageous for the signaller to emit signals close to one of the resonance frequencies of the stem. The input impedance is minimum when in resonance, consequently, force is required to drive the system at a given velocity, and

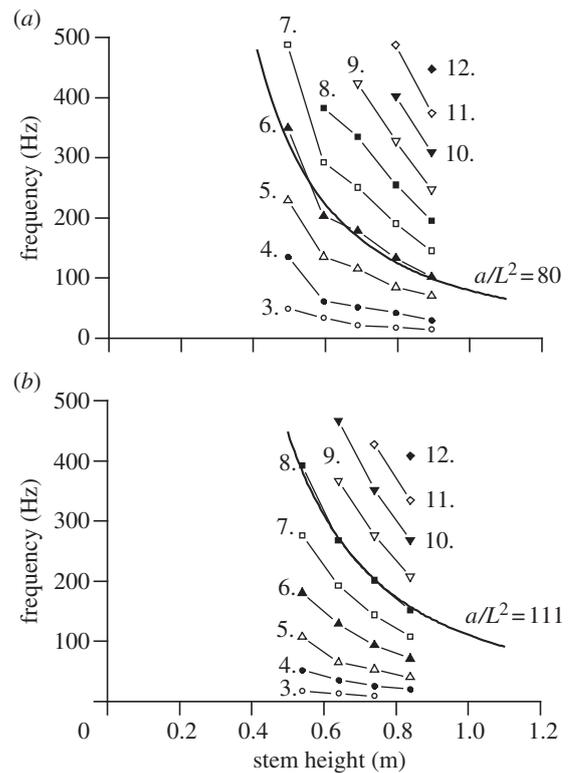


Figure 5. Plots of resonant peaks' frequency versus stem length for the two sedges tested ((a): Cyperus 1, (b): Cyperus 2). Each set of symbols connected with lines within a plot represents one resonance peak, from the third at the bottom (empty circles: around 20 Hz on an intact stem) to the 12th at the top (filled diamond: Cyperus 1: 480 Hz, Cyperus 2: 438.36 Hz). An example of the $y = a/L^2$ fit (see equation (2.8)) is given for each sedge.

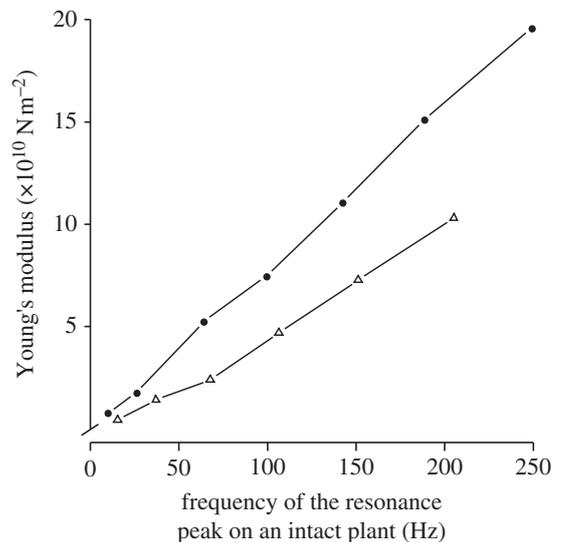


Figure 6. Values of Young's modulus calculated by fitting the function $y = a/L^2$ to the measured dependence of successive eigenfrequencies ν_n on the stem length L (equation (2.9); figure 5), shown for the two Cyperus plants tested.

therefore least mechanical power (energy consumption). Along with the position of nodes and internodes, resonant modes are thus the most obvious mechanical property of an individual plant stem, which any insect

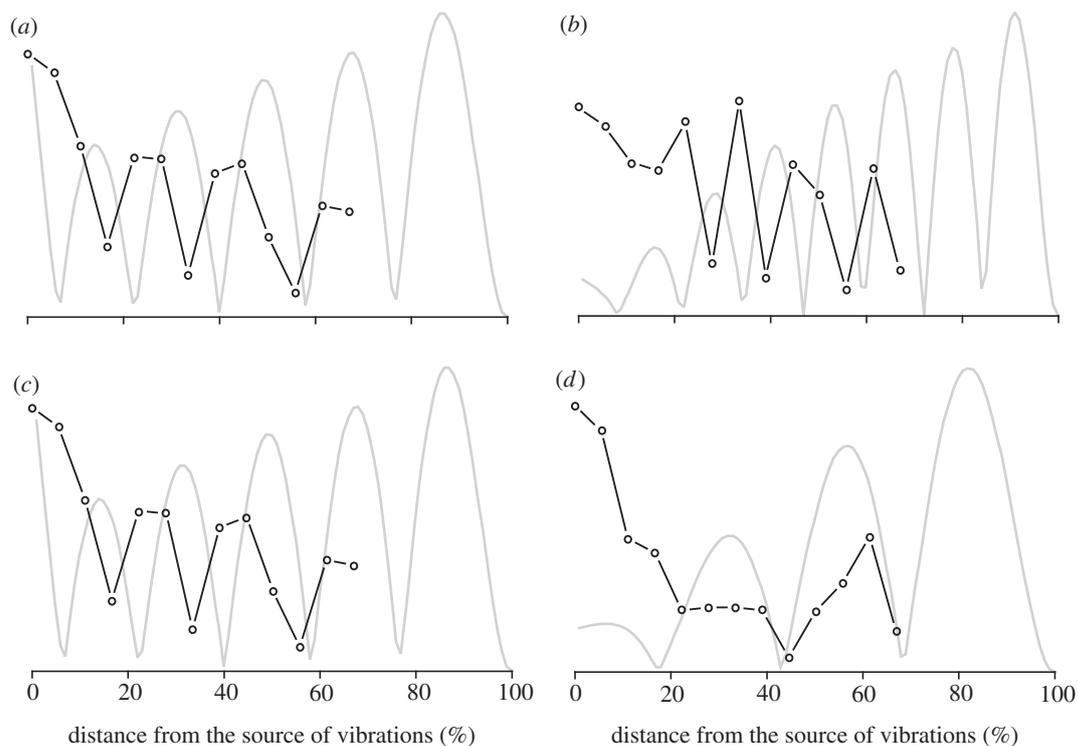


Figure 7. Comparison between observed amplitude variation of pulses with non-resonant frequencies (empty black circles) and calculated values (grey line) for the 89.5 cm high sedge (*Cyperus 2*). Y-axes are arbitrary, and one frequency variant for each pulse type is shown. (a) Twenty hertz sine wave; (b) 200 Hz sine wave; (c) *Nezara* FCS, 89 Hz; and (d) *Podisus* T_{irr} , 50 Hz.

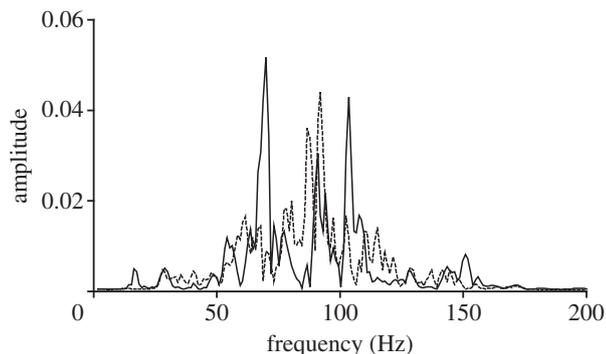


Figure 8. Comparison of frequency spectra of a signal with a wide frequency peak, the *Podisus maculiventris* MS- T_{irr} , with the dominant frequency 90 Hz (table 1 and figure 3), recorded at the source of vibration (dashed line; 0 cm) and 10 cm lower on the stem (solid line). The amplitude scale is linear—not expressed in decibels units as elsewhere—and the same for both spectra, however, values are arbitrary.

using it as a medium is expected to exploit. Additionally, less energy is needed to induce vibration in a material at lower frequencies [29]. Despite that, frequency range used by pentatomid bugs does not extend to the lowest resonance modes of the model system. There are two plausible explanations for such discrepancy: lowest frequencies are more often excited by ambient acoustic noise and wind, which renders them less suitable for use in communication [30]. Secondly, frequency may serve as an index of fitness in sexual selection, thereby driving the frequency range upwards. Attenuation does not appear to have a significant role since it was not influenced by excitation frequency.

In any case, systematic research is needed to correlate signalling with properties of the medium, which will enable conclusions to be drawn regarding the importance of resonance in communication systems of plant-dwelling insects. The basic phenomenon elucidated here is expected to occur on all substrates with comparable material properties (i.e. rod-like parts of herbaceous plants), but experimental data are for now extremely sparse, so the range of variation of parameters relevant for real-life situations remains to be determined.

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