

A method for two-dimensional characterization of animal vibrational signals transmitted along plant stems

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Abstract Conventional approaches to measuring animal vibrational signals on plant stems use a single transducer to measure the amplitude of vibrations. Such an approach, however, will often underestimate the amplitude of bending waves traveling along the stem. This occurs because vibration transducers are maximally sensitive along a single axis, which may not correspond to the major axis of stem motion. Furthermore, stem motion may be more complex than that of a bending wave propagating along a single axis, and such motion cannot be described using a single transducer. Here, we describe a method for characterizing stem motion in two dimensions by processing the signals from two orthogonally positioned transducers. Viewed relative to a cross-sectional plane, a point on the stem surface moves in an ellipse at any one frequency, with the ellipse's major axis corresponding to the maximum amplitude of vibration. The method outlined here measures the ellipse's major and minor axes, and its angle of rotation relative to one of the transducers. We illustrate this method with measurements of stem motion during insect vibrational communication. It is likely the two-dimensional nature of stem motion is relevant to insect vibration perception, making this method a promising avenue for studies of plant-borne transmission.

Keywords Substrate vibration · Animal communication · Laser vibrometry · Signal transmission · *Umbonia crassicornis*

Introduction

Many plant-dwelling insects use substrate-borne vibrations in communication and in detection of predators and prey (Cokl and Virant-Doberlet 2003; Virant-Doberlet and Cokl 2004; Cocroft and Rodríguez 2005; Casas and Magal 2006). Studies of substrate-borne vibrations have shown that in plant stems and leaves, these vibrations propagate in the form of bending waves (Barth 1998; Cocroft et al. 2000; Michelsen et al. 1982). As bending waves propagate along a stem, motion of the substrate is perpendicular to the direction of wave propagation (Cremer et al. 1973). In theory other waves can occur in rod-like structures (Markl 1983; Michelsen et al. 1982), such as quasi-longitudinal waves, which produce particle motion in the same direction as wave propagation. However, only bending waves have been detected in plant stems (Michelsen et al. 1982, p 277; Cocroft et al. 2000 and references therein), and longitudinal motion in the plant stem is ignored in this study.

Transducers commonly used to measure vibrational signals in plant stems, such as laser vibrometers or accelerometers, are only (or at least maximally) sensitive to motion along a single axis. Because of this, use of a single transducer leads to a consistent underestimation of signal amplitude, as usually it is not possible to know a priori how to position the transducer so that its axis of sensitivity coincides with the direction of maximum stem motion. Since bending waves propagate

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along the stem's length and substrate motion is perpendicular to transmission direction, motion at any point occurs within a cross-sectional, two-dimensional (2-D) plane (gray ellipse, Fig. 1). If we assume that it is equally probable for a plant stem to vibrate maximally along any axis within this plane, then it is unlikely that a transducer will be aligned by chance precisely along that axis. However, measurements made along any other axis will underestimate the real amplitude of vibration (Fig. 2). The amplitude measured by the transducer is related to the real amplitude of stem vibration by the cosine of the angle between the axis of measurement and the axis of stem motion (Fig. 2b). Underestimation of the real amplitude of vibration increases exponentially as the angle between the axis of vibration and the transducer alignment increases (Fig. 2c). Thus, in some situations the underestimation may be extreme, such as measuring little to no signal when in fact substantial vibration is present (e.g., Fig. 2a, b, point iii).

In addition to underestimating the amplitude of vibration, a researcher using a single transducer may not accurately characterize stem motion. Stem vibration is likely to be perfectly uniaxial under very limited conditions, if at all. First, when a signaling animal vibrates a stem, it may impart motion along more than one axis. Furthermore, given factors such as the heterogeneity of stem architecture, it is possible that the properties of stem motion will change as a signal

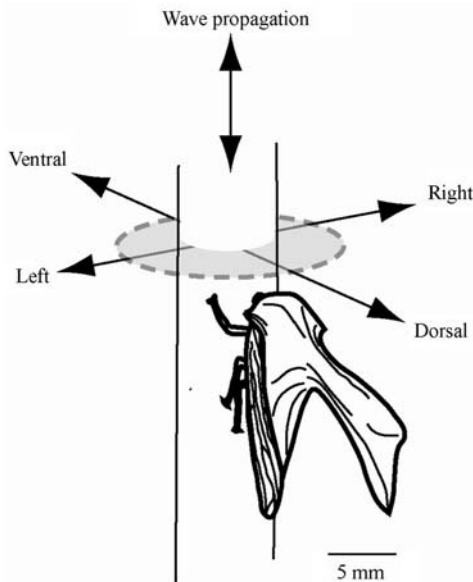


Fig. 1 Vibrations in plant stems are transmitted as bending waves along the longitudinal axis of the stem, with stem motion perpendicular to the direction of propagation. Motion from bending waves at a given point on the stem occurs within a cross-sectional plane (dashed gray ellipse)

propagates (Virant-Doberlet et al. 2006). Previous investigators have provided evidence that measurement along a single axis may not completely describe stem motion (Michelsen et al. 1982; McVean and Field 1996; Virant-Doberlet et al. 2006). However, no formal method has been used to describe the path traced by a stem during transmission of vibrational signals.

The problem of characterizing stem motion within an x - y plane can be solved by applying a method used previously in the field of engineering (below; see also Bachschmid et al. 2004; Lee et al. 1997). The signals from the two transducers, aligned perpendicularly (Fig. 3), provide the x and y coordinates of a point on the stem as its displacement (or velocity or acceleration, depending on the transducer) changes through time. The information obtained from these signals allows calculation of the true amplitude of vibration for any given frequency, as well as the orientation of the axis of vibration relative to one of the

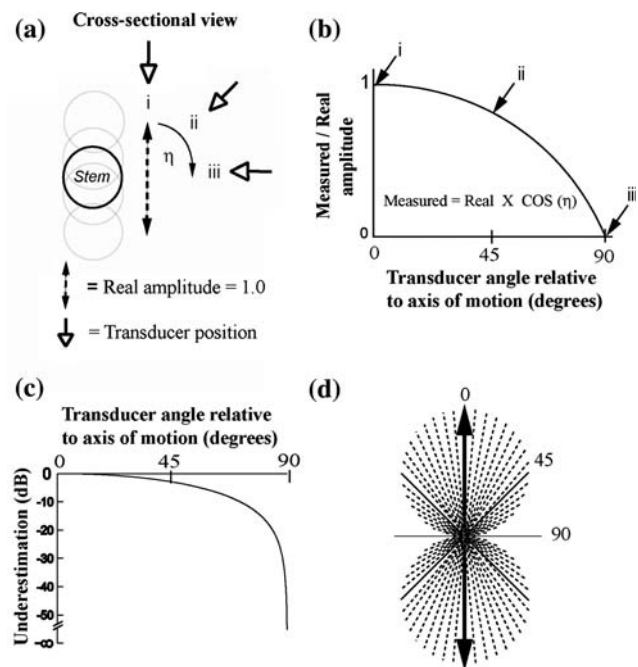


Fig. 2 Illustration of the potential for measurement error when using a single transducer. **a** Stem motion (amplitude not to scale) is assumed to be uniaxial, and the transducer is assumed to be sensitive to motion along only one axis. **b** The measured amplitude is related to the real amplitude by the cosine of the angle (η) between the axis of stem motion and the transducer's axis of sensitivity (e.g., i, ii and iii). **c** The underestimation of amplitude (real/measured) that occurs with single-transducer measurements increases exponentially as transducer alignment approaches 90° relative to the axis of motion. **d** The length of the dashed lines represent the amplitude that would be measured if stem motion is uniaxial and single-transducer measurements are taken around the circumference of a stem in 5° increments. For reference, an additional solid line is placed at 45°

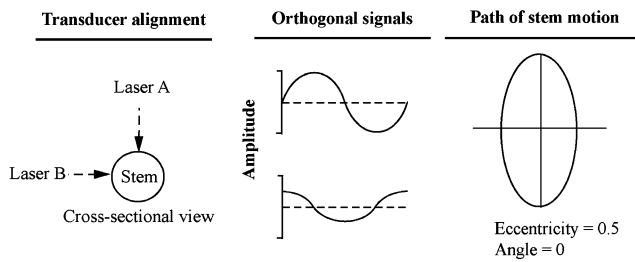


Fig. 3 Orthogonal positioning of two transducers relative to a stem allows characterization of elliptical stem motion within a cross-sectional plane

transducers. This method also provides the information necessary for describing stem vibration more complex than that of bending wave motion along a single axis.

Here, we show how the signals from two orthogonal transducers can be processed to characterize the path of stem motion in two dimensions. We then illustrate the use of this approach with an example of how a plant stem moves when vibrated by signaling insects. Finally, we discuss the situations in which orthogonal measurements may be especially useful, as well as some of the largely unexplored questions about

ellipse (Fig. 4). For our purposes, we are interested in four parameters: (1) the ellipse’s major axis, (2) its minor axis, (3) its angle of rotation relative to one of the transducers, and (4) its eccentricity (obtained from the major and minor axes).

In the equations below, A and B represent the Fast Fourier Transforms (FFT) of $X(t)$ and $Y(t)$, each with real ($\text{Re}[\]$) and imaginary parts ($\text{Im}[\]$) corresponding to magnitude and phase. That is, $A = 2\text{FFT}(X(t))/N$, and $B = 2\text{FFT}(Y(t))/N$, where N is the number of points in the time record. The angle of rotation of the ellipse (η), arbitrarily defined relative to the first signal, $X(t)$, can be found using the equations below (see Supplementary Material for derivations) and the four-quadrant arctangent function (ATAN2) in Matlab (v. 6.5; Mathworks, Natick, Massachusetts):

$$\eta = \frac{1}{2} \left[\text{ATAN2} \left(2 \times (\text{Re}[A] \times \text{Re}[B] + \text{Im}[A] \times \text{Im}[B]), (|A|^2 - |B|^2) \right) \right], \tag{1}$$

From this, the major (a) and minor axis (b) of the ellipse can be found using:

$$a = \sqrt{\text{abs} \left[(|A|^2 \cos^2 \eta) + (|B|^2 \sin^2 \eta) + 2(\text{Re}[AB^*][\sin \eta \cos \eta]) \right]}, \tag{2}$$

$$b = \sqrt{\text{abs} \left[(|A|^2 \sin^2 \eta) + (|B|^2 \cos^2 \eta) - 2(\text{Re}[AB^*][\sin \eta \cos \eta]) \right]}, \tag{3}$$

vibrational communication raised by this more complete description of stem vibration.

Materials and methods

Calculating the two-dimensional properties of stem motion

Consider the motion of a plant stem at a single frequency: two orthogonal sine waves, when plotted against each other, will define an ellipse whose properties depend on the relative amplitude and phase of the signals (Fig. 3). The parameters of interest for each frequency in a signal can be obtained using amplitude and phase information from the signals, $X(t)$ and $Y(t)$, from the two orthogonally aligned transducers. Because each transducer is aligned along one orthogonal axis, together they define a coordinate plane whose axes will be rotated by some unknown angle relative to the major and minor axes of the

where B^* is the complex conjugate of B.

Finally, for a given frequency, eccentricity is given as the ratio of the minor (b) and major (a) axes of the ellipse (eccentricity = b/a). Therefore, values for eccentricity are bounded by 0 (uniaxial) and 1 (circular).

Insect vibrational signals

To illustrate the method outlined above, we characterize in two dimensions the plant stem vibrations produced by signaling insects. We recorded the substrate-borne sexual advertisement signals of each of 15 adult male treehoppers (Hemiptera: Membracidae: *Umbonia crassicornis*) on the stem of a 1-m-tall potted host plant (Mimosaceae: *Albizia julibrissin*). Insects were drawn from a greenhouse colony established with collections near Miami, FL, USA.

To measure the signals we aligned two laser vibrometers (Polytec CLV 1000 with a CLV M030 decoder module; Polytec Inc., Auburn, MA) so that the beams were orthogonal to each other and to the lon-

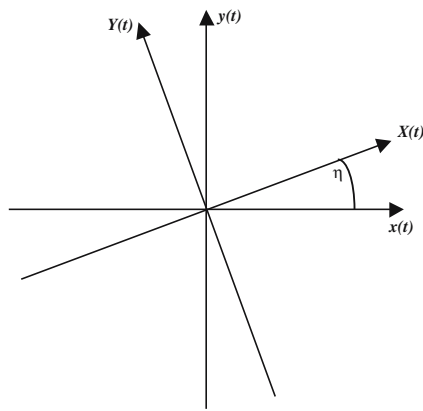


Fig. 4 Rotation of the measurement axes $X(t)$ and $Y(t)$ through the angle η relative to the major and minor axes of the ellipse

gitudinal axis of the stem (Fig. 3). All 15 insects were placed at the same position on the same individual plant. We recorded the signals of each treehopper at three locations: the first was within 1 cm of the insect (stem diameter 4.3 mm; this position referred to hereafter as *source*); the second was 10 cm from the insect but on the same unbranched length of stem (3.5 mm diameter; referred to as *10 cm straight*); and the third was 5 cm from the insect, but on a petiole of a leaf arising from the stem (2.2 mm diameter; referred to as *5 cm branch*).

At the first two locations, *source* and *10 cm straight*, along the plant's vertical main stem, the beam of one laser (laser A) was aligned along the signaling male's dorso-ventral axis, while the beam of the other laser (laser B) was aligned along the male's left-right axis. At the third location, *5 cm branch*, the stem's cross-sectional plane is no longer comparable to the x - y coordinate system established at the source, so we arbitrarily chose to align laser B vertically with respect to gravity, leaving laser A in its original orientation; thus, in all three locations, laser A was aligned parallel with the tabletop. Small pieces of reflective tape (ca. 1 mm²) were attached to the stem at each point of measurement to enhance laser beam reflectance. The temperature of the recording room was maintained at approximately 24°C (range 22.7–25.0°C).

Males of *U. crassicornis* were induced to signal by playing a pre-recorded male-female duet through a loudspeaker (Optimus) from a computer (Macintosh G4). The airborne signal from the loudspeaker was sufficient to induce vibrations in the stem and elicit signaling. The signals of all 15 males were measured at a given location by placing each male in the same position and alignment on the stem. Then the lasers were

re-aligned at the next location and measurements for each male were repeated, again at the same position and alignment on the stem. Between measurements, males were kept in a sleeve cage on a separate *A. julibrissin* plant. The output from the lasers was acquired on a Dell desktop computer using a National Instruments data acquisition board (44,100 Hz sampling rate, 16-bit resolution) and a custom-made program written in Labview (v. 6.0; National Instruments, Austin, TX). The laser signals were high-pass filtered at 70 Hz using a Krohn-Hite 3202 filter (– 24 dB per octave, Krohn-Hite Corp., Brockton, MA). Signals produced by *U. crassicornis* males consist of a frequency-modulated sinusoid (100–200 Hz) lasting 1–2 s. Signals sometimes contain a series of higher-frequency pulses (< 2 kHz) (see Cocroft and McNett 2006), but these are not consistently produced and we did not measure them here.

Results

Underestimation of the real velocity

The amplitude of *U. crassicornis* signals differed between the two lasers (Fig. 5) across all three locations, illustrating the influence of transducer alignment on the measurement of vibrational signals. The underestimation problem that results from variation in the measured signal can be illustrated by comparing single-laser measurements with the real velocity calculated using both laser signals. Because stem motion at *source* and *10 cm straight* was relatively uniaxial and in line with the insects' dorso-ventral axis, laser A illustrates a best-case scenario in which the transducer's axis of sensitivity is aligned with the major axis of vibration (the difference between real velocity and average measured velocity was close to 0 dB at both locations). In contrast, laser B is aligned perpendicularly to the major axis of stem motion, resulting in substantial underestimation (the difference between real velocity and average measured velocity was – 13.8 dB at *source* and – 12.5 dB at *10 cm straight*). At the third location, *5 cm branch*, the velocities measured by both lasers A and B underestimated the real velocity by 3–4 dB.

Path of stem motion

For measurements made at the first two locations, *source* and *10 cm straight*, eccentricity was low (i.e., motion was nearly uniaxial) and relatively constant for frequencies within 10–20 dB of peak amplitude

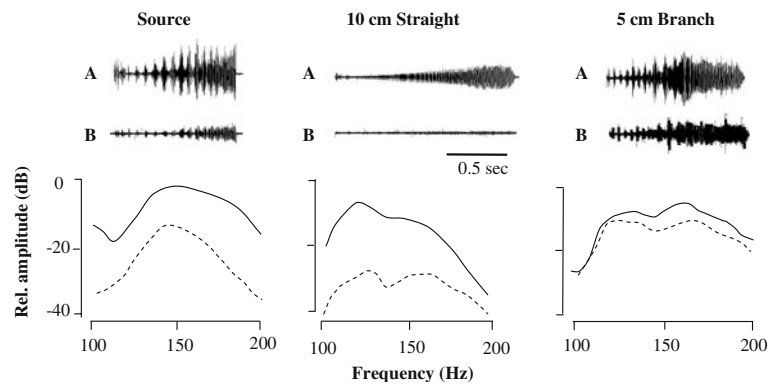


Fig. 5 Signals of a male *U. crassicornis* recorded at three distances from the male using two orthogonally positioned laser vibrometers (A, B). Waveforms from each laser, A and B, are shown with the corresponding amplitude spectra (A = solid line;

B = dotted line) (see the text). Differences between waveforms at a given location highlight the consequences of variation in transducer alignment

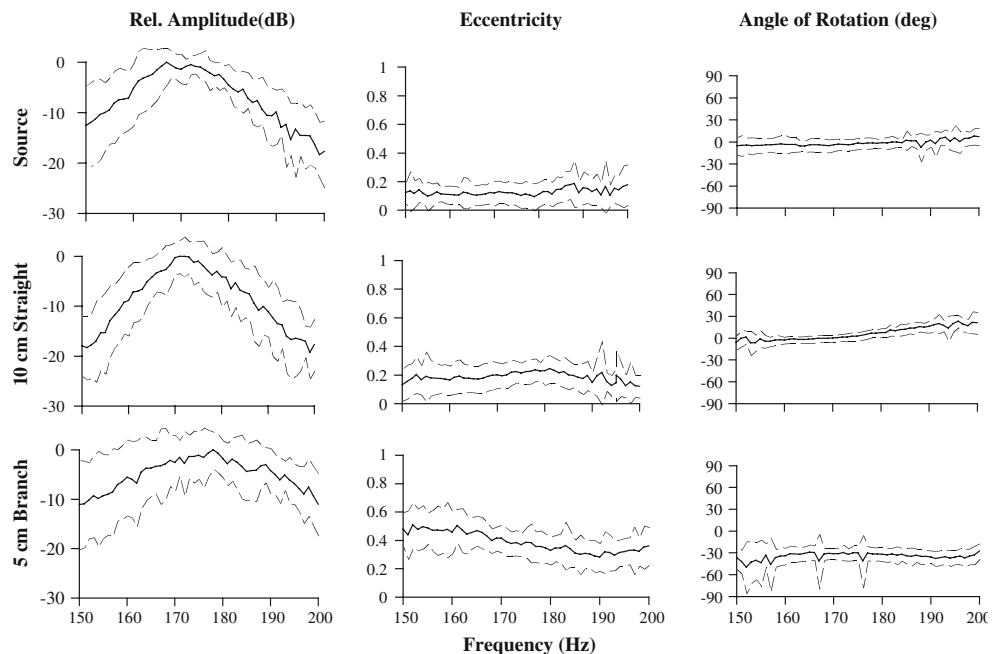
(Fig. 6). Stem motion was more ovoid at the third location, 5 cm branch.

At source and 10 cm branch, the angle of rotation of the major axis of motion relative to laser A deviated little from 0° (Fig. 6). That is, the axis of stem motion was approximately aligned with the male’s dorso-ventral axis for all 15 individuals. Angle of rotation did deviate from a 0° alignment at 5 cm branch; however, as discussed above (see Materials and methods) the *x*–*y* coordinate plane is not comparable once measurements were made on a side branch. At each location, the angles of rotation were relatively consistent across frequencies within 10–20 dB of peak amplitude (Fig. 6).

Discussion

In this paper, we outline a method for accurately characterizing animal signals and other vibrations traveling along plant stems. This method, which uses spectral analysis of the signals from two orthogonal transducers, overcomes two limitations of measurements made with a single transducer. First, it allows calculation of the maximum vibrational amplitude for bending waves in the stem, whether or not one of the transducers is aligned with the major axis of stem motion. Accurate measures of amplitude provide a more rigorous look at a variety of questions, such as the transmission properties of plant substrates. Second,

Fig. 6 Amplitude spectrum, eccentricity, and angle of rotation of male *U. crassicornis* signals measured at three locations on a plant ($x \pm$ s.d., $n = 15$ male signals). Note that at source and 10 cm straight the angle of rotation relative to the insect’s dorso-ventral axis is near zero and eccentricity is low. Eccentricity at 5 cm branch, however, is greater



this method provides a complete description of the elliptical path of motion at any one frequency, which provides an avenue for addressing a range of new questions related to animal vibrational signals in plant stems.

In some cases, the extent to which a researcher using a single transducer will underestimate the major axis of vibration will be minimal: if stem motion at a given frequency is uniaxial, measurements made within 45° of the major axis of motion will underestimate its amplitude by ~ 3 dB at most (see Fig. 2c; note that at 45° the measured amplitude is related to the true amplitude by $\cosine(45^\circ) \approx 0.7$). However, if the measurement axis differs by more than 45° from the axis of motion, underestimation may be more dramatic; for example, at 75° underestimation will be ≈ 12 dB. If the path of stem motion at a given frequency is not uniaxial, then underestimation of the major axis of vibration is decreased, with no measurement error when the path is completely circular. Given these considerations, use of orthogonally aligned transducers will be most important for measuring vibrational amplitude when motion is uniaxial or nearly so, but the axis of this motion cannot be predicted. While the present study used two laser vibrometers, contact vibration sensors such as accelerometers could also be used, at least in situations where the additional mass loading is not problematic.

It would also be possible to use the methods described here using orthogonal measurements of repeatable, mechanically generated signals made at different times with a single transducer. This would require a reference signal that would allow the two measurements to be compared using a common time base. Use of a single transducer in this way is probably limited to non-contact methods of vibration detection, since use of contact methods such as accelerometers will likely impose different mass-loading effects when the transducer is moved 90° around the stem, effectively reducing the repeatability of measurements.

Measurements made around the circumference of plant stem have shown the presence of signal energy along each axis measured (McVean and Field 1996), as well as changes in the distribution of that energy as the signal propagates (Virant-Doberlet et al. 2006). Virant-Doberlet et al. (2006) suggested that such changes might provide a receiver with information about its distance from the vibration source. Interpreting such measurements is difficult, however, because signal energy can be measured at most angles even when motion is uniaxial (see Fig. 4d), and because the phase information is lost between successive measurements. The method described here, by providing information

about the path of stem motion, will facilitate research into questions such as whether the eccentricity of the elliptical motion increases with distance from the source. It would be of interest to investigate how stem motion changes when signals are reflected, as a consequence of impedance changes in the transmission channel (Michelsen et al. 1982).

Receptor sensitivity and 2-D stem motion

If vibration perception is influenced by motion along more than one axis, then describing stem motion within a 2-D coordinate plane may be important for understanding how vibrations are transmitted and perceived.

Sensitivity to orthogonal axes of motion in a vibrational stimulus is important in vibration localization in some scorpions (e.g., Brownell and Farley 1979) and spiders (Barth and Geethabali 1982). Insects have multiple receptors for detecting vibrations (Markl 1983; Kalmring 1985; Yack 2004), among which the subgenual organ has been particularly well studied. In honeybees, the subgenual organ responds to both dorso-ventral and left-right motion, with greater sensitivity to the former (Rohrseitz and Kilpinen 1997). This differential sensitivity implies that the axis of motion of a vibrational stimulus is an important feature of vibration perception. Insects possess subgenual organs in each leg, and in a freestanding insect on a plant stem the legs are arranged in a variable spatial array (Virant-Doberlet et al. 2006). Integration of sensory information from multiple receptors may allow discrimination between uniaxial and more ovoid or circular 2-D motion. Addressing these questions provides fertile ground for further research, and takes us a step closer to understanding how plant-borne vibrations contribute to social and ecological interactions in natural environments.

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