An analytical model for the propagation of bending waves on a plant stem due to vibration of an attached insect

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Abstract

A mathematical model is presented to examine the propagation of bending waves on a plant stem that are induced by vibratory excitation from an attached insect. This idealized model represents the insect body as a mass and the legs as a linear spring along with a general time-varying force that is assumed to act in parallel with the spring. The spring connects the mass to a stem modeled as a beam having uniform geometric and material properties. The linearly elastic beam is assumed to undergo pure vibratory bending and to be infinitely long in each direction. The equations that govern the insect-induced, coupled motions of both the beam and the mass are solved for arbitrary time varying forces produced by the insect’s legs. Solutions for the frequency response indicate that the response is dominated by frequency components near the natural resonant frequency of the attached insect while at higher frequencies the amplitude of the response is strongly influenced only by the properties of the stem.

Keywords: Mechanical engineering, Applied sciences, Insect ecology, Mathematical analysis

1. Introduction

A very substantial percentage of animals communicate through vibrational waves that propagate on solid substrates [1, 2]. Insects that reside on plants can
transmit signals through the plant by vibrating their bodies while grasping a stem. Michelsen [3] showed that of the assortment of types of insect-induced vibrational waves that could occur on plant stems, bending waves predominate. One can therefore obtain insight about this communication channel by considering the stem to be a rather complicated beam undergoing pure bending. The fact that signals having different frequencies propagate on this substrate at different speeds is important information that is a well-known feature of bending wave motion on beams. This feature causes a wave shape that is composed of multiple frequency components to change as it propagates. If the frequency of the signal is increased, one could expect this pure bending behavior to be modified such that other wave types become important. The range of stem parameters and frequencies in which pure bending dominates the motion on plant stems has been sorted out by Casas et al. [4]. A view of a plant stem as a vibrating beam has also motivated studies of signal localization in plant-dwelling insects [5, 6, 7].

The first insight provided by the realization that a plant stem vibrates like a beam in pure bending is thus that it is a dispersive medium, with signals at different frequencies propagating at different speeds. This knowledge follows from the classical analysis of wave motion on beams of infinite length having properties that do not vary with position. Another essential feature of plant stems is that bending waves will no doubt be reflected at locations where the physical properties change dramatically with position, such as at branches and at the stem terminations. Fortunately, again, much is known about the effects of such reflections on beam-like structures. Polajnar et al. [8] studied the effects of these reflections on the motion of plant stems. They showed that the vibration is strongly affected by standing wave resonant frequencies and eigenfunctions that can be accurately represented by an analytical model of an Euler–Bernoulli beam that is clamped at one end and free at the other. The response of the stem was shown to vary significantly in amplitude as a function of spatial location and as a function of frequency.

In addition to dispersion and wave reflections, there are other complicating aspects of signal transmission in this system that are less-well understood. One that comes to mind is the fact that the excitation of the stem is due to an animal that is itself fixed to the stem. The excitation is therefore not due to some ideal externally applied point force. The presence of the insect will no doubt have a significant influence on the resonant properties of the stem. According to Michelsen et al., ‘We have no information about the coupling between animal and plant’ [3]. The main purpose of the present study is to begin to address this deficiency.

While there are well-known computational methods, such as the finite element method, for analyzing the vibration of complicated structures such as a plant, our present aim is to begin with an idealized representation of the system that can lead to an understanding of the key parameters. Our present goal is to derive a model of
the system that captures only certain essential features and is not clouded by too many parameters. We have therefore chosen to begin with a model of the stem as an infinite beam with an attached insect. This, unfortunately, does not account for the effects of wave reflections but it can provide important insight into the influence of the insect on the stem motion.

It should be noted that our present attention is on insects that reside on plant stems rather than leaves. Vibration of plant leaves due to insects has been examined experimentally by Magal et al. [9]. It was shown that anisotropy due to the stems on the leaf had a significant effect on the transmission of vibrational energy around a leaf. The excitation of the leaf was accomplished by dropping small balls on it to minimize the influence of the excitation source on the resulting vibration.

The end result of the mathematical steps described below indicates that there will be a dominant frequency in the insect-induced stem motion which is determined mostly by the properties of the insect rather than of the stem. In addition it is found that the amplitude of the signal at frequencies above the dominant frequency is significantly affected by the properties of the stem.

It is reasonable to expect that the amplitude of the propagating wave for a given stem will strongly depend on the body mass of the insect. A massive insect on a relatively thin stem will no doubt impede the stem’s motion while a very minute insect on a thick stem will not be able to impart significant vibrational energy to the plant.

In addition to the mass of the insect, it is likely to be important to consider the effective stiffness of the appendages that couple the body to the stem. The legs have finite stiffness and it may not be obvious how this stiffness influences the signaling ability of an insect on a given stem.

For our present purposes, the insect may be modeled as an attached spring/mass with a dynamic force applied in parallel with the spring. It is reasonable to expect that the amplitude of the propagating wave will depend on the frequency, the mass, and effective stiffness of the attachment of this mass to the stem. The main purpose of the present study is to examine the coupled motions as a function of the essential properties of the insect and the stem through the use of a simplified analytical model.

Because the beam is a dispersive medium for bending waves it can be challenging to calculate the response due to complicated transient inputs such as those due to a calling insect. The formulation used here provides a means of computing the response of the insect and the beam in the time and/or frequency domain at any location for an arbitrary input waveform. For simple harmonic excitation at the frequency \( \omega \), the steady-state response of the infinite beam will
Figure 1. The mass $m$ is attached to the infinite beam at the origin by a spring $k_s$. Forces $f_0(t)$, and $f_1(t)$ are applied as shown.

have an amplitude that is independent of location everywhere except in close proximity to the source (i.e. in the near-field). For complicated transient excitation, however, the fact that different frequency components propagate at different speeds causes the wave form (and its maximum amplitude) to change dramatically with the distance from the source. As a result, it can be difficult to interpret the results of a model based only in the frequency domain when the excitation is not a pure tone. The approach taken here enables the calculation of the response anywhere on the beam due to arbitrary inputs.

An insect that excites bending waves on a stem may be viewed as an inertial actuator, as is used to drive structures in vibration testing and control applications (see for example [10]). Inertial actuators are used in situations where the loading applied by a shaker would significantly alter the dynamics of the structure. If one wishes to induce vibrations in a very thin structure, such as a stem as considered here, the mass of the inertial actuator can significantly affect the structure’s motion. Because the inertial mass is applied through a flexible spring (or the legs of the insect) the response of the structure may vary significantly for frequencies near the actuator’s resonance frequency.

2. Theory

The system studied here is shown in Figure 1. The mass, $m$, is attached to the infinite beam through the spring $k_s$. A force $f_0(t)$ is applied directly to the beam at $x = 0$, the location of the spring/mass, and a force $f_1(t)$ is applied in parallel with the spring force. In this model we will consider the force $f_1(t)$ to be due to the insect’s muscles. Although not shown, a dashpot $c$ is assumed to act in parallel with the spring $k_s$. The governing differential equations for this system consist of a partial differential equation coupled to an ordinary differential equation. An exact analytical expression is obtained for the response in the frequency domain. The general response due to arbitrary transient excitations is obtained numerically with the aid of the Inverse Fast Fourier Transform.

The governing differential equations and boundary conditions of the system are

$$\rho A \ddot{w} + EI w_{xxxx} = 0 \quad \text{for} \quad x < 0^- \quad \text{and} \quad x > 0^+ \quad (1)$$
\[-EIw_{xx}(0^-, t) + EIw_{xx}(0^+, t) = 0 \quad (2)\]
\[EIw_{xxx}(0^-, t) - EIw_{xxx}(0^+, t) + ks(y - w(0, t)) + c(\ddot{y} - \ddot{w}(0, t)) - f_1(t) + f_0(t) = 0 \quad (3)\]
\[m\ddot{y} + ks(y - w(0, t)) + c(\ddot{y} - \ddot{w}(0, t)) - f_1(t) = 0 \quad (4)\]
\[w(0^-, t) = w(0^+, t), \quad w_x(0^-, t) = w_x(0^+, t) \quad (5)\]

where \( \rho \) is the density, \( A \) is the cross sectional area, \( w(x, t) \) is the transverse displacement of the beam, \( y(t) \) is the displacement of the insect, \( E \) is Young’s modulus of elasticity, and \( I \) is the area moment of inertia of the beam. The spring/mass/damper is assumed to be attached to the beam at \( x = 0 \). The subscript \( x \) denotes partial differentiation with respect to the spatial coordinate. Solutions may be readily obtained to the fourth order partial differential equation (1) and the ordinary differential equation (4) subject to the boundary conditions (5), (2), and (3). In the frequency domain, \( \omega \), equation (4) becomes

\[(k_s + i\omega c - m\omega^2)Y(\omega) - (k_s + i\omega c)W_0(\omega) - F_1(\omega) = 0 \quad (6)\]

where \( Y(\omega) \) is the Fourier transform of \( y(t) \), \( W_0(\omega) \) is the transform of \( w(0, t) \), and \( F_1(\omega) \) is the transform of \( f_1(t) \).

The solution for the response of the beam in the frequency domain may be shown to be

\[\bar{w}(x, \omega) = \frac{((k_s + i\omega c)(\omega) - W_0(\omega)) + F_0(\omega) - F_1(\omega)}{4EI} \times \frac{1}{a^2}(-e^{-a|x|} - ie^{-ia|x|}) \]

\[= W_0(\omega)(e^{-a|x|} + ie^{-ia|x|}) \quad (7)\]

where \( i = \sqrt{-1} \) and

\[a = \sqrt[4]{\omega^2 \rho A \over EI} \quad (8)\]

Evaluating equation (7) at \( x = 0 \) and using equation (6) give

\[\begin{bmatrix}
\frac{4EIA^3}{1+i} - (k_s + i\omega c) & (k_s + i\omega c) \\
-(k_s + i\omega c) & (k_s + i\omega c) - m\omega^2
\end{bmatrix}
\begin{bmatrix}
W_0(\omega) \\
Y(\omega)
\end{bmatrix} = \begin{bmatrix}
F_1(\omega) - F_0(\omega) \\
F_1(\omega)
\end{bmatrix} \quad (9)\]

or,

\[W_0(\omega) = \frac{-(k_s + i\omega c)(F_0(\omega)) - (F_1(\omega) - F_0(\omega))m\omega^2}{(\frac{4EIA^3}{1+i} - k_s - i\omega c)(k_s + i\omega c - m\omega^2) + (k_s + i\omega c)^2} \]

\[= \frac{-((k_s + i\omega c)(F_0(\omega)) - (F_1(\omega) - F_0(\omega))m\omega^2}{\frac{4EIA^3}{1+i}(k_s + i\omega c - m\omega^2) + (k_s + i\omega c)m\omega^2} \quad (10)\]

and,

\[Y(\omega) = \frac{(F_1(\omega))\frac{4EIA^3}{1+i} - F_0(\omega)(k_s + i\omega c)}{\frac{4EIA^3}{1+i}(k_s + i\omega c - m\omega^2) + (k_s + i\omega c)m\omega^2} \quad (11)\]
The general solution in the time domain can be obtained by an inverse transform from the frequency $\omega$ to time, $t$,

$$w(x, t) = \int_{-\infty}^{\infty} e^{i\omega t} \overline{w}(x, \omega) d\omega$$

$$y(t) = \int_{-\infty}^{\infty} e^{i\omega t} Y(\omega) d\omega$$  \hspace{1cm} (12)

Our remaining challenge is to evaluate the integrals in equations (12). This can be rather awkward, even in the special case where $F_0(\omega)$, and $F_1(\omega)$ are independent of $\omega$. Note that $a$ in equation (8) also depends on $\omega$. Rather than attempt an analytical evaluation of the integrals in equations (12), we utilize the Fast Fourier Transform algorithm to construct a computationally efficient means of calculating the response at any point on the stem due to any combination of driving forces.

Consider the situation where the only force is that applied in parallel with the spring, $F_1(\omega)$ so that $F_0(\omega) = 0$. To examine the effect of varying system parameters on the amplitude of the wave on the beam, it is helpful to rewrite equation (10),

$$W_0(\omega) = \frac{-F_1(\omega)\omega^2}{4EIa^3(\omega_m^2 + 2\omega_m i\omega \zeta - \omega^2) + m(\omega_m^2 + 2\omega_m i\omega \zeta)\omega^2}$$  \hspace{1cm} (13)

where

$$\omega_m^2 = \frac{k_s}{m}$$  \hspace{1cm} (14)

and

$$\zeta = \frac{c}{2\sqrt{k_s m}}$$  \hspace{1cm} (15)

We will use equation (8) and let

$$\alpha = 4EIa^3\omega^{-3/2} = 4(\rho A)^{3/4}(EI)^{1/4}$$  \hspace{1cm} (16)

If the stem has a circular cross section of radius $r$, $A = \pi r^2$ and $I = \pi r^4/4$. Equation (16) then becomes

$$\alpha = 4\rho^{3/4}\pi^{5/2}\sqrt{E/2}$$  \hspace{1cm} (17)

$\alpha$ is thus a fairly strong function of the radius $r$ and a weak function of $\rho$ and $E$. The constant $a$ in equation (8) becomes

$$a = \left( \frac{2}{E} \right) \sqrt{\frac{\omega}{r}}$$  \hspace{1cm} (18)
Equation (10) becomes
\[ W_0(\omega) = \frac{-F_1(\omega)\omega^2}{a\omega^{3/2}} \]
\[ + \frac{1}{1+i}(\omega_m^2 + 2\omega_m\hat{\omega}\zeta - \omega^2) + m(\omega_m^2 + 2\omega_m\hat{\omega}\zeta)\omega^2 \]  
\[ \times (e^{-\alpha|x|} + e^{-\beta|x|}) \]  
\[ \text{(19)} \]

The response at any location along the stem is then obtained from equations (7) and (19),
\[ \tilde{w}(x, \omega) = \frac{-F_1(\omega)\omega^2}{a\omega^{3/2}} \]
\[ + \frac{1}{1+i}(\omega_m^2 + 2\omega_m\hat{\omega}\zeta - \omega^2) + m(\omega_m^2 + 2\omega_m\hat{\omega}\zeta)\omega^2 \]
\[ \times (e^{-\alpha|x|} + e^{-\beta|x|}) \]  
\[ \text{(20)} \]

Note that as the distance, \( x \), from the insect increases, the term \( e^{-\alpha|x|} \) is reduced exponentially. As the distance increases beyond \( x \approx 1/a \), this term has negligible effect relative to \( e^{-\beta|x|} \), which affects the phase, or time delay but has no impact on the response amplitude. The constant \( 1/a \) may be considered to be the length of the near-field where evanescent waves contribute to the response. For distances sufficiently far from the insect that near field effects are negligible, the motion becomes periodic in \( x \) with a wavelength of \( \lambda = 2\pi/a \).

It has been pointed out by Casas et al. [4] that if the stem radius becomes sufficiently large relative to the wavelength, the simple Euler–Bernoulli model of simple bending will no longer be adequate and non-dispersive waves may dominate the response. It was found that the simple bending model is appropriate for ratios of stem radius to wavelength that satisfy \( r/\lambda < 0.03 \). In the systems examined in the present study, the Euler–Bernoulli bending theory is then predicted to be appropriate for frequencies less than about 1 kHz.

If the dashpot constant \( c \) (and hence \( \zeta \)) is sufficiently small, at the frequency \( \omega = \omega_m \), equation (19) reduces to
\[ W_0(\omega_m) \approx -\frac{F_1(\omega)}{k_s} \]  
\[ \text{(21)} \]

where we have used the fact that \( k_s = m\omega_m^2 \). If the dashpot constant \( c = 0 \), the maximum response at resonance thus becomes independent of the properties of the beam.

At frequencies where \( \omega >> \omega_m \), equation (19) becomes
\[ W_0(\omega) \approx \frac{F_1(\omega)(1+i)}{a\omega^{3/2}} \]  
\[ \text{(22)} \]

At frequencies well above the resonance frequency of the insect, \( \omega_m \), the response depends on the inverse of \( a \) and is independent of the properties of the insect (i.e. on \( k_s, m, \) and \( c \)). For these frequencies, thinner, more compliant stems will produce greater response since these correspond to smaller values of \( a \).
3. Results

Numerical results are presented in the following to illustrate the effect of key parameters on the predicted response of the system. Parameters in the model have been roughly estimated to represent the treehopper *Umbonia crassicornis* on a natural host plant stem. A much more detailed investigation is required to obtain accurate parameter estimates.

In our highly simplified model, the stem is represented by only three parameters: Young’s modulus of elasticity, \(E\) (N/m\(^2\)), density \(\rho\) (kg/m\(^3\)) and the radius \(r\) (m) or diameter, \(d = 2r\). The Young’s modulus of elasticity of plant stems has been estimated to be approximately \(E \approx 10^9\) N/m\(^2\) and the density is approximately \(\rho = 1\) gm/cm\(^3\) or, in our preferred units \(\rho = 1000\) kg/m\(^3\) [11]. *U crassicornis* typically resides on stems having a diameter of between 3 mm and 6 mm [12].

With these estimates of the essential parameters of the stem, equations (8) and (20) enable us to calculate the length of the near-field, \(1/a\) (m) as discussed after equation (20). For a stem having a diameter of 0.5 cm, this near-field distance is found to vary from about 4.5 cm at 100 Hz to 1 cm at 2 kHz. At distances from the insect greater than about 5 cm, near-field effects are predicted to not have a significant impact. Without the exponential decay of these evanescent waves, we can expect the energy to propagate without attenuation over long distances. This, of course, is a result of us representing the stem as a lossless, infinite beam; in real stems one will always find attenuation with distance due to energy dissipation and spatial nonuniformities.

Having estimates of the three parameters that characterize the stem, we must now determine physically reasonable estimates of the mass \(m\), stiffness \(k_s\), and damping constant \(c\), that represent the insect. Of these three constants, the mass is easiest to measure directly. We will take \(m = 45\) mg based on measurements reported in reference [13]. We will assume the stiffness of the legs results in the mass of the insect supported on the legs to have a resonant frequency \(\omega_m = \sqrt{k_s/m}\) so that the stiffness is \(k_s = m\omega_m^2\). The natural frequency of the insect is taken to be equal to the dominant frequency observed in the communication signal as in Cocroft et al. [14], approximately 160 Hz so that \(\omega_m = 2\pi 160\). This gives a spring constant equal to \(k_s = 45.47\) N/m.

The damping constant \(c\) is also difficult to measure directly. In the present study, this will be set to a value so that the ratio of \(c\) relative to the critical damping value, \(2\sqrt{k_sm}\) is equal to \(\zeta = 0.015 = c/(2\sqrt{k_sm})\). Again, the task of obtaining more reliable estimates of \(k_s\) and \(c\) will be left for future studies.

The response of plant stems due to vibrational communication of the treehopper *Umbonia crassicornis* has been reported by Cocroft et al. [14]. Measurements of
Figure 2. Frequency response for varying stem diameters from 3 mm to 6 mm. The distance from the insect is taken to be $x = 5$ cm. The results are in reasonable qualitative agreement with those shown in [14].

the stem vibration due to excitation from a calling insect were obtained at a distance of 5 cm and 15 cm from the insect. The response on a stem due to excitation from the insect consists of a dominant frequency component at roughly 160 Hz along with higher frequency components having a response level that is roughly 40 dB below that of the dominant frequency.

Our examination of equation (20) reveals that in the special case where the frequency content of the force applied by the legs, $F_1(\omega)$, is a constant at all frequencies, if $\alpha$ is not too small, the response will be dominated by frequencies close to $\omega \approx \omega_m$, the resonant frequency of the insect. For the set of parameters selected above, we find that $\alpha = 0.1385$.

The predicted response as a function of driving frequency $\omega$ is shown in Figure 2. The figure shows the motion to be dominated by that at the resonance frequency of the insect, $\omega_m$, with the response at higher frequencies at substantially lower levels in qualitative agreement with those of [14]. It is also clear that the response at higher frequencies is significantly reduced as the stem diameter increases.

To see the effect of stem diameter on the response at the resonance frequency of the insect, the data of Figure 2 are re-plotted with an expanded scale around the resonance frequency in Figure 3. Comparing Figures 2 and 3 shows that varying the stem diameter from 3 mm to 6 mm affects the response at resonance by only about 7 dB while reducing the response at 1 kHz by about 15 dB. The influence of the stem diameter on the response at resonance depends on the damping ratio, $\zeta$, as can be seen in equation (19). Lower values of damping will cause the stem diameter to have less influence on the response at resonance. As discussed above,
Figure 3. Zoomed in view of the frequency response data shown in Figure 2.

when $\zeta = 0$, the diameter of the stem is predicted to have no influence on the response at $\omega = \omega_m$. Figure 3 also shows that the stem diameter has only a modest effect on the frequency at which maximum response occurs.

The results shown above indicate that if the force applied in parallel with the spring that represents the legs is independent of frequency, the response is predicted to be strongly influenced by frequencies that are close to the resonant frequency of the spring/mass/damper. Of course, the force exerted by the animal, while not known precisely, is likely to be dependent on frequency. However, because the response is so strongly affected by contributions near the animal’s resonant frequency, the force does not need to be carefully tuned to this frequency to elicit a similar response. This is illustrated in Figures 4 and 5 which show the predicted time domain response for two rather different excitation forces.

Figure 4 shows the predicted response in the time domain when the excitation consists of brief pulses having a full cycle at 150 Hz. Figure 5 shows the predicted response when the excitation pulses consist of single cycle oscillations at 500 Hz, significantly above the system’s dominant resonance. In this case, the response levels are significantly lower but the response is still dominated by the oscillation at the resonant frequency of the spring/mass (i.e. the insect’s body supported by its legs). The insect may be able to achieve a similar oscillatory response by a wide range of transient force inputs; it is necessary only to excite the system’s impulse response which is dominated by this resonance.

4. Discussion & conclusions

It should be emphasized that the intent of the present study is not to construct a comprehensive and reliable predictive tool. The aim is to identify the simplest
Figure 4. Predicted response versus time due to brief excitation pulses consisting of one full cycle at a frequency of 150 Hz, which is also the resonant frequency of the spring/mass. $w(t)$ is the response of the stem (shown at $x = 5$ cm and $x = 15$ cm with the insect at $x = 0$). $y(t)$ is the predicted response of the insect. Both the stem and the body of the insect show oscillatory response at 150 Hz.

Figure 5. Predicted response versus time due to brief excitation pulses consisting of one full cycle at a frequency of 500 Hz. $w(t)$ is the response of the stem (shown at $x = 5$ cm and $x = 15$ cm with the insect at $x = 0$). $y(t)$ is the predicted response of the insect. Both the stem and the body of the insect show oscillatory response at 150 Hz, which is the resonant frequency of the spring/mass. The system’s impulse response is dominated by the resonance at 150 Hz which can be excited by a wide range of transient inputs.

possible model of the system that captures certain essential effects. We have idealized the stem as an infinite beam with uniform geometric and material properties throughout its domain. The present model may be appropriate in situations where the stem is indeed very long and has sufficient foliage at its ends to dissipate energy and hence attenuate waves that are reflected at its ends. Branches and other nonuniformities will doubtless cause reflections that are not accounted for here.
While the model described here is highly simplified, it does predict an important effect that has been lacking in our previous view of the system as an infinite beam subjected to a harmonic point load; the resonance of the insect’s mass and stiffness can result in a dominant narrowband response at a frequency that depends almost entirely on the properties of the insect, not the properties of the stem. This feature causes the signal to be much more representative of and determined by the insect rather than the stem.

The present study could be extended to account for nonuniformities, branches, and finite boundaries in the stem. This could be accomplished using computational tools such as the finite element method. It is unfortunate however, that results obtained using detailed computational models often can be nearly as difficult to interpret as experimental results. A key assumption here is that a carefully chosen, highly idealized model can result in equations that are simple enough to permit interpretation and insight.

Declarations

Author contribution statement

Ronald Miles: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

The author received no funding from an external source.

Competing interest statement

The author declares no conflict of interest.

Additional information

No additional information is available for this paper.
Acknowledgements

I would like to thank R.B. Cocroft of the University of Missouri and C.I. Miles and M. Losinger of SUNY Binghamton for numerous helpful discussions on this topic.

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