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Analysis of vibrational behaviors of microtubules embedded within elastic medium by Pasternak model

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ABSTRACT

Microtubules in living cells are very important component for various cellular functions as well as to maintain the cell shape. Mechanical properties of microtubules play a vital role in their functions and structure. To understand the mechanical properties of microtubules in living cells, we developed an orthotropic-Pasternak model and investigated the vibrational behavior when microtubules are embedded in surrounding elastic medium. We considered microtubules as orthotropic elastic shell and its surrounding elastic matrix as Pasternak foundation. We found that due to mechanical coupling of microtubules with elastic medium, the flexural vibration is increased with the stiffening of elastic medium. We noticed that foundation modulus (H) and shear modulus (G) have more effect on radial vibrational mode as compared to longitudinal vibrational mode and torsional vibrational mode.

1. Introduction

Microtubules (MTs) are the stiffest biopolymers of a network of proteinous filaments of the cell cytoskeleton [1]. MTs are interconnected with actomyosin microfilaments and intermediate filaments to form composite cytoskeleton which maintains the cell shape and largely responsible for the mechanical rigidity of the cell. MTs are structural and dynamical basis of the cell [2]. Physiologically; MTs are involved in many cellular functions such as cell division, cell motility and intracellular transport. MTs act as routes for motor proteins and are essential part of moving core of cilia and flagella [3]. Geometrically; MTs are long, hollow nanoscale elastic cylinders that are made of α-β tubulin heterodimers assembled into 13 parallel, laterally associated protofilaments with outer and inner diameters of about 30 and 20 nm, respectively, whose length can vary from tens of nanometers to hundreds of microns [4].

Mechanics of MTs play important role in their various cellular functions [5] and it is the known fact that mechanical properties of MTs are affected when subjected to surrounding elastic matrix [6]. Therefore, mechanics of MTs coupled with surrounding elastic medium, has been the topic of many researchers during the last few years [7]. MTs vibrate during their functions such as transporting organelles and maintaining the cell shape hence, vibration of MTs is of major interest [8,9]. In particular, since MTs are embedded in the surrounding elastic cytoplasm; the vibration of MTs embedded in the elastic medium has been investigated in the last decade [10]. A detailed study has been carried out [11], by modeling MTs as isotropic membrane shell immersed in fluid. Three axisymmetric modes and an infinite set of nonaxisymmetric modes have been obtained. In [12] the MTs are modeled as a nonlocal shear deformable cylindrical shell which contains small scale effect and surrounding elastic matrix as Pasternak foundation. However, these models cannot be used to study more complex localized 2D shell like behavior of hollow MTs, such as 2D localized shell-like vibration mode of MTs [13]. Therefore, it is needed to give a reliable model to describe 2D localized shell-like behavior of MTs embedded in surrounding elastic medium. In [13], orthotropic elastic shell model is used to study vibrational behavior of free MTs because MTs structure reveals that the longitudinal bonds between αβ-tubulin dimmers along protofilaments are much stronger than the lateral bonds between adjacent protofilaments [3]. In particular, shear modulus of MTs is much lower than elastic modulus along longitudinal direction [14,15] and elastic modulus along the circumferential direction is lower than elastic modulus along longitudinal direction by a few orders of magnitude. These results suggest that, instead of isotropic shell model, MTs should be more accurately modeled as an orthotropic elastic shell.

Based on these ideas, an orthotropic shell model was developed [13] to study the vibrational behaviors of MTs. A good agreement has been found between this model, available discrete models and experiments. Due to its valid applications [7,13], the present paper will further extend the model to analyze the vibrational

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behavior of embedded MTs in surrounding elastic matrix. We modeled the surrounding of MTs as Pasternak foundation to account normal stress and shear stress between MTs and surrounding elastic matrix. This model has been used to account the surrounding effects of elastic medium for buckling behavior of MTs [16,17]. On these grounds, an orthotropic-Pasternak model is developed in the present paper and is employed to study the vibrational behavior of embedded MTs.

2. Methods

2.1. Orthotropic-Pasternak model

An orthotropic elastic shell model is used for the free vibration [13] and wave propagation pattern of MTs [18]. Now, we will extend this model for investigation of vibration of MTs embedded in the elastic medium. Since, an orthotropic-Pasternak model has independent material constants (including longitudinal modulus E_x, circumferential modulus E_θ, shear modulus $G_{x\theta}$, Poisson ratio υ_x along the longitudinal direction, non-dimensional foundation parameter H and non-dimensional shear modulus G [19]) the range of the values of these material constants for MTs are identified from the data available in the literature, and summarized in Table 1. In particular, following the literature, the cross section of MTs will be treated as an equivalent circular annular shape, with an equivalent thickness $h \approx 2.7$ nm [20,21]. Thus, all elastic moduli, in-plane stiffnesses, and the mass density ρ are defined based on such a thickness $h = 2.7$ nm. On the other hand, the bending stiffness of MTs is determined largely by a so-called "bridge" thickness of MTs [8]. Thus similar as single-walled carbon nanotubes [22], the effective bending stiffness of MTs, modeled as an elastic shell, should be considered to be an independent material constant. According to experimental data on shell-like buckling of individual MTs, the bending stiffness of MTs can be estimated by an effective thickness determined in Ref. [8] which is about 1.6 nm.

2.2. Governing equations of MTs

The governing equations for MTs in surrounding elastic matrix can be written as below [7,17]

$$\left\{\begin{array}{c} R^2\frac{\partial^2}{\partial x^2} \\ +\left(\frac{K_{x\theta}R^2+D_{x\theta}}{R^2K_x}\right)\frac{\partial^2}{\partial\theta^2}\end{array}\right\}u+\left\{\frac{R(\upsilon_xK_\theta+K_{x\theta})}{K_x}\frac{\partial^2}{\partial_x\partial_\theta}\right\}\upsilon+\left\{\begin{array}{c} -\frac{R\upsilon_xK_\theta}{K_x}\frac{\partial}{\partial x} \\ +\frac{RD_x}{K_x}\frac{\partial^3}{\partial x^3} \\ -\frac{D_{x\theta}}{RK_x}\frac{\partial^3}{\partial x\partial\theta^2}\end{array}\right\}w=\frac{\rho h}{K_x}R^2\frac{\partial^2 u}{\partial t^2}$$

$$\left\{R\left(\upsilon_\theta+\frac{K_{x\theta}}{K_x}\right)\frac{\partial^2}{\partial x\partial\theta}\right\}u+\left\{\begin{array}{c}\frac{K_\theta}{K_x}\frac{\partial^2}{\partial\theta^2} \\ +\left(\frac{K_{x\theta}R^2+3D_{x\theta}}{K_x}\right)\frac{\partial^2}{\partial x^2}\end{array}\right\}\upsilon+\left\{\begin{array}{c}-\frac{K_\theta}{K_x}\frac{\partial}{\partial\theta} \\ +\left(\frac{\upsilon_\theta D_x+3D_{x\theta}}{K_x}\right)\frac{\partial^3}{\partial x^2\partial\theta}\end{array}\right\}w=\frac{\rho h}{K_x}R^2\frac{\partial^2\upsilon}{\partial t^2}$$

$$\left\{\begin{array}{c}\upsilon_\theta R\frac{\partial}{\partial x} \\ -R\frac{D_x}{K_x}\frac{\partial^3}{\partial x^3} \\ +\frac{D_{x\theta}}{RK_x}\frac{\partial^3}{\partial x\partial\theta^2}\end{array}\right\}u+\left\{\begin{array}{c}\frac{K_\theta}{K_x}\frac{\partial}{\partial\theta} \\ -\frac{(\upsilon_xD_\theta+3D_{x\theta})}{K_x}\frac{\partial^3}{\partial x^2\partial\theta}\end{array}\right\}\upsilon+\left\{\begin{array}{c}-R^2\frac{D_x}{K_x}\frac{\partial^4}{\partial x^4} \\ -\left(\frac{\upsilon_xD_\theta+\upsilon_\theta D_x+4D_{x\theta}}{K_x}\right)\frac{\partial^4}{\partial x^2\partial\theta^2} \\ -\frac{D_\theta}{R^2K_x}\left(\frac{\partial^2}{\partial\theta^2}+1\right)^2-\frac{K_\theta}{Kx}\end{array}\right\}w+\frac{R^2P}{K_x}=\frac{\rho h}{K_x}R^2\frac{\partial^2 w}{\partial t^2} \quad (1)$$

Table 1
The values of orthotropic material constants for microtubules.

Parameters	Values	References
Longitudinal modulus H	0.5–2 GPa	[18,20]
Circumferential modulus E_θ	1–4 MPa	[18]
Shear modulus in x–θ plane $G_{x\theta}$	~1 MPa	[14,18]
Poisson's ratio in axial direction υ_x	0.3	[18,21]
Mass density per unit volume ρ	1.47 g/cm^3	[11]
Equivalent thickness h	2.7 nm	[20,11]
Effective thickness for bending h_0	1.6 nm	[20]

where x and θ are axial and circumferential angular coordinates; u, υ and w are axial, circumferential and radial displacements; ρ is the mass density, and R is the average radius of MTs, and $\gamma = h_0^3/(12hR^2)$. In addition, υ_x and υ_θ are Poisson ratios satisfying $\upsilon_\theta/\upsilon_x = E_\theta/E_x$, and

$$K_x = E_xh/(1-\upsilon_x\upsilon_\theta), K_\theta = E_{\theta x}/(1-\upsilon_\theta\upsilon_x), K_{x\theta} = G_{x\theta}h$$

are in-plane stiffnesses in longitudinal and circumferential directions, and in-plane stiffness in shear, respectively, and,

$$D_x = [E_xh_0^3/12(1-\upsilon_x\upsilon_\theta)], D_\theta = [E_\theta h_0^3/12(1-\upsilon_x\upsilon_\theta)], D_{x\theta} = G_{x\theta}h_0^3/12$$

are the effective bending stiffnesses in longitudinal and circumferential directions, and bending stiffness in shear, respectively. In what follows, we define.

$$\alpha = \frac{\upsilon_\theta}{\upsilon_x} = \frac{E_\theta}{E_x} = \frac{K_\theta}{K_x} = \frac{D_x}{D_\theta}, \beta = \frac{G_{x\theta}}{E_x} = \frac{G_{x\theta}}{E_x}(1-\alpha\upsilon_x^2) = \frac{D_{x\theta}}{D_x} = \frac{K_{x\theta}}{K_x}$$

and $S_L = \sqrt{\frac{E_x}{\rho}}$ ($\alpha v_x \to 0$ see Table 1). The pressure of the surroundings is p.

2.3. Governing equations of surrounding elastic medium

Here, let us consider the effect of the surrounding elastic medium on the vibration of MTs. The outer surface of MTs is in contact continuously with an elastic medium. Upon vibration of the MTs, the surrounding medium of filament network is deformed. In turn, the elastic filaments exert a distributed force on the MTs in the opposite direction of the vibration amplitude.

The elastic medium of MTs acts as an elastic foundation represented by Pasternak model [12,16]. This model is used to include normal stress as well as the shear stress between MTs and surrounding elastic matrix. The Pasternak model is given as;

$$P = Kw - \overline{G}\nabla^2 w \quad (2)$$

Where 'P' is the force per unit area, 'K' is the Winkler foundation stiffness per unit length and '$\overline{G}$' is the shearing layer stiffness of the foundation. ∇^2 is the Laplace operator in x and θ

$$\nabla^2 = \left(\frac{\partial^2}{\partial^2 x} + \frac{1}{r^2}\frac{\partial^2}{\partial^2\theta}\right)$$

It is the established fact that cytoplasm which surrounds the MTs is elastic and heterogeneous in nature, so, Winkler foundation stiffness and shearing layer stiffness assume different values in different conditions and regions and hence calculated over a wide range of values.

2.4. Analysis of elastically complaint mts in surrounding matrix

Considering MTs, simply supported at both ends, the solution of Eq. (1) can be given as;

$$\begin{aligned} u(x,\theta,t) &= U\cos k_xx.\cos n\theta.e^{i\omega t}, \\ \upsilon(x,\theta,t) &= V\sin k_xx.\sin n\theta.e^{i\omega t}, \\ w(x,\theta,t) &= W\sin k_xx.\cos n\theta.e^{i\omega t}, \end{aligned} \quad (3)$$

where U, V and W represent the vibration amplitude of MTs in longitudinal, circumferential and radial direction, k_x is the wave vector along longitudinal direction, n is the circumferential wave number, t is the time and ω is angular frequency, which is related to frequency f by $\omega = 2\pi f$.

Upon substitution of Eqs. (2) and (3) into (1), we obtain following three algebraic equations.

$$\left\{k^2+\beta(1+\gamma).n^2-\Omega^2\right\}U+\{-(\alpha v_x+\beta).k.n\}V+\left\{\alpha v_x.k+\gamma.(k^2-\beta.n^2).k\right\}W=0$$

$$\{-(\alpha v_x+\beta).k.n\}U+\left\{\alpha.n^2+\beta.(1+3\gamma).k^2-\Omega^2\right\}.V+\left\{\begin{matrix}-\alpha.n\\ -\gamma.(\alpha v_x+3\beta).k^2.n\end{matrix}\right\}W=0$$

$$\left\{\begin{matrix}\alpha v_x.k\\ +\gamma.(k^2-\beta.n^2).k\end{matrix}\right\}U+\left\{\begin{matrix}-\alpha.n\\ -\gamma.(\alpha v_x+3\beta).k^2.n\end{matrix}\right\}V+\left\{\begin{matrix}\gamma.k^4\\ +2\gamma.(\alpha v_x+2\beta).k^2.n^2\\ +\alpha\gamma.(n^2-1)^2+\alpha-\Omega^2\\ +H+G(k^2+n^2)\end{matrix}\right\}W=0 \tag{4}$$

Where $\Omega=\frac{r\omega}{S_L}$ is dimensionless frequency and $k = rk_x$ is dimensionless wave vector. Moreover $H=\frac{r^2K}{K_x}$ is nondimensional foundation parameter and $G=\frac{\overline{G}}{K_x}$ is nondimensional shear modulus. The frequency determinant of Eqs. (4) has the form

$$H(n,k,\Omega)_{3\times3} \tag{5}$$

where H is the coefficient matrix of Eq. (4). A nontrivial solution of the algebraic equations system (4) for U, V and W exists only when frequency determinant is equal to zero, i.e.

$$\det[H(n,k,\Omega)_{3\times3}]=0 \tag{6}$$

Solving Eq. (6), one can get Ω as a function of n and k with the effect of nondimensional parameters H and G for MTs. The frequency f is calculated as $f=(\frac{S_L}{2\pi r})\Omega$.

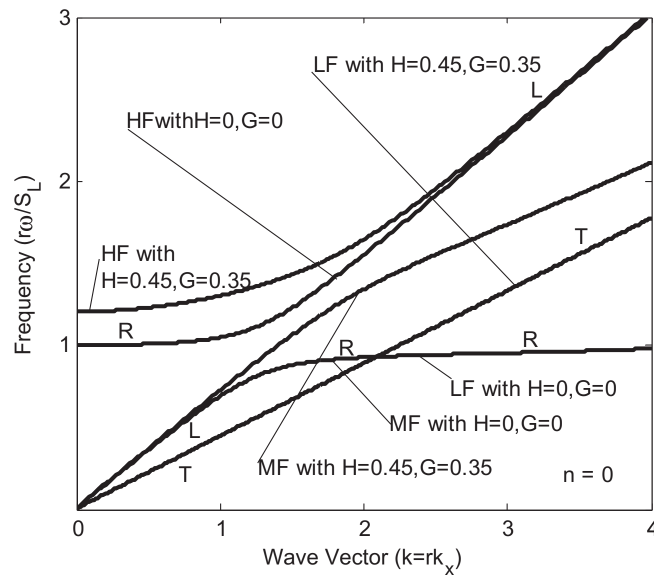

Fig. 1. Effect of elastic medium on dispersion relation of an embedded (H = 0.45, G = 0.35) and free (H = 0, G = 0) microtubule within elastic medium for axisymmetric (G) mode of vibration. (L, longitudinal mode; T, torsional mode; R, radial mode; LF, lowest frequency; MF, middle frequency; HF, highest frequency; H, foundation modulus; G, shear modulus).

3. Results and discussion

MTs embedded in elastic medium are analyzed to determine the vibrational behaviors under the influence of foundation parameters H and G. The dispersion relation of MTs is obtained for each pair of wave vector k and circumferential wave numbers n which yields three natural frequencies corresponding to three mode shapes.

In axisymmetric ($n = 0$) vibrations of embedded and free MTs with $R = 12.8nm$, $E_x = 1GPa$, $\upsilon_x = 0.3$, $E_\theta = 1$ MPa, $\alpha = 0.001$, $\beta = 0.001$, $\gamma = 0.0008$, and length from 0.01 to 4 μm approximately, uncoupled torsional (T) mode is represented by one of the three roots, whereas the other two non-torsional modes involve longitudinal (L) and radial (R) motions.

Fig. 1 shows the phonon-dispersion curves for embedded and free MTs between dimensionless frequency Ω and wave vector k for axisymmetric mode ($n = 0$).

The effect of nondimensional foundation parameters H and G on the lowest eigenfrequency (LF) of MTs for axisymmetric mode ($n = 0$) is noticed and it indicates that for the wave vector $k > 2$, the lowest eigenfrequency coincides with radial (R) mode of vibration for foundation parameters H and G whereas for $k < 1.8$, it corresponds to torsional (T) mode of vibration. The lowest frequency is as sensitive to foundation parameters H and G as is the radial mode for $k > 2.5$. We observe that with the rise in the values of foundation parameters H and G for the surrounding elastic medium of MTs, there is a rise in the frequency curve for $k > 2$, on the other hand it remains unchanged for $k < 2$. This shows that effect of foundation parameters H and G on the torsional vibrational mode is insignificant. These observations show that foundation parameters H and G are expected to influence only the radial vibration mode of MTs, as it does to the frequency pattern lying beyond $k > 2$. Besides this, we notice that with the rise in the values of foundation parameters H and G, the component of the frequency curve in the range $k > 2$ shows torsional behavior for higher and higher values of k.

For the middle eigenfrequency (MF) of embedded MTs, the foundation parameters H and G have no significant effect on the frequency curve in the domain $k < 1$. However, in the range $k > 1$ the effect of foundation parameters H and G is audible. The reasons can be assimilated very easily as the mode of vibration for the domain $k < 1$ is longitudinal.

As for as the highest eigenfrequency (HF) of embedded MTs is concerned for axisymmetric mode ($n = 0$), the foundation parameters H and G have significant effect only for $k < 2$ and is negligible in the range $k > 2$. This is because the vibration mode is radial for $k < 2$ and on the other hand, it is totally longitudinal for $k > 2$. It shows that only radial mode of MTs is influenced by foundation modulus.

It is clearly indicated from Fig. 1 that the frequency of radial mode of vibration of embedded MTs is increased with the increase of values of the foundation parameters H and G. This behavior of radial frequency is reasonable, since with the stiffening of the foundation, the flexural vibration of MTs is bound to increase. The effect of foundation parameters H and G is more pronounced on radial vibrational mode, to a lesser extent on torsional vibrational mode and least on longitudinal vibrational mode of embedded MTs.

Non-axisymmetric mode of vibration for $n = 1$ of embedded and free MTs with the same parameters as in Fig. 1 is demonstrated in Fig. 2. We should remember that for the circumferential wave number $n \geqslant 1$, all the modes of vibration of MTs are coupled. Without regard to this case, where for $k \leqslant 0.5$, the lowest frequency belongs to radial mode. The effect of foundation parameter of MTs is assimilating in this portion of the curve. It might be noted that the effect of foundation parameter on the frequency curves is higher as compared to axisymmetric mode. Here, it is also noted that effect of foundation parameter is not only for radial mode but it also affects the other modes, particularly, torsional frequency curve has increased considerably for lowest frequency of embedded MTs. This is reasonable as MTs mechanically couple with the surrounding elastic medium.

Now we investigate in Fig. 3, the behavior of vibrational frequency in GH_Z versus wave vector for embedded and free MTs for R = 12.8 nm, $E_x = 1GPa$, $\upsilon_x = 0.3$, $E_\theta = 1MPa$, $\alpha = 0.001$, $\beta = 0.001$, $\gamma = 0.0008$, and length from 0.03 to 4 μm with $n = 0$ and having different values of nondimensional foundation modulus H and nondimensional shear modulus G. Here, we denote the highest frequency with $f1$, the middle one as $f2$ and the lowest with $f3$.

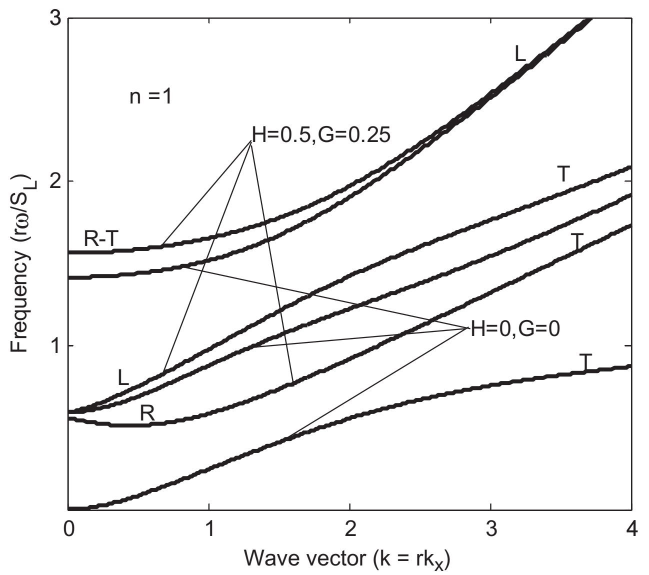

Fig. 2. Effect of elastic medium on dispersion relation of an embedded ($H = 0.5$, $G = 0.25$) and free ($H = 0$, $G = 0$) microtubule within elastic medium for non-axisymmetric (E_θ) mode of vibration. (L, longitudinal mode; T, torsional mode; R, radial mode; R–T, radial and torsional combined mode).

We noticed that the highest eigenfrequency of embedded MTs increases considerably with the rise in the values of H and G. The radial mode of vibration lies in the component of the curve for $k \leqslant 0.03$ for $H = 0$ and $G = 0$ but with the increase in the values of these parameters, i.e., for embedded MTs in elastic medium, the range of curve for radial mode of vibration has increased and value of frequency has also increased. The middle eigenfrequency has also increased with the rise in the values of H and G. The lowest frequency corresponds to torsional mode of vibration is not significantly affected by foundation parameters.

In Fig. 4, we noticed the effect of elastic matrix of MTs with the same parameters as in Fig. 3 on its various frequencies for circumferential wave number $n = 3$ and noticed that with the mechanical coupling of MTs with elastic medium, the radial frequency has increased remarkably, particularly for the highest frequency $f1$. For $n = 3$, the lowest frequency corresponding to torsional mode of vibration of embedded MTs has also increased noticeably.

In conclusion, an orthotropic-Pasternak foundation model is developed to study vibrational behaviors of embedded MTs within elastic medium. Special attention is paid to the non-dimensionlization of the parameters of foundation elastic medium.

We found that the foundation modulus (H) and shear modulus (G) influence radial vibrational mode more than longitudinal vibrational mode and torsional vibrational mode. This is because of the fact that flexural vibration of MTs is increased with the stiffening of the foundation. It is clear from the figures that the dynamic behavior of the embedded MTs in the elastic foundation is very sensitive to the foundation parameters. Obtained results have been evaluated against those available in the literature for free MTs (with $H = 0$, $G = 0$). Our theoretical and numerical results confirm the experimental findings indicated in Ref. [6] and in [23] that due to mechanical coupling with the surrounding elastic medium, microtubules stiffness is bound to increase.

It is well known that mitochondria are aligned along MTs and cooperation between mitochondria and MTs is a unique physical process.

Our results may help to understand some biochemical and biological aspects of cells in abnormal conditions also; such as, in mitochondrial dysfunction, which occurs in cancerous cells, the surrounding medium of MTs is disturbed, and damping of oscillations in MTs in tumors is enlarged [24]. Mechanical coupling of MTs with elastic medium may therefore provide a physical basis by which the MTs can vibrate in cell and thereby control cell behavior that is critical for tissue development. Using similar approach described here, we can determine the influence of elastic medium on the mechanical properties of other cytoskeletal polymers.

Further experiments based on this quantitative model are needed to explore a unified protocol to measure various subcellular mechanical properties of living cell.

Finally, it is worthwhile to indicate that for the considered orthotropic MTs with anisotropic parameters $\alpha = 0.001$, $\beta = 0.001$, the isotropic model is applicable when length of the MTs is long enough such that $k < 0.01$, which corresponds to the length of 8.04 µm. A comprehensive study has been done [25] by taking into

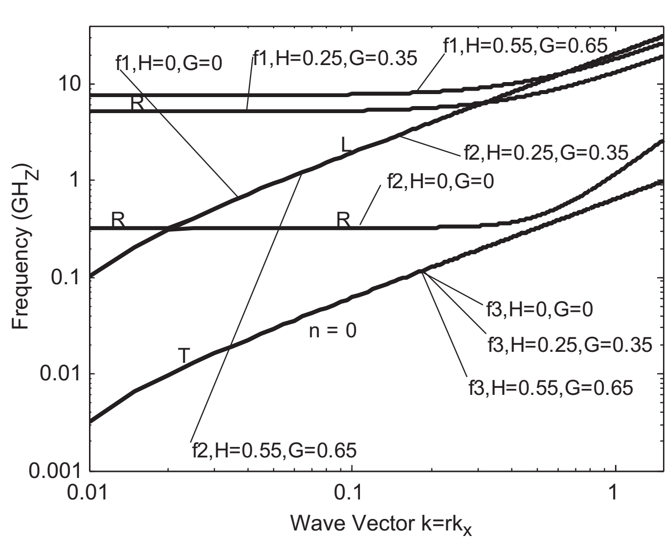

Fig. 3. Effect of elastic medium on the frequencies (GH_Z) of an embedded ($H = 0.25$ and 0.55, $G = 0.35$ and 0.65) and free ($H = 0$, $G = 0$) microtubule within elastic medium for 1–4 MPa (L, longitudinal mode; T, torsional mode; R, radial mode).

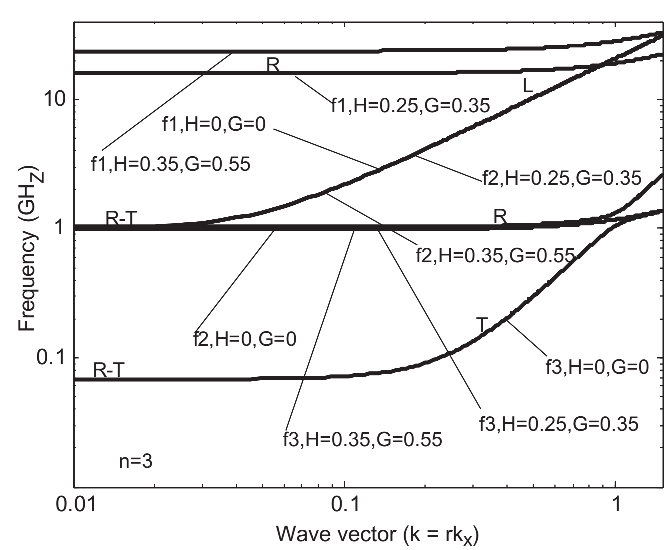

Fig. 4. Effect of elastic medium on the frequencies (GH_Z) of an embedded ($H = 0.25$ and 0.35, $G = 0.35$ and 0.55) and free ($H = 0$, $G = 0$) microtubule within elastic medium for θ (L, longitudinal mode; T, torsional mode; R, radial mode; R–T, radial and torsional combined mode).

account the anisotropic properties of MTs to explore the unexplained length dependence of young's modulus in the existing data. Such unrealistic length dependence was deduced to be a result of the anisotropy of MTs.

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