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Research Paper

Analysis of wave propagation in orthotropic microtubules embedded within elastic medium by Pasternak model

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ABSTRACT

Microtubules are embedded within elastic medium in living cells, where they perform a wide variety of functions; in cell motility and division, in organelle transport, and in cell organization. Waves propagate along microtubules in performing their physiological functions, so, wave propagation along microtubules has been the topic of research in the past decade. In the present article, the wave propagation in microtubules embedded in the elastic medium has been investigated on the basis of orthotropic-Pasternak model. We considered microtubules as orthotropic elastic shell and its surrounding elastic matrix as Pasternak foundation. We found that the flexural rigidity of microtubules has been increased with the stiffening of the elastic medium. Moreover, we observed that due to the mechanical coupling of microtubules with the elastic medium, their radial wave velocity has increased considerably as compared to other two wave velocities, i.e., longitudinal wave velocity and torsional wave velocity. The effect of foundation parameters *H* and *G* is more pronounced on radial wave velocity, to a lesser extent on torsional wave velocity and least even negligible on longitudinal wave velocity.

1. Introduction

Microtubules (MTs) are hollow proteinous component of the cytoskeleton (Alberts et al., 2005), a composite material in living cells formed by interconnection of MTs with actomyosin filaments and intermediate filaments through cross linking proteins (López-Huertas et al., 2010). MTs are basic structural and functional units of the cells and are deeply involved in maintaing the cell shape (Yoshio Fukui et al., 1990; Kivelä and Uusitalo, 1998). MTs also perform various vital functions unique to them: they are the building blocks of the mitotic spindle formed during the cell division (Julia and Andrea, 2002), and are engaged in the distribution of chromosomes in cell division; also cell motility is made possible by the continuous reorganization of the MTs (Gunning, 1990). Further, MTs translate and input the information carried by the electrophysiological impulses that enter in the brain cortex (Georgiev, 2003), and may act as electrical transmission lines (Hagan et al., 2002; Adames and Cooper, 2000). In plants, the axiality of cell growth in interphase cells is

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reinforced by the direction of cellulose deposition which is controlled through microtubule bundles (David Boal, 2012).

Structurally, MTs are made up of two tubulin protein heterodimers, i.e. α- and β-tubulin, with more or less different biochemical properties (Carter and Cross, 2005). These heterodimers are assembled to form 13 parallel, laterally bonded protofilaments which constitute long, hollow nanoscale cylindrical MTs with outer and inner diameters of about 30 and 20 nm respectively and varying length from tens of nanometers to hundreds of microns (de Pablo et al., 2003). MTs are the stiffest biopolymers of the cytoskeleton, and their bending rigidity is about 100 times larger than that of actin filaments with persistence length of about 6 mm (Gittes et al., 1993; Lin et al., 2010).

Understanding the mechanics of MTs is crucial to appreciate its various functions within cells. Many methods have been applied both experimentally and theoretically to explore the mechanical properties of the MTs. By the experimental techniques like laser trap and atomic force microscopy, the elastic response, buckling, instability (Schaap et al., 2006) and mechanical anisotropy of MTs (Kis et al., 2002) are tested. Meanwhile, mathematical models have also been developed for exploring the mechanical properties of MTs in the past few years. These theoretical models have been employed to study the elastic buckling (Wang et al., 2006a; Li, 2008; Taj and Zhang, 2011), vibrational behaviors (Wang et al., 2006b; Taj and Zhang, 2012) and predicting the flexural rigidity of MTs (Tuszynski et al., 2005).

Wave propagation along MTs is one of the major issues in various cellular functions, such as; cell signaling, cell division, translating information carried by the electrophysiological impulses, acting as transmission lines and controlling stomatal opening and closing in plant cells (Brokaw, 1998; Chretien and Wade, 1991), also by force generating at the cell's periphery which travel in the cells through MTs (Das et al., 2008). Furthermore, waves propagate along MTs in the movement of cells by cilia and flagella: a structure possessing a central bundle of MTs, called the axoneme, in which nine outer doublet MTs surround a central pair of singlet MTs.

Ciliary and flageller beating is characterized by a series of bends. Beating can be planar or three dimensional; like waves. The bends push against the surrounding elastic medium, propelling the cell forward (Lodish et al., 2000).

Some studies have been done to investigate wave propagation along MTs (Brokaw, 1998; Qian et al., 2007). In these studies, free MTs are considered but it is a known fact that MTs are embedded in the elastic medium and mechanical reinforcement of the elastic medium increases the flexural rigidity of MTs (Brangwynne et al., 2006). Moreover, MTs are permanently colliding with water and other cytoplasmic molecules (Kasas et al., 2004). This collision generates waves along MTs, so it is essential to study wave propagation along MTs within the elastic medium. In (Qian et al., 2007), an orthotropic elastic shell model is used to study wave propagation of MTs because its structure reveals that the longitudinal bonds between αβ-tubulin dimmers along protofilaments are much stronger than the lateral bonds between adjacent protofilaments (Schoutens, 2004). In particular, shear modulus of MTs is much lower than elastic modulus along longitudinal direction (Kis et al., 2002; Nogales et al., 1999) 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.

Inspired by these ideas, an orthotropic shell model was developed (Qian et al., 2007), to study wave propagation along MTs. A good agreement has been found between this model and available discrete models and experiments. Due to its valid applications (Taj and Zhang, 2011, 2012; Wang et al., 2006a; Qian et al., 2007), the present paper will further extend the model to analyze the wave propagation behavior of embedded MTs in the surrounding elastic matrix. We modeled the surrounding of MTs as Pasternak foundation to account normal stress and shear stress between MTs and the surrounding elastic matrix. This model has been used to account the surrounding effects of elastic medium for vibrational and buckling behavior of MTs (Taj and Zhang, 2012; Shen, 2010, 2011). On these grounds, an orthotropic-Pasternak model is developed in the present paper and is employed to study the wave propagation of embedded MTs.

2. Methods

2.1. *Orthotropic-Pasternak model*

Here, let us develop an orthotropic-Pasternak model to study waves propagation in MTs embedded in Pasternak foundation. 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 (Ventsel

Table 1 – The values of orthotropic material constants for microtubules.

Parameters	Values	References
Longitudinal Modulus, E_x	0.5 – 2 GPa	(de Pablo et al., 2003; Taj and Zhang, 2011)
Circumferential Modulus, E_θ	1 – 4 MPa	(Qian et al., 2007)
Shear Modulus in x-θ plane, $G_{x\theta}$	1 MPa	(Kis et al., 2002; Taj and Zhang, 2011)
Poisson's ratio in axial direction, υ_x	0.3	(Taj and Zhang, 2011; Wang et al., 2006)
Mass density per unit volume, ρ	1.47 g/cm^3	(Qian et al., 2007)
Equivalent thickness, h	2.7 nm	(Qian et al., 2007; Flugge, 1960)
Effective thickness for bending, h_0	1.6 nm	(Flugge, 1960)