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Cell cytoskeleton and tensegrity

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Abstract. The role of tensegrity architecture of the cytoskeleton in the mechanical behavior of living cells is examined by computational studies. Plane and spatial tensegrity models of the cytoskeleton are considered as well as their non-tensegrity counterparts. Local buckling including deep postbuckling response of the compressed microtubules of the cytoskeleton is considered. The tensioned microfilaments cannot sustain compression. Large deformation of the whole model is accounted and fully nonlinear analysis is performed. It is shown that in the case of local buckling of the microtubules non-tensegrity models exhibit qualitatively the same linear stiffening as their tensegrity counterparts. This result raises the question of experimental validation of the local buckling of microtubules. If the microtubules of real cells are not straight, then tensegrity (in a narrow sense) is not a necessary attribute of the cytoskeleton architecture. If the microtubules are straight then tensegrity is more likely to be the cytoskeletal architecture.

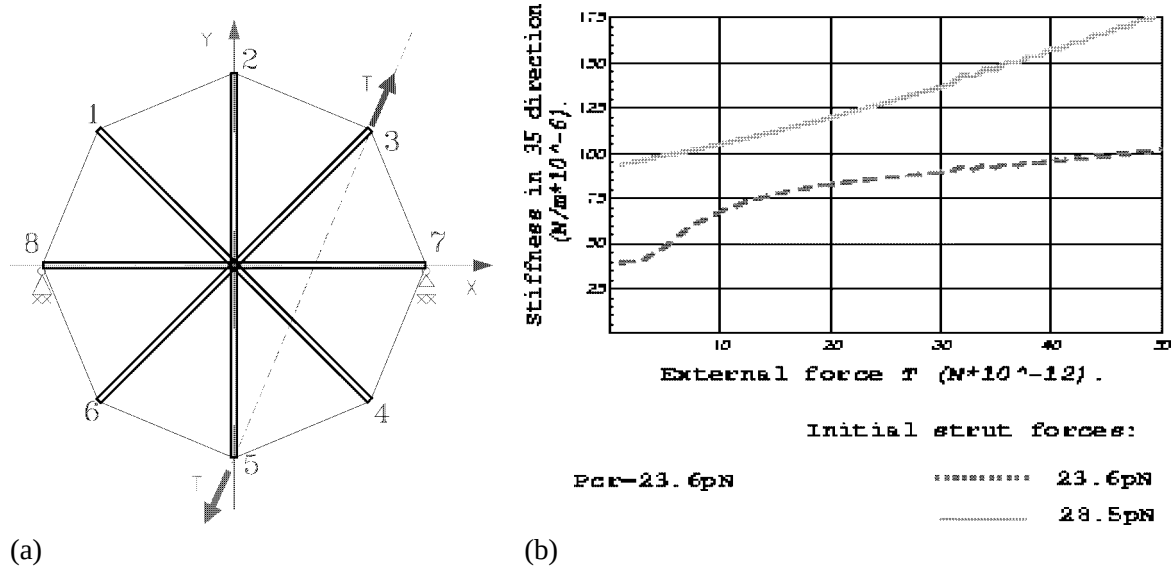
1. Introduction

The cell mechanism of transition of mechanical signals (deformations) into biochemical output is not well understood and various scenarios have been proposed for the explanation of the aforementioned mechanotransduction. Among other are [7]: modification of electrical potentials; variations in the chemical environment of cells; G-protein-linked receptors; mechanically activated ion channels; and cytoskeleton. The latter one [1] is a result of recent experiments refuting the traditional fluid balloon model of a cell [3,5]. It was discovered that a microstructural framework comprising microtubules and microfilaments is responsible for the cell contractility. This cytoskeletal framework is spread over the cell and it seems to be the main load-bearing element of the cell. Ingber [1,4] proposed that the cytoskeletal framework enjoys a specific architecture called *tensegrity*. By using tensegrity model shown in Fig. 3 [2,6,9] it was possible to explain the experimentally observed linear stiffening of living cells [8,10,11].

Tensegrity architecture of the cytoskeleton implies that isolated compressed microtubules are attached at every node of the tensioned network of the microfilaments. An important feature of tensegrity assemblies (in a narrow sense) is that they are statically and kinematically indeterminate. Static indeterminacy means possibility of pre-stressing and stabilization of the whole assembly. This stabilization is necessary because kinematic indeterminacy means existence of small displacements that do not produce elongations of microtubules and microfilaments. As a result of the kinematic indeterminacy the mechanical response of cytoskeletal frameworks is nonlinear and linear stiffening of the cell may be observed. However, the lack of constraints of tensegrity structures is not the only possible reason of the nonlinear cell response and its linear stiffening. Also, local buckling of microtubules of a fully constrained cytoskeleton can be the main source of cell non-linearity. A question suggests itself: what is a mechanical response of a non-tensegrity and fully constrained cytoskeletal model? Is it possible to observe the linear stiffening as a result of the buckling of microtubules only without involvement of geometrical degeneracy of tensegrity? The goal of this note is to answer this question. Computer simulations examine plane and spatial under-constrained tensegrity models as well as their fully constrained “counterparts”.

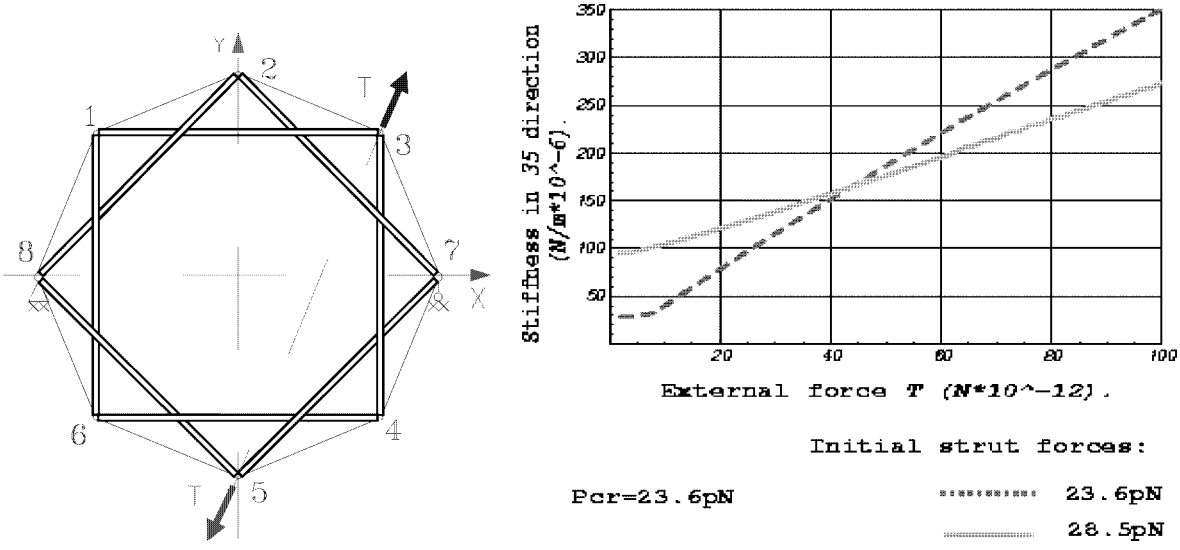
2. Computer simulation

Four cytoskeletal models shown in Figs 1–4 are considered. First two models are plane (2D) and latter ones are spatial (3D). Models shown in Figs 1(a) and 3(a) are kinematically indeterminate underconstrained tensegrity assemblies while their "counterparts" shown in Figs 2(a) and 4(a) are kinematically determinate fullyconstrained and non-tensegrity. All models are statically indeterminate and allowed for pre-stressing. Double line in figures marks microtubules and regular line marks microfila-



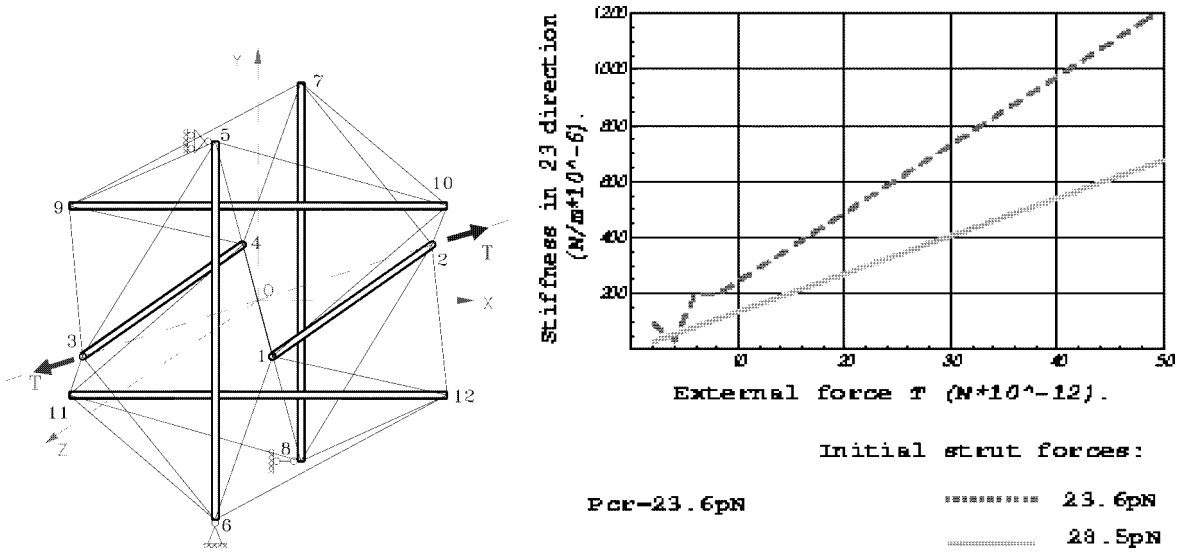
(a) (b)

Fig. 1. Plane kinematically indeterminate underconstrained tensegrity cell (a); stiffness versus force (b).



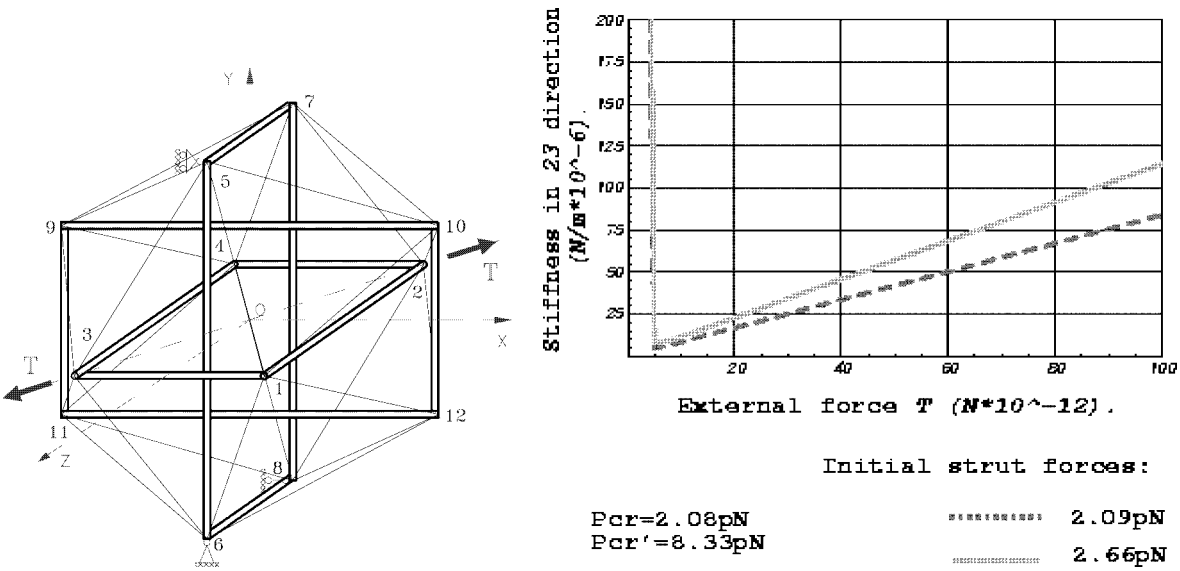
(a) (b)

Fig. 2. Plane kinematically determinate fullyconstrained non-tensegrity cell (a); stiffness versus force (b).



(a) (b)

Fig. 3. Spatial kinematically indeterminate underconstrained tensegrity cell (a); stiffness versus force (b).



(a) (b)

Fig. 4. Spatial kinematically determinate fullyconstrained non-tensegrity cell (a); stiffness versus force (b).

ments. Three degrees of freedom are prohibited for 2D models and six degrees of freedom are prohibited for 3D models in order to exclude rigid body motions. Elasticity modulus is $E_{\mathrm{S}} = 1.2$ GPa for struts-microtubules; and $E_{\mathrm{C}} = 2.6$ GPa for cables-microfilaments. The bending stiffness of struts and cross-sectional areas of struts and cables are accordingly $(EI)_{\mathrm{S}} = 2.15 \cdot 10^{-23}\ \mathrm{N\,m^2}$, $A_{\mathrm{S}} = 190\ \mathrm{nm^2}$, $A_{\mathrm{C}} = 18\ \mathrm{nm^2}$ for three first models (Figs 1–3). The corresponding magnitudes of the fourth model (Fig. 4) are $(EI)_{\mathrm{S}} = 1.9 \cdot 10^{-24}\ \mathrm{N\,m^2}$, $A_{\mathrm{S}} = 40\ \mathrm{nm^2}$, $A_{\mathrm{C}} = 2.6\ \mathrm{nm^2}$. The relations between pre-stressing

forces in struts and cables and their lengths *at the reference state* shown in figures take the following forms:

$$\text{Fig. 1(a):} \qquad P_{\mathrm{S}} = 2P_{\mathrm{C}}\cos(3\pi/8), \qquad L_{\mathrm{C}} = L_{\mathrm{S}}\sqrt{2-\sqrt{2}}/2;$$

$$\text{Fig. 2(a):} \qquad P_{\mathrm{S}} = P_{\mathrm{C}}\sin(\pi/8)/\sin(\pi/4), \qquad L_{\mathrm{C}} = L_{\mathrm{S}}\sqrt{4-2\sqrt{2}}/4;$$

$$\text{Fig. 3(a):} \qquad P_{\mathrm{S}} = P_{\mathrm{C}}\sqrt{6}, \qquad L_{\mathrm{C}} = L_{\mathrm{S}}\sqrt{3/2}/2;$$

$$\text{Fig. 4(a):} \qquad P_{\mathrm{S}} = P_{\mathrm{C}}2\sqrt{6}, \qquad P'_{\mathrm{S}} = P_{\mathrm{C}}\sqrt{6}, \qquad L_{\mathrm{C}} = L_{\mathrm{S}}\sqrt{3/2}/2, \qquad L'_{\mathrm{S}} = 0.5L_{\mathrm{S}}.$$

All microtubules possess the same length *at rest* $L_0 = 3$ μm except for the short microtubules in Fig. 4(a) with the corresponding length $0.5L_0$. This length defines constitutive relations for microtubules [9]. Controlling the pre-stressing force in microtubules it is possible to fit the rest of parameters of the models.

Stiffness versus forces are shown in Figs 1(b)–4(b). The stiffness is defined as the ratio of the applied force to the elongation in its direction. Two cases of pre-stressing are accounted. First, microtubules are compressed up to the critical buckling load. Second, microtubules are buckled at the reference state. It is readily seen that all models exhibit linear stiffening response independently of their architecture.

3. Closure

Computer simulations of under- (tensegrity) and fully-constrained cytoskeletal models have been presented. Results of these simulations show that independently of the specific structural geometry (regular or degenerate) the linear stiffening is observed due to the local buckling of microtubules. In the light of these theoretical results the experimental observation of the buckling of microtubules is of interest. If there are non-straight buckled microtubules then the tensegrity architecture (in a narrow sense) is not the only possible cytoskeletal architecture. If only straight unbuckled microtubules are observed then the cytoskeletal architecture is geometrically degenerate and it may be tensegrity.

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