

On Tensegrity in Cell Mechanics

K. Y. Volokh*

“Systems of interacting forces and stimuli do not have to be very complicated before the unaided human intuition can no longer predict accurately what the net result should be. At this point computer simulations, or other mathematical models, become necessary. Without the aid of mechanicians, and other skilled in simulation and modeling, developmental biology will remain a prisoner of our inadequate and conflicting physical intuitions and metaphors.”

Albert Harris

Abstract: All models are wrong, but some are useful. This famous saying mirrors the situation in cell mechanics as well. It looks like no particular model of the cell deformability can be unconditionally preferred over others and different models reveal different aspects of the mechanical behavior of living cells. The purpose of the present work is to discuss the so-called tensegrity models of the cell cytoskeleton. It seems that the role of the cytoskeleton in the overall mechanical response of the cell was not appreciated until Donald Ingber put a strong emphasis on it. It was fortunate that Ingber linked the cytoskeletal structure to the fascinating art of tensegrity architecture. This link sparked interest and argument among biologists, physicists, mathematicians, and engineers. At some point the enthusiasm regarding tensegrity perhaps became overwhelming and as a reaction to that some skepticism built up. To demystify Ingber’s ideas the present work aims at pinpointing the meaning of tensegrity and its role in our understanding of the importance of the cytoskeleton for the cell deformability and motility. It should be noted also that this paper emphasizes basic ideas rather than carefully follows the chronology of the development of tensegrity models. The latter can be found in the comprehensive review by Dimitrije Stamenovic (2006) to which the present work is complementary.

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1 Introduction

Man needs to understand how living cells work. Such an understanding will help to develop new biomedical technologies leading to dramatic changes in the life of human beings. The progress is slow, however. While various components of the cell have been identified their connections and functionality largely remain to be understood. The cell problem is interdisciplinary yet biochemistry dominated the cell studies in the past century. It was realized recently that the cell deformability might also be crucial for the understanding of the cell motion and mechanotransduction – see Chen et al (1997), for example. Thus, mechanics of the cell appeared on the stage.

Cell mechanics is a relatively new science of deformation and motion of living cells which stands at the crossroad of various disciplines including physics, chemistry and biology. Contrary to more traditional areas of mechanics cells are difficult to study experimentally. The major experimental techniques include: micropipette aspiration; cell poker; particle tracking; magnetic twisting cytometry; atomic force microscopy; microplate manipulation; cytoindentation; optical tweezers etc. Most techniques are used to reveal the mechanical response of the cell to the locally applied loads. Unfortunately, the interpretation of the outcome of the experiments is not trivial at all and the diversity of the experimental schemes and results also requires various guiding theories. However, no particular theory of the cell deformability can be unconditionally preferred over others and different theories reveal different aspects of the mechanical behavior of living cells.

The purpose of the present work is to discuss the so-called *tensegrity* theories of the cell cytoskeleton. It seems that the role of the cytoskeleton in the overall mechanical response of the cell was not appreciated until Ingber (1993, 1997, 1998, 2003a, 2003b) put a strong emphasis on it. It was fortunate that Ingber linked the cytoskeletal structure to the fascinating art of tensegrity architecture. This link sparked interest and argument among biologists, physicists, mathematicians, and engineers. At some point the enthusiasm regarding tensegrity perhaps became overwhelming and as a reaction to that some skepticism built up. To demystify Ingber's ideas this paper aims at pinpointing the meaning of tensegrity and its role in our understanding of the importance of the cytoskeleton for the cell deformability and motility. It should be noted also that the present work emphasizes basic ideas rather than carefully follows the chronology and subtleties of the development of tensegrity models. The latter can be found in the comprehensive reviews by Stamenovic (2006) and Stamenovic and Ingber (2009) to which the present work is comple-

mentary.

We start with a brief review of theoretical approaches in cell mechanics in Section 2. Then the crucial experiments underlying tensegrity models are considered in Section 3 and the concept of tensegrity is introduced in Section 4. Some results on modeling tensegrity architecture are presented in Section 5. And a closing discussion of the role of tensegrity models appears in Section 6.

2 Approaches in cell mechanics

Cell mechanics, i.e. cell deformation and motion, is a relatively new subject with a few monographs partially or completely devoted to it: Fung (1993); Bray (2000); Howard (2001); Pollack (2001); Boal (2002); Mofrad and Kamm (2006). Theoretical models describing mechanics of the cell can be provisionally divided into *structural* and *continuum*.

Historically continuum models of the cell appeared first. They were triggered by the intuitively appealing vision of the cell as a liquid drop surrounded by a membrane. The liquid comprised all the interior cell components dominated by cytoplasm. First models considered the Newtonian liquid (Evans and Kukan, 1984) and they were subsequently complicated by introducing non-Newtonian liquids (Tsai et al, 1993), solids (Mijailovich et al, 2002; Dao et al 2003), and solid-fluid mixtures with various rheological properties (Ateshian et al, 2006). Though the continuum theories are phenomenological, somewhat subtle physical reasoning can underlie their development as in the case of the soft glassy material models by Fabry et al (2001). Needless to say, the use of the continuum theory is a gross approximation. The inner space of the eukaryotic cells is heterogeneous with the inclusion of nucleus. Nonetheless, continuum models are simple and pleasure to deal with. They are useful when the whole-cell response is of interest. For example, the Suresh group (Suresh et al, 2005) used continuum models to detect the disease state of the malaria infected red blood cells. They modeled and observed that the infected red blood cells underwent significant structural changes and their bulk stiffness increased. The stiffness increase affected the motility of the infected cells during their advance inside the pipette and such cells could be easily identified. Various aspects of continuum models in cell mechanics were recently reviewed by Lim et al (2006). It is reasonable to assume based on the works in this direction that the choice of a continuum model should depend on the targeted application. In this way even a rough model opened for criticism in general can be useful and successful under particular circumstances.

While continuum models are based on the idea of the homogenization of the cell constituents, the structural models emphasize the different roles of the different

constituents in the design of the cell. Among the structural models, we mention the open-cell foams that consider networks of interconnected struts (Budiansky and Kimmel, 1987; Warren and Kraynik, 1997; Satcher and Dewey, 1996; Satcher et al, 1997) and tensegrity systems considering cytoskeleton as an assembly of the pre-stressed microtubules and microfilaments (Coughlin and Stamenovic, 1997; Wendling et al, 1999; Volokh et al, 2000). Tensegrity models will be considered at length below. Though the structural models can gain interesting qualitative insights in the mechanical behavior of the cell they are computationally intensive and, because of that, limited by a small number of elements.

Finally, we should separately mention the polymer-based cell models that link different length scales analogously to the statistical theories of rubber-like materials: MacKintosh et al (1995); Gardel et al (2004); Storm et al (2005).

3 Crucial experiments

In this section simple experiments are described that led to the introduction of the tensegrity models that we consider afterwards.

Intuition, occasionally based on our high-school microscope observations, suggests that a fluid-like cellular inner space is preserved due to the bounding soft membrane. This intuition is a simple motivation for the viscous fluid balloon model. Putting aside viscosity one can even consider a rubber balloon filled with water as a large scale physical model of the cell. Such a balloon will tend to spread over a thin substrate being placed on it freely – Fig. 1.

This thought experiment can also be tried with the real cells. Such cell experiment was actually done by Harris et al (1980) and the results were amazing. Unexpectedly, the thin rubber substrate folded under the spread cells – Fig. 2.

The folding is hardly imaginable if the cell is a fluid balloon. To give a rational explanation for the observation of the substrate folding one should assume that something exists inside the cell that contracts during the cell spreading and this contraction is transmitted to the substrate through the attachment sites of the cell. The ‘something’ can only be formed by the cytoskeleton comprising microfilaments, intermediate filaments, and microtubules. At this point we do not discuss the architecture of the cytoskeleton yet conclude that it has the load-bearing capacity and plays a significant role in the mechanical response of the cell. The latter idea is of fundamental importance and it should be examined in independent experiments. For example, it is natural to try pulling the receptors on the surface of the cell while tracking the nucleus response deep inside the cell. Such a scenario guided the experiments by Maniotis et al (1997) who used micropipette to disturb the cell receptors and observed immediate changes in the position of the nucleus.

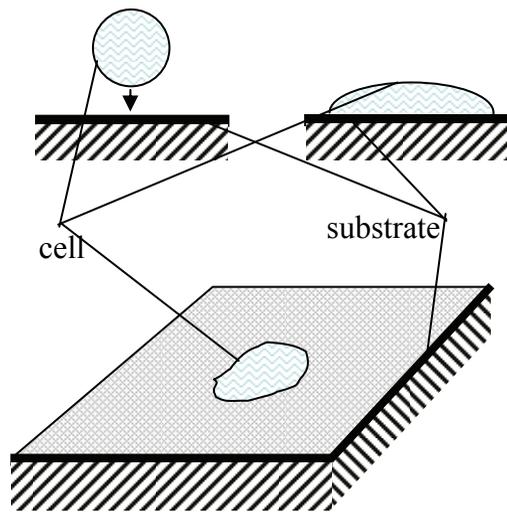


Figure 1: Expected behavior of the fluid cell-balloon on a substrate.

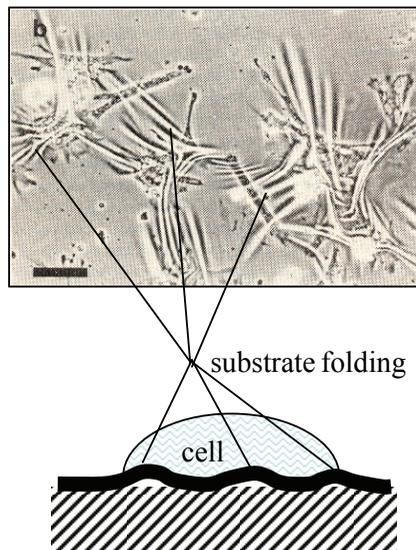


Figure 2: Amazing substrate folding in Harris et al (1980) experiments.

The described experiments bear witness of the ability of the cell interior to sustain

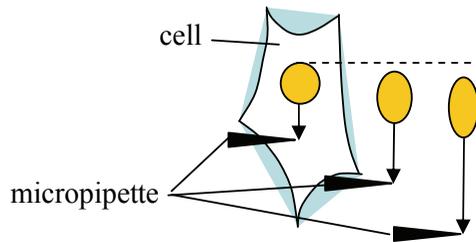


Figure 3: Unexpected immediate rearrangements inside the cell after pulling surface receptors by Maniotis et al (1997).

tension. The cytoskeleton is the network that provides the cell stiffness. Donald Ingber – Fig. 4 – suggested that this network has the so-called tensegrity architecture where the tension of the microfilaments is induced through the compression of microtubules.



Figure 4: Donald Ingber.

Ingber's many publications include discussions of various implications of the idea of the tensegrity structure of the cytoskeleton and we turn now to the concept of tensegrity.

4 The meaning of tensegrity

Tensegrity is a marriage of *tension* and *integrity*. This name was coined by the artist Buckminster Fuller – Fig. 5 – who is also famous for the *fullerene* structures popular in materials science and physics.

Whether Fuller invented tensegrity structures is a delicate question and we leave the exciting studies of the priority issues to the reader. It should be stated, however,

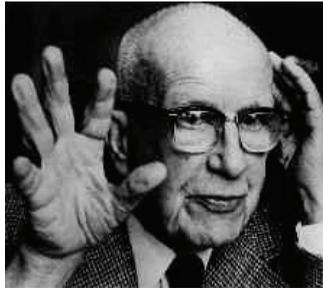


Figure 5: Buckminster Fuller.

that the key figure in the development of the tensegrity concept was another artist – Kenneth Snelson – Fig. 6.



Figure 6: Kenneth Snelson.

Snelson defined tensegrity as follows: *‘Tensegrity describes a closed structural system composed of a set of three or more elongate compression struts within a network of tension tendons, the combined parts mutually supportive in such a way that the struts do not touch one another, but press outwardly against nodal points in the tension network to form a firm, triangulated, prestressed, tension and compression unit’.*

A simple spatial tensegrity structure is shown in Fig. 7.

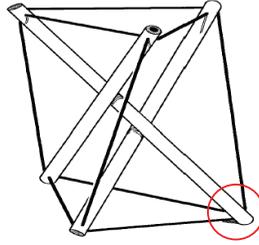


Figure 7: Simple tensegrity structure.

It is emphasized in the figure that only one strut enters a node while the number of cables-tendons entering the node is not restricted. To formalize the notion of tensegrity structures we consider an assembly of pin-jointed struts in some reference state and assume, for the sake of the stability analysis only, that all elements undergo small displacement perturbations, $\delta \mathbf{u}$, at the nodes.

The energy stored by the assembly can be written in the form

$$\Psi = \sum_{n=1}^N \psi_n, \quad (1)$$

where ψ_n is the stored energy of the n th element and N is the number of elements.

The assembly is in equilibrium when the first perturbation of the total energy, including the stored energy and the energy of the external forces, with respect to the nodal displacements equals zero. This condition is used for formulating equilibrium equations and finding the element forces and displacements. However, not every formal solution of the equilibrium equations can be observed in reality. Only stable solutions have physical meaning. The structural stability criterion takes the following form

$$\delta^2 \Psi = \delta \mathbf{u}^T \mathbf{K} \delta \mathbf{u} > 0, \quad (2)$$

where the *tangent stiffness matrix* can be presented in the form

$$\mathbf{K} = \mathbf{B}^T \mathbf{C} \mathbf{B} + \mathbf{D}. \quad (3)$$

Here the matrix of direction cosines, \mathbf{B} , is N by M where M is the number of the nodal degrees of freedom. The entries of the matrix can be calculated as follows: $B_{nm} = (X_m - X_k)/L_n$, where X_m designates nodal coordinates; L_n designates the

referential chord length of the n th element; m and k are proper indices of the element coordinates. The uncoupled stiffness matrix, \mathbf{C} , is N by N diagonal with entries: $C_{mn} = S_n/L_n$, where S_n is the axial stiffness of the n th element. The geometric stiffness matrix, \mathbf{D} , is M by M symmetric with entries: $D_{mm} = \sum_{n=1}^j P_n/L_n$; $D_{mt} = -P_n/L_n$, where P_n is a pre-stress force in the n th element. The sum is over all j elements joined at the node with the m th degree of freedom. Index t is the properly chosen degree of freedom at the second edge of the n th element.

Since the displacement perturbations are arbitrary, condition (2) implies that the tangent stiffness matrix \mathbf{K} must be *positive definite* to provide the stability of the assembly. At this point we arrive at two different possibilities to provide the stability of the structural assembly. The first possibility is that matrix $\mathbf{B}^T \mathbf{C} \mathbf{B}$ is positive definite. In this case since the element axial stiffness is usually much greater than the possible pre-stress, $S_n \gg P_n$, the second term on the right hand side of (3) can be ignored as compared to the first one and we have

$$\mathbf{K} \cong \mathbf{B}^T \mathbf{C} \mathbf{B}. \quad (4)$$

Such approximation is characteristic of the classical structures whose stability is due to the material elastic properties. The infamous structure of this type is shown in Fig. 8.



Figure 8: Eiffel tower – regular structure.

It can occur, however, that $\mathbf{B}^T \mathbf{CB}$ is singular

$$\det(\mathbf{B}^T \mathbf{CB}) = 0, \quad (5)$$

and the account of the second term on the right hand side of (3) becomes crucial. Of course, in this case the pre-stress should exist and it should stabilize the structure providing the positive definiteness of \mathbf{K} .

Condition (5) takes place in a very special case of structures that lack constraints. The latter is the reason to call such structures *underconstrained* – see Fig. 9 and Kuznetsov (1991) or Volokh and Vilnay (1997a), for example. Tensegrity structures fall within the class of underconstrained structures obeying condition (5).



Figure 9: Snelson tower – underconstrained tensegrity structure.

It is crucial to realize that though the pre-stress can regularize the tangent stiffness matrix, $\det \mathbf{K} \neq 0$, it may not be enough to stabilize the assembly providing the positive definiteness of \mathbf{K} . In the case of *all pre-tensioned* elements the mathematical proof exists that the assembly is always stable because \mathbf{K} is positive-definite (Volokh and Vilnay, 2000). If, however, the assembly comprises both tensioned and compressed members, as in the case of tensegrity structures, its stability cannot be taken for granted (Volokh and Vilnay, 1997b; Li et al, 2010).

In summary, tensegrity structures are singular structures and their stability is provided due to pre-stress rather than the elastic properties of the elements (see also Volokh (2003) for discussion). The pre-stress is achieved with the help of the stiff struts that can bear compression. The compressed struts sustain tension in cables that can stabilize the whole assembly.

5 Tensegrity models

Tensegrity architecture is sophisticated and it requires nonlinear analysis of stress and deformation. Two features make the analysis difficult. First, microfilaments are cables or tendons from the structural mechanics standpoint, which means that they do not bear compression. Only tension is possible in microfilaments as well as in intermediate filaments. Second, microtubules are struts from the structural mechanics standpoint, which means that they can bear both tension and compression. However, microtubules are not stiff enough to remain straight during deformation. They buckle. A nice photograph of a buckled microtubule can be found in Wang et al (2001), for example. Thus, the unilateral response of cables and buckling of struts¹ should be taken into account in analysis. These features make simulations intensive computationally and complicated algorithmically. The latter explains why the simple tensegrity model shown in Fig. 10 was primarily used in computer modeling.

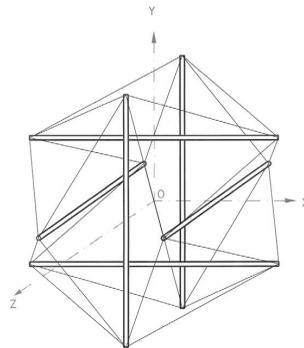


Figure 10: Spatial tensegrity model of the cytoskeleton.

This model was analyzed in the pioneering work by Coughlin and Stamenovic (1997) and in the numerous subsequent studies of Stamenovic – Fig. 11 – and his collaborators – see Stamenovic (2006) for references.

Later Wendling et al (1999) also used this model to show the stiffening behavior of the cell under deformation. The deep postbuckling behavior of the microtubules and the unilateral response of microfilaments was accounted for in Volokh et al (2000). A typical deformed model is shown in Fig. 12.

It is interesting to note that microtubules can bear compression in the buckled state

¹ See also Appendix.

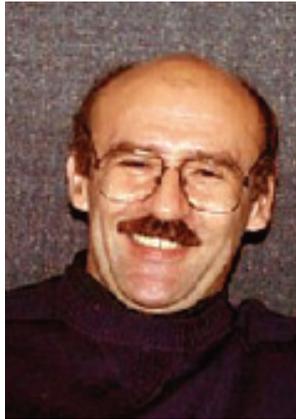


Figure 11: Dimitrije Stamenovic.

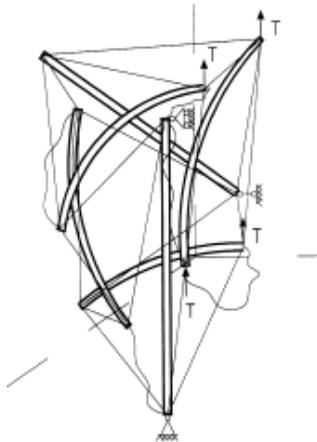


Figure 12: Deformed tensegrity model (from Volokh et al, 2000).

while microfilaments cannot.

The tensegrity model can readily explain the substrate folding in Harris's experiments assuming that some nodal points are connected to the substrate. Moreover, tensegrity models explained the stiffening of the cell during deformation. Such stiffening is commonly observed in experiments. Besides, based on the tensegrity model Volokh et al (2000) also found a possible softening response of the cell due to buckling of microtubules. Of course, the softening response may be local and it

depends strongly on the specific skeleton structure in the area of the applied force. Since tensegrity in the narrow sense defined by Snelson is quite odd it was interesting to examine a non-tensegrity model similar to the tensegrity one. Such a model shown in Fig. 13 was examined in Volokh et al (2002).

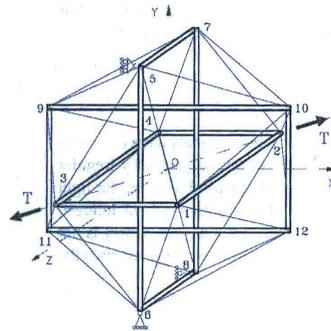


Figure 13: Non-tensegrity model (from Volokh et al, 2002).

It should be emphasized that two struts meet at every node in Fig. 13 contrary to the definition of tensegrity. Numerical analysis showed that the non-tensegrity model also exhibited stiffening under loading. Thus the stiffening response is not a privilege of tensegrity architecture only. For more modeling examples of tensegrity we refer to Stamenovic's (2006) review.

6 Discussion

In the present work we discussed *tensegrity models* of the cytoskeleton tracking their architectural roots, connection to biological experiments, and their meaning from the perspective of structural mechanics.

We have to distinguish between the narrow and wide meanings of tensegrity. In the narrow meaning tensegrity is an odd structure whose stiffness and stability are provided due to the pre-stress rather than elastic properties of its elements. Moreover, the requirement that only one compressed microtubule is linked to microfilaments at every node of the cytoskeleton is hardly in peace with reality. We also doubt that all these structural subtleties were meant by the trained biologist Donald Ingber who pushed the tensegrity idea into cell mechanics. Evidently, tensegrity should be interpreted in a wide meaning as the idea of the internal filamentous net of the cytoskeleton that can be stabilized and stiffened by microtubules without strictly following the Snelson definition.

Ingber's idea was important because it emphasized the load bearing capacity of the cytoskeleton. That was a breakthrough. An interesting question is whether the microtubules play a crucial role in mechanics of the cytoskeleton. Of course, such 'massive' elements as microtubules cannot be ignored in structural analysis on the one hand. On the other hand their mechanical role is probably more modest than the tensegrity models suggest because the number of microtubules is much smaller than the number of microfilaments.

Probably, the cytoskeleton bears cells mechanically in a way similar to spokes bearing the wheel loads – Fig. 14.



Figure 14: Wheel with spokes.

The spokes, similarly to filaments, are very flexible and they cannot bear significant compression without buckling. The spokes, however, are perfect in bearing tension. During the wheel motion only a fraction of the spokes in tension is mobilized to bear the load on the wheel. It is reasonable, in our opinion, to assume similarly that during the cell deformation and motion only a fraction of the tensioned filaments is mobilized to bear the load.

Another interesting point to be mentioned here is the observed stiffening behavior of the cell. This behavior is well explained by the tensegrity models. In a wider perspective, however, the stiffening behavior is typical of rubberlike materials and soft biological tissues. The reason for stiffening is that the long polymer chains unfold during deformation and their straightening leads to the material bulk stiffening. Similar alignment and straightening of the cytoskeletal net in the direction of tension is observed in the cell experiments.

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Appendix: Buckled Strut

Computer analysis of tensegrity models is complicated and it requires modeling buckling of struts. Below we present a simple new way to account for such buckling.

We start with the consideration of compression and postbuckling of a strut as shown in Fig. A1.

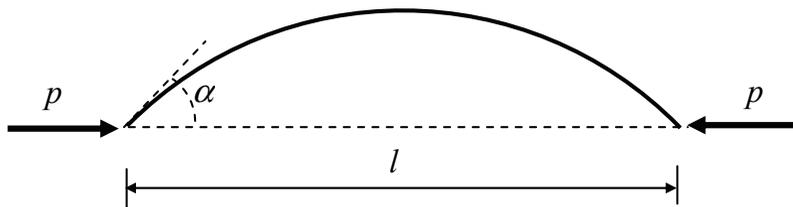


Figure A1: Buckled strut – the elastica solution

For the sake of simplicity and because of the high flexibility of the microtubules we ignore the option of unbuckled compression and assume that microtubules are buckled when compressed. The well-known elastica solution (Timoshenko and Gere, 1961) describes the buckled strut implicitly:

$$L = 2\sqrt{YI/pK}[\sin^2(\alpha/2)], \quad (\text{A1})$$

$$l = 4\sqrt{YI/pE}[\sin^2(\alpha/2)] - L, \quad (\text{A2})$$

where Y is the Young modulus; I is the cross-sectional inertia moment; L is the strut length; l is the distance between the strut edges; α is the edge slope; and the complete elliptic integrals of the first and second kind take the following forms accordingly

$$K[\beta] = \int_0^{\pi/2} \frac{d\varphi}{\sqrt{1 - \beta \sin^2 \varphi}}. \quad (\text{A3})$$

$$E[\beta] = \int_0^{\pi/2} \sqrt{1 - \beta \sin^2 \varphi} d\varphi. \quad (\text{A4})$$

The critical Euler load is obtained from (A1) for $\alpha = 0$: $p_c = \pi^2 YI/L^2$.

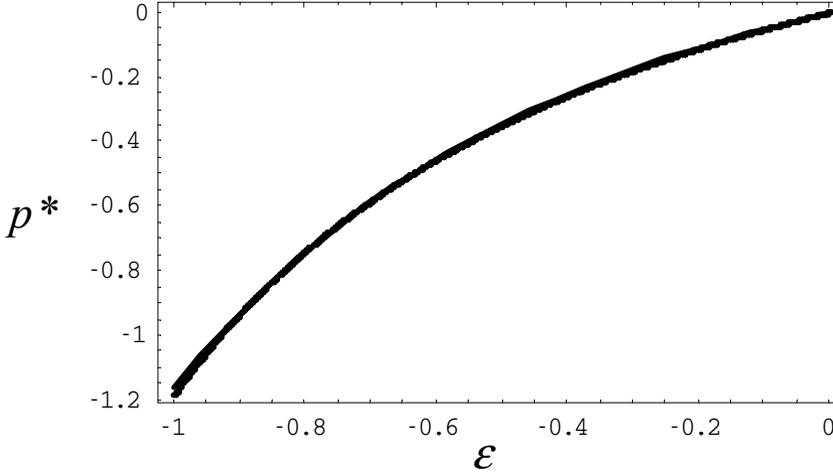


Figure A2: Tabulated and fitted stress-strain curves coincide

In order to establish the force-elongation, $p \sim \Delta = l - L$, relationship it is necessary to exclude slope α from (A1)-(A2). The analytical solution of the latter problem is not found yet. It is possible, however, to produce a highly accurate approximation of the solution numerically. In order to do that we rewrite (A1) and (A2) in the following form

$$\frac{p}{p_{cr}} + 1 \equiv p^* = -4 \frac{K^2}{\pi^2} + 1, \tag{A5}$$

$$\frac{\Delta}{L} \equiv \varepsilon = 2 \frac{E}{K} - 2, \tag{A6}$$

where p^* is a 'relative' axial force; $p_{cr} = \pi^2 EY/L^2$ is an absolute magnitude of the critical buckling load of the hinged strut. It was taken into account that compressive stresses are negative.

It is remarkable that the right-hand sides of (A5) and (A6) do not depend on the geometrical and physical properties of the considered strut. The latter prompts the idea to relate p^* and ε by tabulating the right-hand sides of (A5) and (A6) numerically and, then, fitting the tabulated data with polynomials. To accomplish this plan we determine the range of the argument of the elliptic integral where the tabulation will take place. Evidently, the buckling starts from $\alpha = m = 0$ and proceeds until the strut is bent into a ring. In the latter case, we have $m = 0.826$ and

$\alpha = 130.69^\circ$, which is a solution of equation: $l/L = 2E(m)/K(m) - 1 = 0$. After determining the range of the argument, we can tabulate the stress-strain relation, $p^* \sim \varepsilon$, for the buckled strut and fit it by a polynomial. Fig. A2 shows the tabulated numerical curve $p^* \sim \varepsilon$ for the mesh of the uniformly distributed 1001 points and the analytical curve produced by the Mathematica 'Fit' procedure for the chosen polynomial: $p^* = 0.536317 \varepsilon + 0.622645 \varepsilon^3$.

Now, the force-elongation relationship in compression, $p \sim \Delta$, can be written as follows

$$p = [0.536317 \Delta/L + 0.622645 \Delta^3/L^3] \pi^2 YI/L^2. \quad (A7)$$

Based on (A7) we can write the stored energy of a strut in compression as follows

$$\psi_C = YI \pi^2 L^{-2} [0.536317 (\Delta + \Delta_0)^2 / (2L) + 0.622645 (\Delta + \Delta_0)^4 / (4L^3)], \quad (A8)$$

where we added the initial elongation, Δ_0 , which accounts for the deformed configuration of a strut in its reference state.