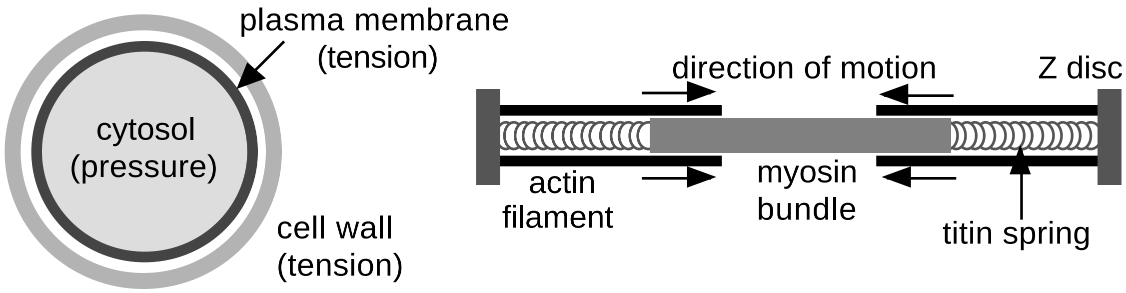
TENSEGRITY AND BUCKLING

To be covered:

- tension/compress couplets
- filament buckling
- limits to cell division

Tension / compression

Newton's third law tells us that at equilibrium, a cell must have elements under compression to balance those under tension. In the simplest arrangements, a fluid region, like the interior of the cell, is under compression and filaments are under tension:

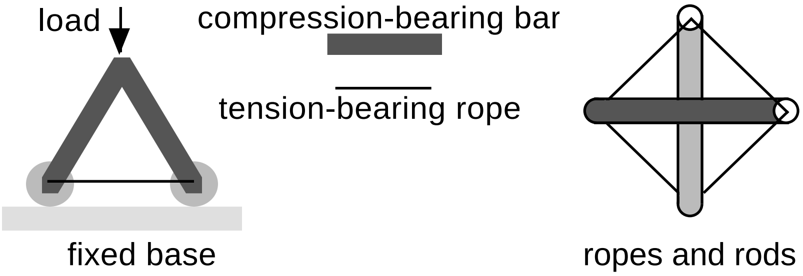


From this diagram, the tension-bearing filaments can be arranged in an intriguing number of ways; in muscles, for example:

- actin and myosin filaments are under tension
- titin under tension (used in part to keep myosin bundles aligned)
- compression is borne by the bone to which muscle is attached

Within the families of filaments, the thinest (actin, spectrin) have the smallest compression resistance, while microtubules have the largest.

It has been proposed that filaments themselves can form tension / compression couplets like the *tensegrity* structures of Buckminster Fuller.



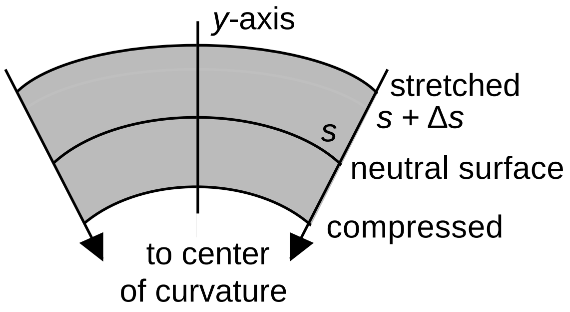
Whether these structures are feasible in a cell depends on whether the compression-bearing elements buckle.

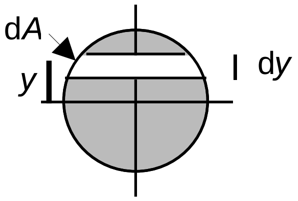
Buckling

Suppose that we gently bend an otherwise straight bar by applying a torque about its ends, as shown below. The top surface of the bar is stretched and the bottom surface is compressed; near the middle lies the *neutral surface* (no lateral strain).

For a small enough segment of the bar

- the bend is very gentle
- the neutral surface runs through the midplane
- the radius of curvature R is constant.





The section has an arc length s along the neutral surface and a length $s + \Delta s$ at a vertical displacement y, where $\Delta s > 0$ when $y > 0$. Because the arcs have a common center of curvature, then

$$(s + \Delta s)/s = (R + y)/R$$

or

$$\Delta s/s = y/R.$$

However, $\Delta s/s$ is the strain in the longitudinal direction, so

$$[\textit{longitudinal strain}] = y/R \qquad \text{(strain depends on } y\text{)}$$

The stress is the force per unit area at y, which we write as $\mathrm{d}F/\mathrm{d}A$, where dA is shown in the diagram. Now,

$$[\textit{stress}] = Y\,[\textit{strain}]$$

which becomes

$$\mathrm{d}F/\mathrm{d}A = Yy/R$$

or

$$\mathrm{d}F = (yY/R)\,\mathrm{d}A$$

This element of force results in a torque around the mid-plane equal to $y\,\mathrm{d}F$, which can be integrated to give the bending moment $\mathcal{M}$:

$$\mathcal{M} = \int y\,\mathrm{d}F = (Y/R)\int y^2\,\mathrm{d}A,$$

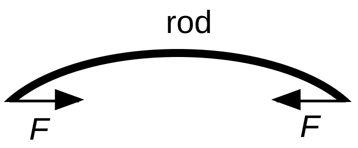
Equivalently

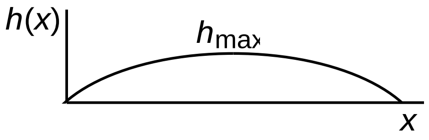
$$\mathcal{M} = Y\mathcal{I}/R \qquad (1)$$

where $\mathcal{I}$ is the moment of inertia of the cross section

$$\mathcal{I} = \int_{\text{cross section}} y^2 \, dA$$

We now apply Eq. (1) to the buckling problem, specifically the forces applied to the ends of a bar





Coordinates:

- $x = 0$ at one end of the bar
- contour length = L_c

As a function of height $h(x)$, the bending moment $\mathcal{M}$ from the force F applied to the ends of the bar is

$$\mathcal{M}(x) = Fh(x) \qquad \text{(from torque = } \mathbf{r} \times \mathbf{F}\text{)}$$

Replace $\mathcal{M}$ using Eq. (1) to obtain

$$Y\mathcal{I}/R(x) = Fh(x) \qquad (2)$$

The radius of curvature R is a function of position. To find its value, we use

$$d^2\mathbf{r}/ds^2 = \mathbf{n}/R,$$

where

- position = $\mathbf{r}$
- arc length = s along the curve
- unit normal = $\mathbf{n}$.

For gently curved surfaces,

$$d^2\mathbf{r}/ds^2 = d^2h/dx^2$$

so that

$1/R = -d^2h/dx^2$ (the minus sign arises because d^2h/dx^2 is negative here).

Thus, Eq. (2) becomes a differential equation for $h(x)$

$$d^2h/dx^2 = -(F/Y\mathcal{I})h(x) \qquad (3)$$

We recognize this equation has the same functional form as simple harmonic motion, so its solution must be

$$h(x) = h_{\max} \sin(\pi x/L_c) \qquad (4)$$

where $h_{\max}$ is the maximum displacement of the bend, occurring at $x = L_c/2$ in this approximation. As required, $h(0) = h(L_c) = 0$.

We can relate F to L_c by taking the second derivative of Eq. (4)

$$d^2h/dx^2 = -(\pi/L_c)^2\, h_{\text{max}} \sin(\pi x/L_c) = -(\pi/L_c)^2 h(x)$$

Comparing this to Eq. (3) gives $F/Y\mathcal{I} = (\pi/L_c)^2$, or

$$F_{\text{buckle}} = \pi^2 Y\mathcal{I}/L_c^2 = \pi^2 \kappa_f/L_c^2. \tag{5}$$

Physical meaning:

- if $F_{\text{applied}} < F_{\text{buckle}}$, the beam will just compress
- if $F > F_{\text{buckle}}$, the rod buckles.

Applications to cytoskeleton filaments

- persistence length of actin and spectrin is much less than cell dimensions; --> floppy
- what about microtubules?
  take $\xi_p \sim 3$ mm (experimental is 1-6 mm)
  flexural rigidity $\kappa_f = k_B T \xi_p = 1.2 \times 10^{-23}$ J•m
  take $F_{\text{max}} = 5$ pN
  Eq. (5) says microtubule will buckle if $L_c > 5$ µm.

Experimental observations (Elbaum *et al*., 1996):

- single microtubule in a floppy phospholipid vesicle, the vesicle has the appearance of an American football, whose pointed ends demarcate the ends of the filament.
- as tension is applied to the membrane by aspiration, the microtubule ultimately buckles and the vesicle appears spherical.
- microtubule of length 9.2 µm buckled at $F_{\text{buckle}} = 10$ pN.

Tensegrity?

- long filaments in the cell will buckle, not stiff enough for tensegrity structures unless present in bundles.