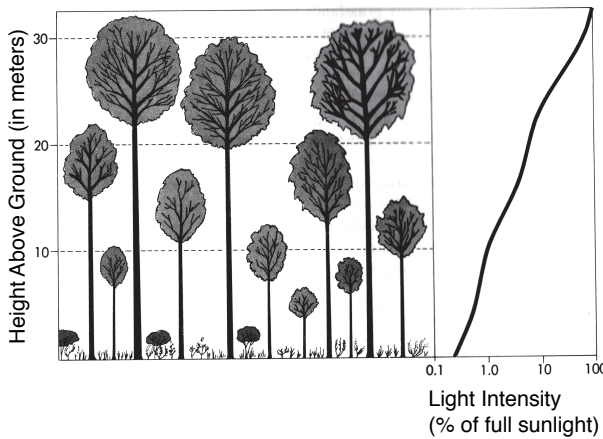
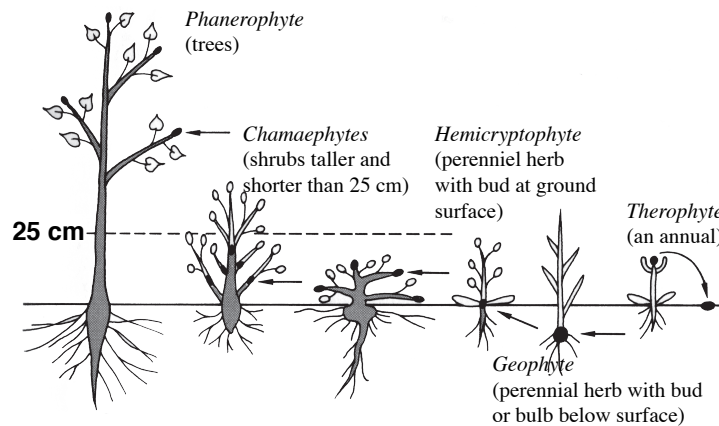


How high can a tree grow? Actually, a more basic question is why would a tree grow high? The answer to that is both simple and complex. The simple reason is to out-compete other trees in search of maximal sunlight intensities for utilization in photosynthesis.



In a forest, shading by taller trees results in a very strong attenuation of sunlight intensity: to levels 0.1 to 1% of full sunlight^[1]. So, it's natural to propose that tallness will confer a strong adaptive fit for a tree species. A more complex answer is related to adaptation to niche. In other words, growing tall expends a great deal of energy. Some species adapt to low light intensities, stay short and avoid the energetic cost of being tall. Other species splurge and grow tall.

In many ecosystems, trees don't necessarily dominate the landscape, dependent on environmental and other conditions. One way to illustrate this is by using taxonomic descriptions of plant forms (from Raunkiaer, a famous figure in European plant ecology) to assess the relative proportion of trees in different communities.

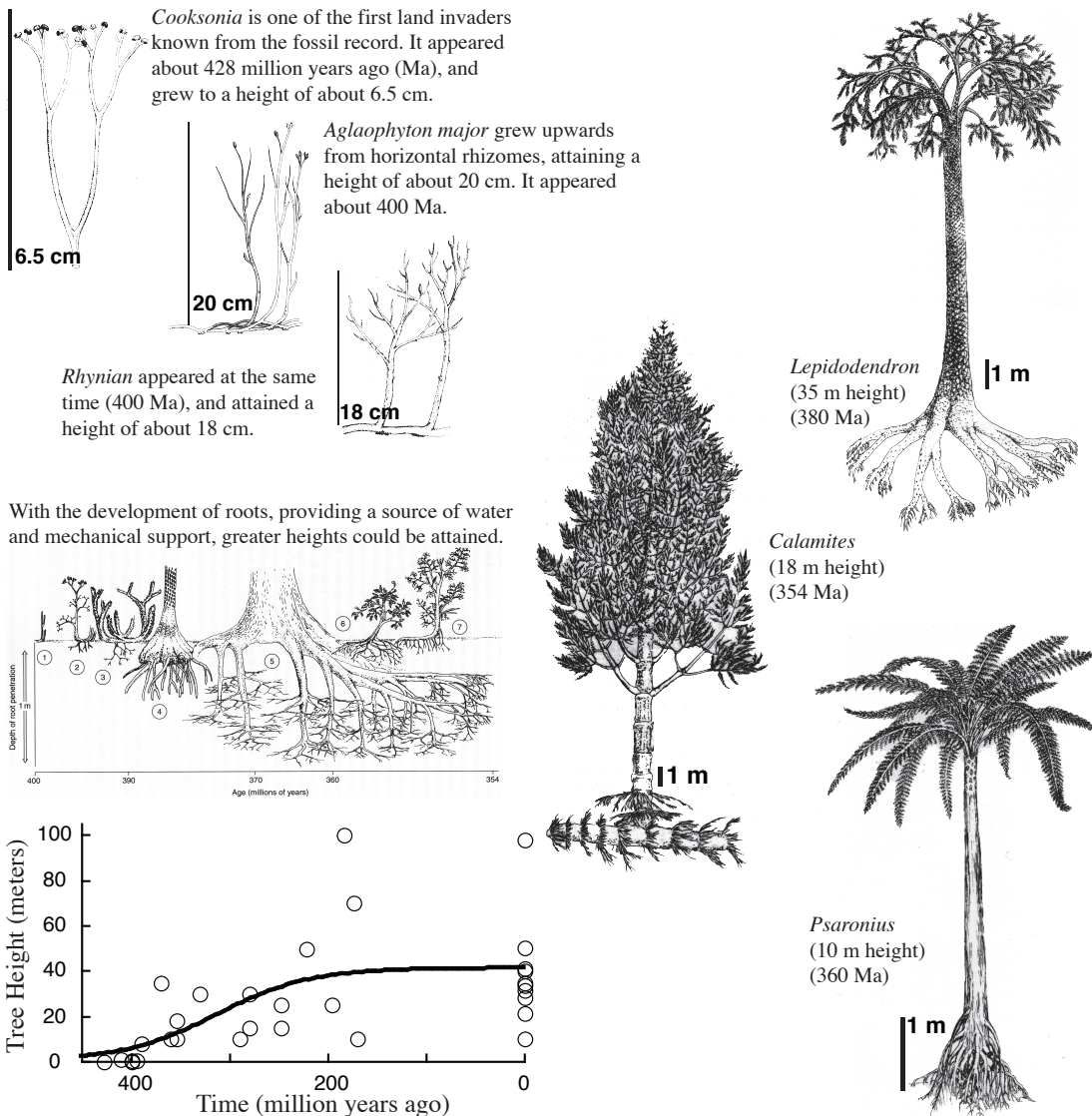


Tropical Rain Forest	96%	2%	2%		
Cold-temperate Forest	10%	17%	54%	12%	7%

In a tropical rain forest, trees dominate, overwhelmingly so. In a cold-temperate forest (similar to Ontario), short shrubs dominate^[1]. So, growing high can have advantages, but there are costs; trees are not necessarily the dominant growth form, and environmental conditions don't always favor a tall tree. Nevertheless, tall trees have appeared relatively recently in evolutionary time.

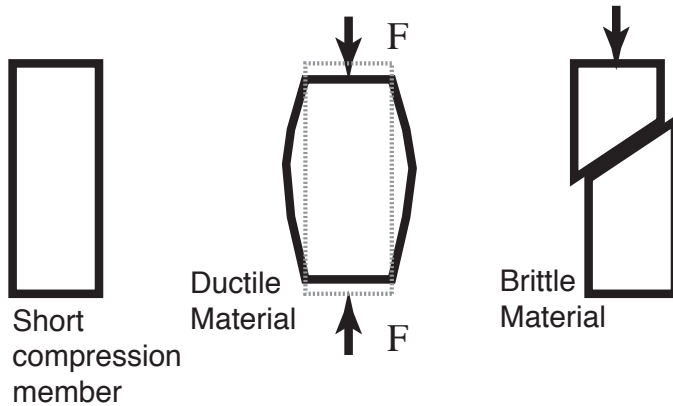
^[1]Whittaker RH 1975. Communities and Ecosystems. MacMillan Publishing Co. New York. pp. 60–67.

In the context of evolutionary time, the invasion of land by plants is relatively recent, only 500 million years ago. Plants had to evolve many adaptive properties to allow them to survive in a dry environment. Their life cycles were modified to protect their offspring from desiccation, they developed root systems to *drink* water from the newly developed soils, they evolved an increasingly complex vasculature to move both water and nutrients long distances. And, they grew to greater and greater heights.



^[1]Source: Willis, K.J. and J.C. McElwain 2002. The Evolution of Plants. Oxford University Press.

So, trees do grow high to compete, and have evolved to greater heights over the past 400 million years, But, how high *can* a tree grow? One factor which may affect tree height is the mechanical properties of the tree. The mechanical nature of a tree is best modeled by a column. The major (constant) stress a tree or column undergoes is compression.



Compression failure depends upon the length of the column (or tree) and its thickness relative to its length. For short columns, when compressive axial force ($\sigma = F/A$ where F is the force and A the area of the columnar end) is applied, failure may be deformation if the material is ductile, or fracture if the material is brittle^[1].

For a tree, the compressive force is equal to the height times the wood density: The density (ρ) of wood varies with species, but the value for a Sequoia tree may be appropriate: 436 kg m^{-3} . Measurements of compression to rupture are known for a Sequoia, about 42.4 MN m^{-2} . We can calculate the maximum height a tree can attain before it undergoes compressive rupture.

$$\text{compression} = \rho \cdot h$$

$$h_{critical} = \frac{\text{compression}}{\rho}$$

$$h_{critical} = \frac{42.4 \cdot 10^6 (\text{N} \cdot \text{m}^{-2}) \cdot \frac{1(\text{kg}(\text{f}))}{9.80665(\text{N})}}{436(\text{kg} \cdot \text{m}^3)}$$

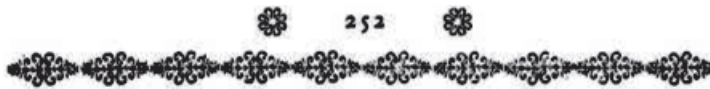
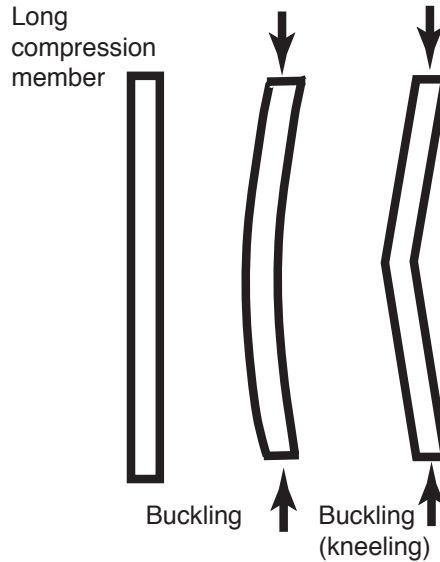
$$h_{critical} = 9916.5(\text{m})$$

Note that 9.80665 newtons are equal to 1 kg(f) under standard gravity.

Very high, indeed.

^[1]Engineering Fundamentals (www.efunda.com) “Buckling of Columns”

But a calculation using compression = $\rho \cdot h$ is too simple. Rather than being a short compressive member, trees are more similar to a long column. For long columns, columnar geometry (length versus diameter) and stiffness (Young’s modulus) become important. In this case, buckling occurs prior to failure. Like the short column, failure will depend upon the stiffness. Inelastic buckling results in kneeling^[1].



SUR
LA FORCE DES COLONNES.
PAR M. EULER.

I

Quand je développai dans le supplément de mon Traité sur les Iso-périmètres les courbes des lames élastiques, j’en ai tiré une règle pour juger de la force des colonnes, qui me parut d’abord fort remarquable. Il s’agit de déterminer le poids qu’une colonne peut soutenir, sans être sujette à se plier. La Règle que j’ai trouvée, regarde les colonnes, qui sont également fortes par toute leur longueur; & si l’on nomme la hauteur d’une telle colonne = a , & le moment de son ressort = Ekk , dont j’ai expliqué tant la signification, que les moyens pour en trouver la juste valeur en chaque cas; le poids que cette colonne est capable de soutenir sans se plier, est $= \pi\pi \cdot \frac{Ekk}{aa}$, où π marque la circonférence d’un cercle dont le diamètre est = 1: d’où l’on voit que ce poids suit la raison renversée du carré de la hauteur de la colonne. Mais pour faire usage de cette règle, il est bon que je rapporte ici ce qu’il faut entendre par l’expression Ekk , que je viens de nommer *Moment du Ressort*.

The effect of buckling on column failure was originally addressed by M. Euler in a paper entitled “Sur La Force des Colonnes” published in 1759 in *Memoires de l’academie des sciences de Berlin* 13, 1759, pp. 252-282.

^[1]Source: Engineering Fundamentals (www.efunda.com) “Buckling of Columns”

For trees, the column is clamped at the bottom by the root system. The critical buckling load is obtained from modifications of the generalized form of Euler's formula. Where, F_{cr} is the critical buckling load (elastic stability limit), E is the Young's modulus of the wood (column material), I is the area moment of inertia (see next page) (for a circular cross section of a tree, $I = \pi \cdot r^4 / 4$, r being the radius, or $I = \pi \cdot d^4 / 64$, d being the diameter), and L_{eff} is the effective length of the column. L_{eff} depends upon how the column is supported. For a column with one end clamped and the other free, $L_{eff} = 2 \cdot L$ (where L is the height of the column).

$$F_{cr} = \frac{E \cdot I \cdot \pi^2}{L_{eff}^2}$$

Generalized form of Euler's formula^[1]

One major assumption that should be borne in mind when this equation is used to determine the maximum height of a tree is that trees are only columnar to a first approximation, because they taper with height. This should effectively increase the height they can attain without columnar failure. This will be counterbalanced by the fact that axial compressive force is only one potential force: wind results in significant shear. Finally, mechanical failure of trees often occurs as a consequence of uprooting, thus the assumption of a clamped and free end are violated.

^[1]Source: Niklas, Karl J 1992. Plant Biomechanics. An engineering approach to plant form and function. University of Chicago Press.

In Euler's formula for the strength of columns, the area moment of inertia, I , is a crucial term.

$$F_{cr} = \frac{E \cdot I \cdot \pi^2}{L_{eff}^2}$$

Generalized form of Euler's formula

The area (or second) moment of inertia along the x-axis is described by:

$$I_x = \int y^2 dA$$

area moment of inertia about the x-axis

perpendicular distance to the area element dA from the x axis

elemental area

Similarly, along the y-axis:

$$I_y = \int x^2 dA$$

The intuitive explanation for the area moment of inertia is that the force acting on the column (or some other shape) will vary linearly with distance from a given axis. So, the area moment of inertia measures the resistance to bending in response to an applied force. It does so by summing the contribution of each small area element. The greater the area moment of inertia, the greater the resistance to bending.

For a circular cross section of radius r :

The area of the ring is the circumference: $2 \cdot \pi \cdot R$ times the increment dR :

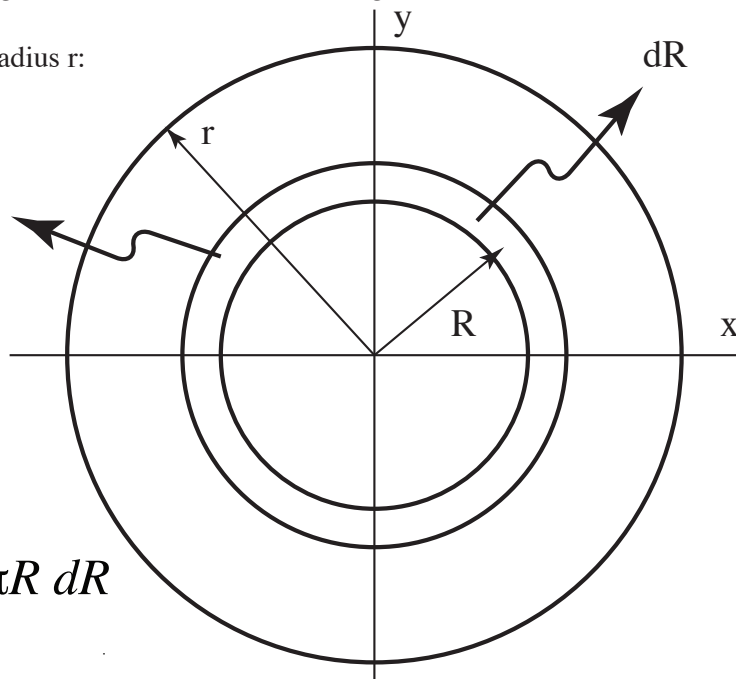
$$2 \cdot \pi \cdot R \cdot dR$$

The general form of the area moment of inertia^[1]:

$$I = \int R^2 dA$$

becomes:

$$I = \int_0^r R^2 2\pi R dR$$



^[1]Nota bene: $x^2 + y^2 = R^2$

The area moment of inertia

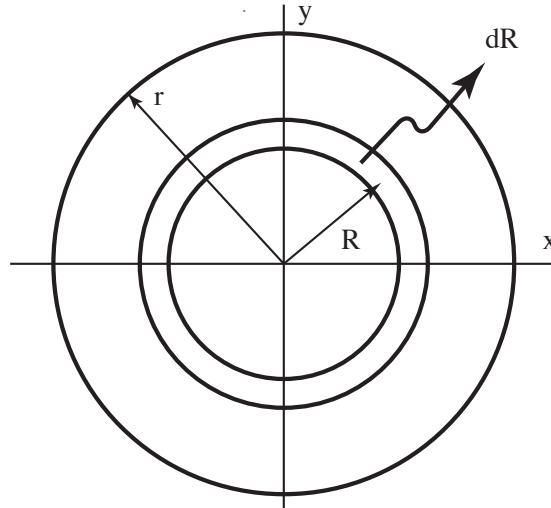
$$I = \int_0^r R^2 2\pi R dR$$

can be simplified:

$$I = 2\pi \int_0^r R^3 dR$$

and evaluated:

$$\begin{aligned} I &= 2\pi \frac{R^4}{4} \Big|_0^r \\ &= 2\pi \frac{[r^4 - 0^4]}{4} \\ &= \frac{\pi \cdot r^4}{2} \end{aligned}$$



Since $\frac{d}{dR} R^4 = 4R^3$, or $\frac{d}{dR} \frac{R^4}{4} = R^3$

then, $\int R^3 dR = \frac{R^4}{4}$ Plus a constant for the indefinite integral.

Nota bene: $I = I_x + I_y$, by symmetry, $I_x = I_y$

so, $\frac{\pi \cdot r^4}{2} = 2 \cdot I_x$, thus $I_x = \frac{\pi \cdot r^4}{4}$

Therefore, for a tree with a circular cross section, the area moment of inertia is:

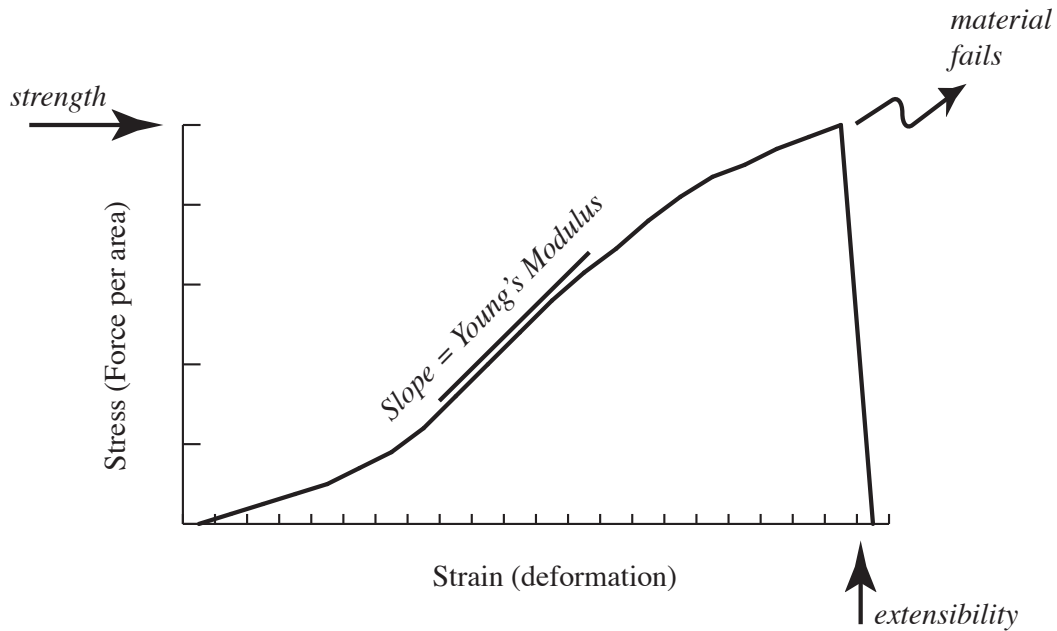
$$I_x = \frac{\pi \cdot r^4}{4}$$

In Euler's formula for the strength of columns, besides the area moment of inertia (I), Young's modulus (E) also deserves closer scrutiny.

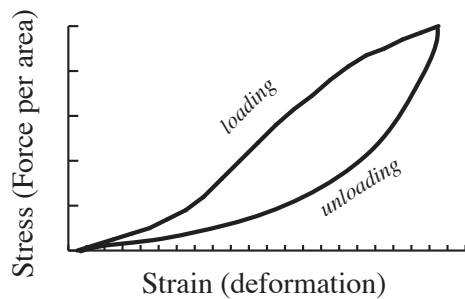
$$F_{cr} = \frac{E \cdot I \cdot \pi^2}{L_{eff}^2}$$

Generalized form of Euler's formula

If we apply a stress (a force per area) on some material, the structure will be deformed (strain). Strain is a fractional deformation, hence dimension-less.



The steeper the slope (the greater the value of Young's modulus, in units of force per area), the stiffer (less deformable) the material.



Experimentally, materials may be 'viscoelastic', leading to a stress-strain relation in which load and unloading of the force follow different paths of deformation.

^[1]Source: Vogel, Steven (1988) Life's Devices. The physical world of animals and plants. Princeton University Press. pp. 183–184.

With a solution for the area moment of inertia ($I = \pi r^4/4$) and data for Young's modulus of elasticity (shown elsewhere), we can arrange Euler's formula to determine the critical height of a tree¹¹ by equating it with the weight of the tree.

$$F_{cr} = \frac{E \cdot I \cdot \pi^2}{L_{eff}^2}$$

Generalized form of Euler's formula

$$F_{cr} = \frac{E \cdot \frac{\pi \cdot r^4}{4} \cdot \pi^2}{(2 \cdot h)^2}, \text{ and } F_{cr} = \rho \cdot \pi \cdot r^2 \cdot h$$

where $\rho \cdot \pi \cdot r^2 \cdot h$ is the weight of the tree.

where $L_{eff} = 2 \cdot h$ (h is the height),

and F_{cr} (in kg(f)) is equal to the density (ρ) times the cylinder volume ($\pi \cdot r^2 \cdot h$). Then,

$$\rho \cdot \pi \cdot r^2 \cdot h = \frac{E \cdot \frac{\pi \cdot r^4}{4} \cdot \pi^2}{(2 \cdot h)^2}$$

Combining the two equations.

Solving for the height, h ,

$$h^3 = \frac{E \cdot \frac{\pi \cdot r^4}{4} \cdot \pi^2}{4 \cdot \rho \cdot \pi \cdot r^2}$$

$$h^3 = \frac{E \cdot r^2 \cdot \pi^2}{16 \cdot \rho}$$

$$h = \left[\frac{\pi^2}{16} \right]^{1/3} \cdot \left[\frac{E}{\rho} \right]^{1/3} \cdot r^{2/3}$$

$$h = 0.851 \cdot \left[\frac{E}{\rho} \right]^{1/3} \cdot r^{2/3}$$

Note the 2/3 power dependence on tree radius, and the cube root of the ratio of Young's modulus to wood density.

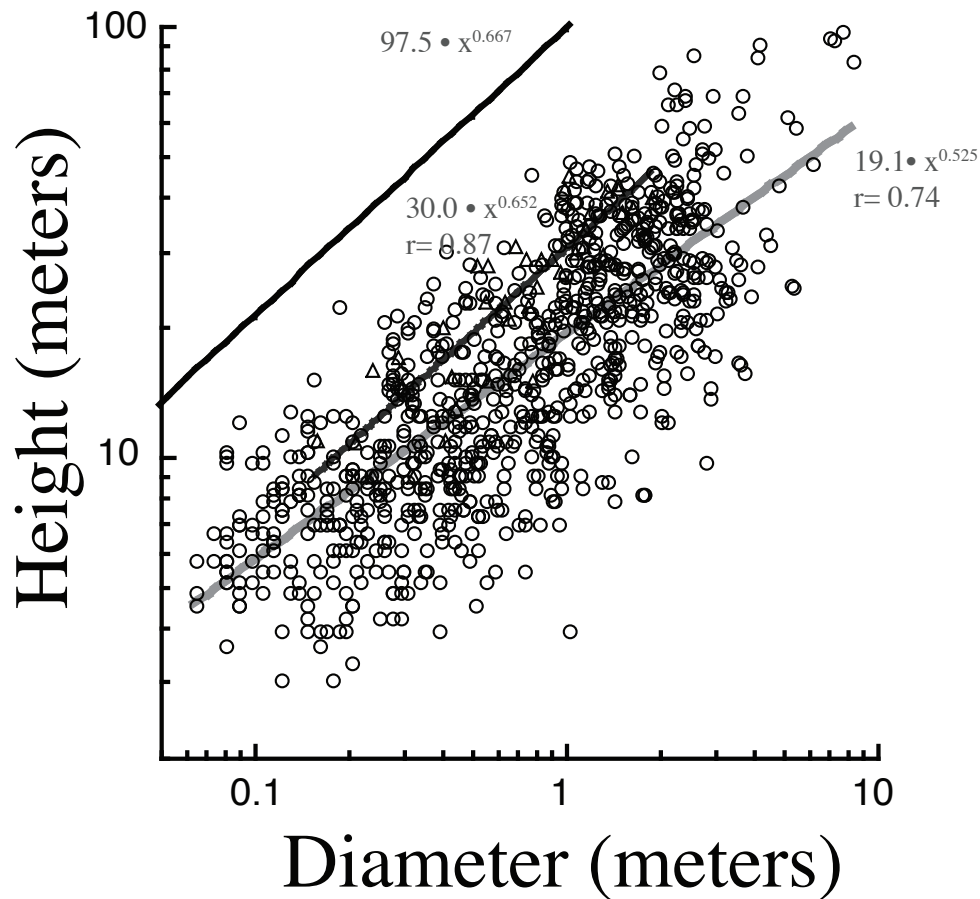
¹¹Source: McMahon, T. (1973) Size and shape in biology. Science 179:1201–1204.

Below are some data for example trees. Diameters and heights are for the largest known examples of the various species. Modulus of rupture is the force (per area) required for compressive failure of the wood. Modulus of elasticity is the Young's modulus. Also included are the rupture force for compression parallel to the grain^[1].

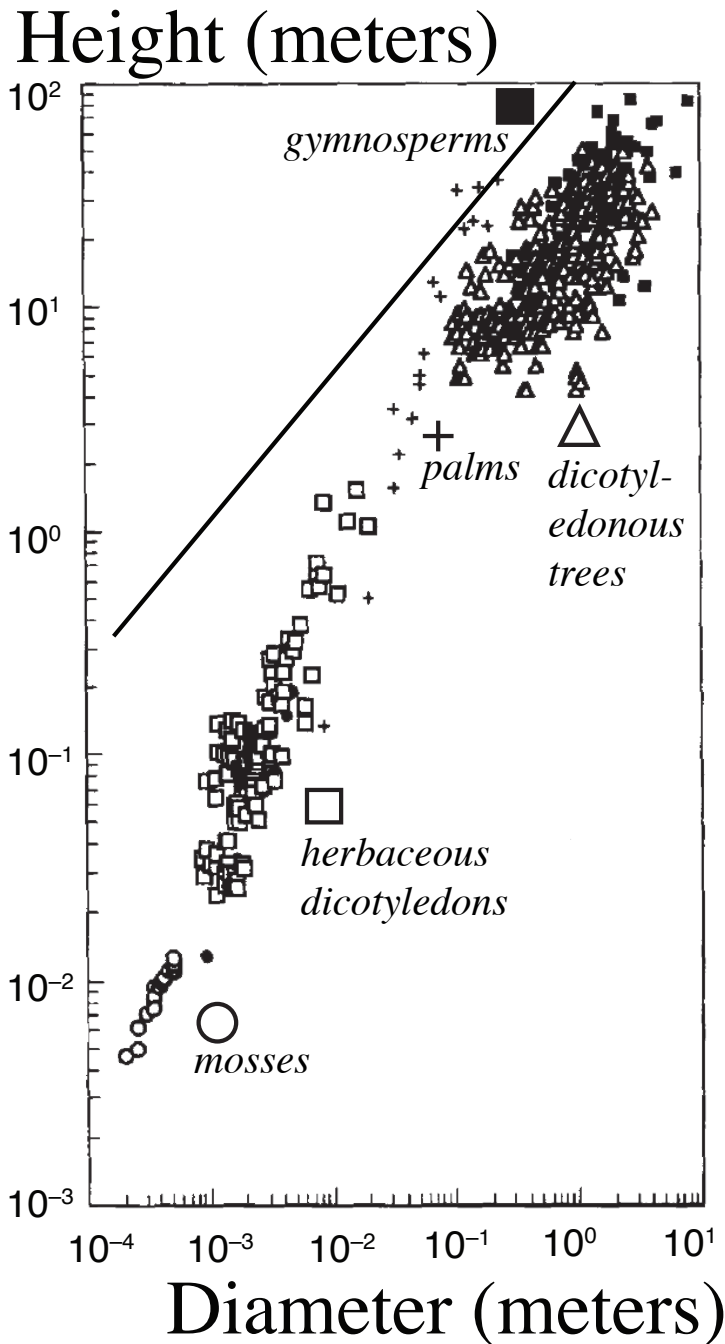
common name	species	diameter meters	height meters	Modulus of Rupture GN·m ⁻²	Modulus of Elasticity GN·M ⁻²	density kg m ⁻³	compression parallel to grain MN·m ⁻²
Redwood	<i>Sequoia sempervirens</i>	7.6808	97.8408	0.074	9.40	436	42.4
Eastern Hemlock	<i>Tsuga canadensis</i>	1.6332	50.2920	0.059	8.30	431	21.2
Trembling Aspen	<i>Populus tremuloides</i>	0.9702	41.4528	0.059	8.22	401	14.8
White Pine	<i>Pinus strobus</i>	2.4174	40.2336	0.061	8.81	373	16.8
Sugar Maple	<i>Acer saccharum</i>	1.8030	35.0520	0.108	12.65	676	27.7
Yellow Poplar	<i>Liriodendron tulipifera</i>	3.0238	33.8328	0.064	10.38	427	18.3
Yellow Birch	<i>Betula lutea</i>	1.5038	31.6992	0.117	14.53	668	23.3
Black Locust	<i>Robina pseudoacacia</i>	2.5225	28.6512	0.134	14.20	798	70.2
Eastern Cottonwood	<i>Populus deltoides</i>	3.5898	28.3464	0.060	9.53	433	15.7
Hornbeam	<i>Ostrya virginiana</i>	0.9298	21.3360	0.100	11.76	762	n/a
Common Apple	<i>Malus sylvestris</i>	1.1400	21.3360	0.088	8.77	745	n/a
Dogwood	<i>Cornus florida</i>	0.8894	10.0584	0.105	10.64	796	n/a
			means	0.086	10.599	578.8	27.822

^[1]Sources: diameter and height from American Forestry Register of Big Trees.
Moduli and densities from Niklas, KJ (1992) Plant Biomechanics. Table 2.3, page 114.
Compression from Forest Products Laboratory (1999) Wood Handbook. USDA Forest Service

Here are plotted the height versus diameters of the largest trees for a variety of species^[1]. The critical height (above which failure would occur) is also shown. Note that the predicted slope for critical height is $D^{0.667}$, and that both American Big Trees and British Champion Trees have lower slopes: $D^{0.525}$ and $D^{0.652}$, respectively. One might conclude, reasonably, that trees do not grow to a height which would result in structural failure through compressive loading/buckling.



^[1]Sources: American Forests National Register of Big Trees (www.americanforests.org) (869 trees), and British Champion Trees (www.treeregister.org) (38 trees)
McMahon, T. (1973) Size and shape in biology. *Science* 179:1201–1204.

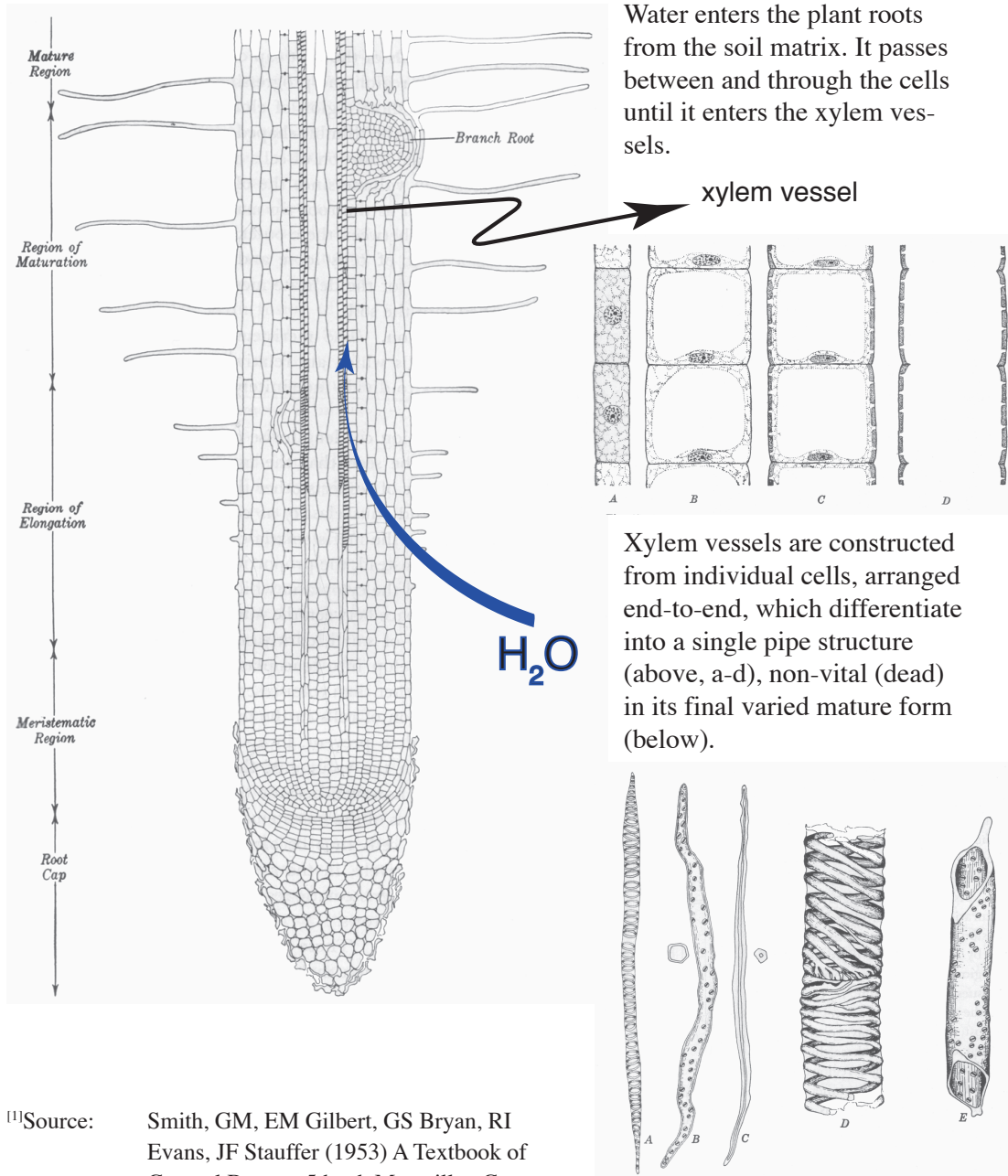


Scaling of height versus stem diameter can be extended by examining smaller plants (non-tree)^[1]. The critical buckling height limit is re-drawn from the graph of 'Big Trees'. With the range of heights and diameters extended over many orders of magnitude, it is clear that heights are normally significantly below the mechanical limit described by the Euler formula.

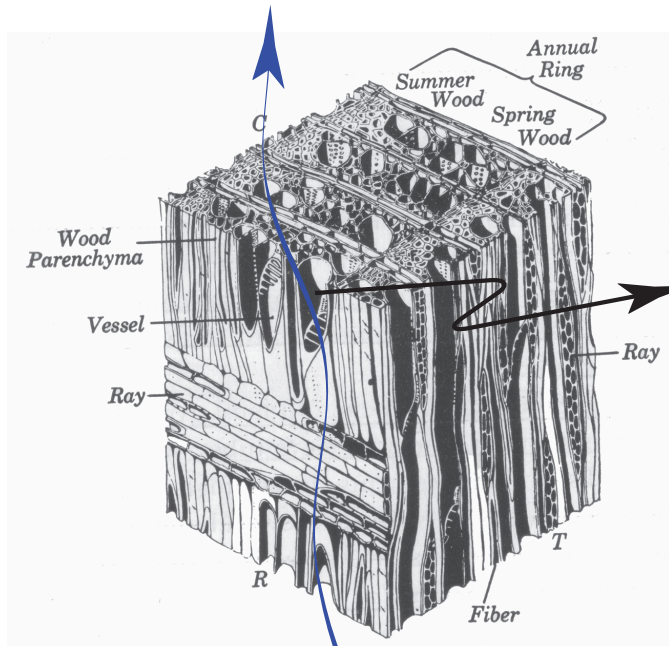
Besides mechanical constraints, the height of a tree will also be limited by the availability of water, which must be drawn to extraordinary heights in opposition to the force of gravity.

^[1]Niklas, KJ (1993) The scaling of plant height: A comparison among major plant clades and anatomical grades. *Annals of Botany* 72:165–172.

Water is essential for biological life, which is why the ability to draw water to the maximal height of the tree is crucial for survival and may constrain the height of a tree. To explore the physical limits on elevating water, we must first explore the structure and function of the water transport system in a tree (or other vascular plant)^[1].



^[1]Source: Smith, GM, EM Gilbert, GS Bryan, RI Evans, JF Stauffer (1953) A Textbook of General Botany. 5th ed. Macmillan Co.

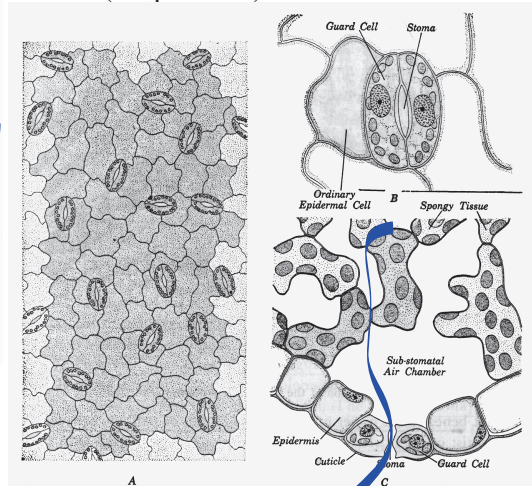
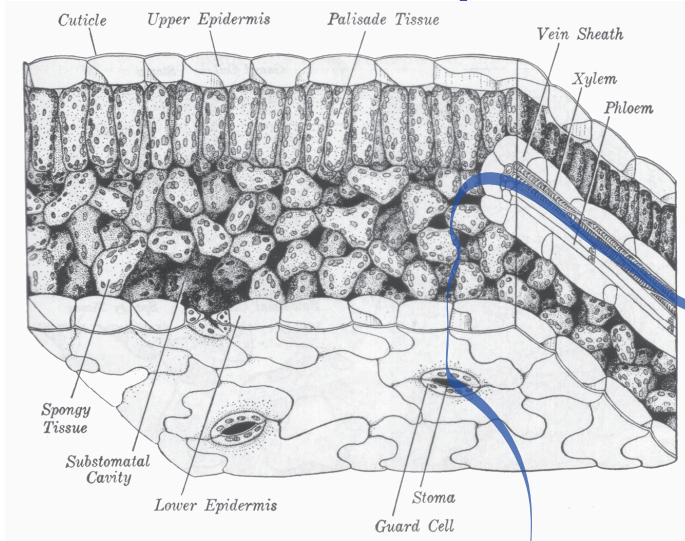


In the stem of a tree, the architecture of the vasculature can be very complex, with numerous cell types including the water-transporting xylem vessels^[1].

xylem vessel

The size of the xylem vessels varies, some can be quite large, about 150 μm in diameter (range 20–300 μm in dicotyledonous trees, about 50 μm in conifers). Nevertheless, this is still a small tube in the context of hydrodynamics. In fact, microfluidic.

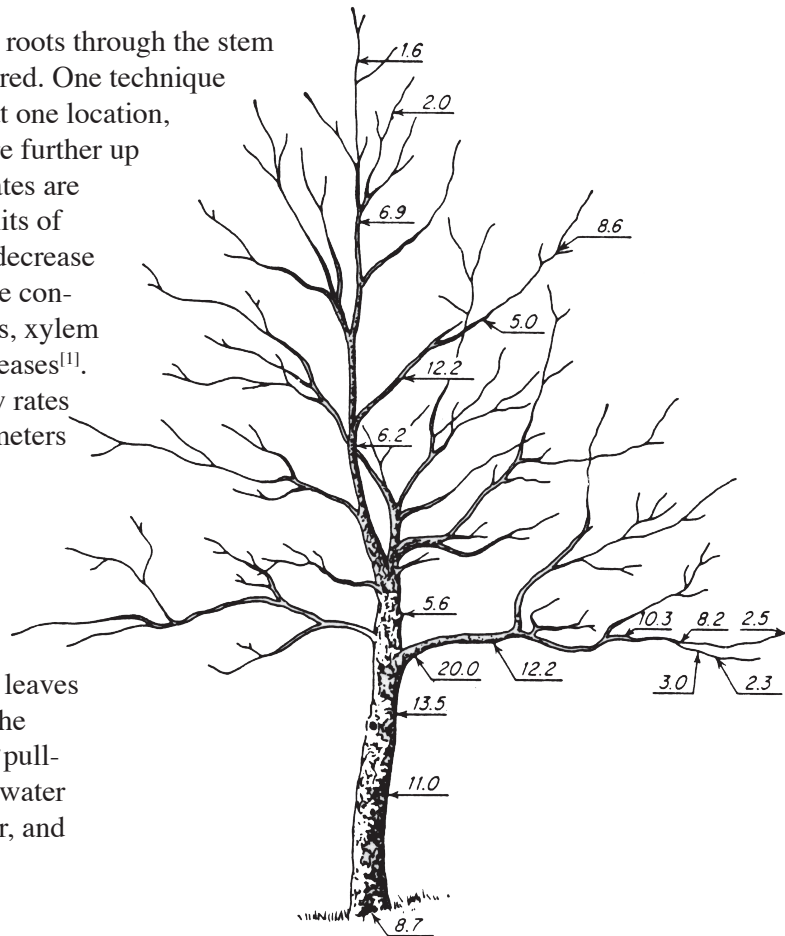
In the leaves, water continues to be transported through the xylem, but then passes through and between cells for a final exit from the plant through the stomata, via transpiration (evaporation).



^[1]Source: Smith, GM, EM Gilbert, GS Bryan, RI Evans, JF Stauffer (1953) A Textbook of General Botany. 5th ed. Macmillan Co.

H₂O

The flow of water from the roots through the stem and branches can be measured. One technique is to apply a pulse of heat at one location, and monitor the temperature further up the stem or branch. Flow rates are shown for an oak tree in units of meters per hour. The rates decrease towards the top, because the conducting surface ratio (that is, xylem cross area to leaf area) increases^[1]. In a variety of species, flow rates vary from about 0.1 to 60 meters per hour.



The rates of flow are strongly affected by the atmospheric relative humidity, since it is evaporation of water at the leaves that ‘pulls’ water up from the soil. The energetics of the ‘pulling’ force are given by the water potential of the water vapor, and its dependence on relative humidity^[2]:

$$\Psi_{wv} = \frac{RT}{\bar{V}_w} \ln\left(\frac{\% \text{ relative humidity}}{100}\right) + \rho_w gh$$

where R is the gas constant (8.314 m³ Pa mol⁻¹ °K⁻¹), T is the temperature (°K), \bar{V}_w is the partial molal volume of water (1.805•10⁻⁵

m³ mol⁻¹ at 20°C [293°K]). At 20°C, the term RT/ \bar{V}_w is 135 MPa. The second term is the gravitational potential: ρ_w is the density of water (998.2 kg m⁻³ at 20°C), g is the gravitational constant (9.807 m sec⁻²) and h is the height. For a tree 100 m high, $\rho_w gh$ is 978 kPa. Even at a relatively high relative humidity (95%), the water potential is about –6 MPa, more than sufficient to ‘pull’ water from the soil, providing the flow through the xylem vessels (the hydraulic tubes of the tree) is not limiting.

^[1]Source: Kramer, PJ (1983) Water Relations of Plants. Academic Press. pp. 274-275

^[2]Source: Nobel, PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp. 91-95.

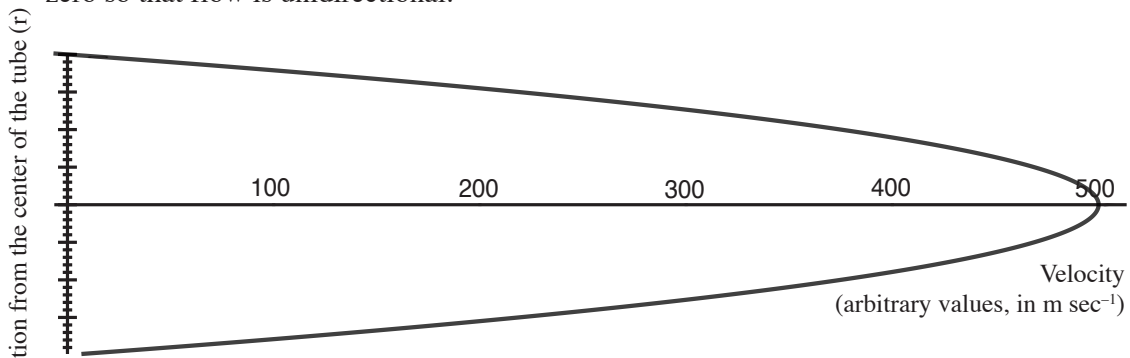
The basic equation describing the flow velocity of a liquid through a tube (such as a xylem vessel) is the Poiseuille equation¹¹:

$$v = \left(\frac{\Delta p}{l} \right) \left(\frac{1}{4 \cdot \eta} \right) (R^2 - r^2)$$

velocity (meters sec⁻¹) pressure difference (Pascal = 1 kg m⁻¹ sec⁻¹) tube radius

distance (meters) viscosity (water = 0.01 gm cm⁻¹ sec⁻¹, or Pa sec) distance from center of tube

The equation describes a parabolic velocity profile within the tube, dependent upon the pressure gradient (dP/dx, which is linear along the tube, thus Δp/l) and the viscosity of the liquid. Note that this formulation requires laminar flow, that is, dP/dy and dP/dz are both zero so that flow is unidirectional:



The fastest velocity is at the center of the tube (r = 0):

$$v = \left(\frac{\Delta p}{l} \right) \left(\frac{1}{4 \cdot \eta} \right) R^2$$

¹¹Sources: Landau, LD and EM Lifshitz (1959) Fluid Mechanics (Pergamon Press) is the ‘classic’ text. Zimmerman MH (1974) Transport in Xylem *in* Zimmerman MH and CL Brown (eds.) Trees. Structure and Function (Springer-Verlag) presents the material in the context of water transport in trees

Rather than flow velocity of a liquid through a tube, the Poiseuille equation is often cast in the form of the volume of liquid passing through the tube. Thus, the volume must be considered^[1]. A volume passing each second through any section of the tube is described by:

A volume $2 \cdot \pi \cdot r \cdot v \, dr$

passes through an annular element

$2 \cdot \pi \cdot r \, dr$

of the cross - sectional area. Thus, the volume flow is:

$$J_v = 2 \cdot \pi \int_0^R r \cdot v \, dr$$

Using

$$v = \left(\frac{\Delta p}{1} \right) \left(\frac{1}{4 \cdot \eta} \right) (R^2 - r^2)$$

The solution is:

$$J_v = \left(\frac{\Delta p}{1} \right) \left(\frac{\pi}{8 \cdot \eta} \right) \cdot R^4$$

$$J_v(r) = 2 \cdot \pi \cdot r \cdot \left(\frac{\Delta p}{l} \right) \left(\frac{1}{4 \cdot \eta} \right) (R^2 - r^2) \, dr$$

re - arranging and simplifying :

$$J_v(r) = \pi \cdot \left(\frac{\Delta p}{l} \right) \left(\frac{1}{2 \cdot \eta} \right) (r \cdot R^2 - r^3) \, dr$$

integrating

$$J_v = \pi \cdot \left(\frac{\Delta p}{l} \right) \left(\frac{1}{2 \cdot \eta} \right) \int_0^R (r \cdot R^2 - r^3) \, dr$$

from $\frac{d}{dr} r^4 = 4 \cdot r^3$ and $\frac{d}{dr} r^2 = 2 \cdot r$, then

$$\left(\frac{1}{2} r^2 R^2 - \frac{1}{4} r^4 \right) \Big|_0^R = \frac{1}{2} R^4 - \frac{1}{4} R^4 = \frac{1}{4} R^4, \text{ and}$$

$$J_v = \pi \cdot \left(\frac{\Delta p}{l} \right) \left(\frac{1}{8 \cdot \eta} \right) \cdot R^4$$

Thus, volume flow depends upon the the tube radius to the fourth power. However, in the context of water transport in a tree, velocity is far easier to measure than volume flow. As noted before, the use of the Poiseuille equation to describe flow depends upon an very important assumption, that the flow is laminar in nature: No Turbulence (otherwise the flow will not be unidirectional). This will only be true for low Reynolds number.

^[1]Sources: Landau, LD and EM Lifshitz (1959) Fluid Mechanics. Pergamon Press is the 'classic' text. Zimmerman MH (1974) Transport in Xylem *in* Zimmerman MH and CL Brown (eds.) Trees. Structure and Function. Springer-Verlag presents the material in the context of water transport in trees

A low Reynolds number is a pre-requisite for laminar, non-turbulent flow through the xylem vessel. The Reynolds number is a dimension-less ratio of inertial components of velocity to the resistance to flow:

$$R_e = \frac{\rho \cdot v \cdot l}{\eta}$$

density (water = 1 gm cm⁻³)
 velocity (cm sec⁻¹)
 tube diameter (cm)
 viscosity (water = 0.01 gm cm⁻¹ sec⁻¹)

When inertial components dominate, turbulence of the medium will occur, so that pressure gradients are no longer uni-directional (dP/dy and dP/dz are not 'zero'). When viscosity dominates, the flow will be laminar.

For a xylem vessel of 150 micron diameter and a flow rate of 20 meters hour⁻¹, the Reynolds number is:

$$R_e = \frac{1 \text{ (gm cm}^{-3}\text{)} \cdot 0.56 \text{ (cm sec}^{-1}\text{)} \cdot 0.015 \text{ (cm)}}{0.01 \text{ (gm cm}^{-1}\text{ sec}^{-1}\text{)}} = 0.84$$

This is much lower than the cut-off for turbulent flow (about 2000)^[1], so the Poiseuille equation is valid.

Using the Poiseuille equation for velocity, we can calculate the pressure gradient required for water transport in a tree:

$$v = \left(\frac{\Delta p}{l} \right) \left(\frac{1}{4 \cdot \eta} \right) R^2$$

$$\left(\frac{\Delta p}{l} \right) = \left(\frac{4 \cdot \eta}{R^2} \right) \cdot v = \left(\frac{4 \cdot 0.01 \text{ (Pa} \cdot \text{sec)}}{0.015^2 \text{ (cm}^2\text{)}} \right) \cdot 0.56 \text{ (cm} \cdot \text{sec}^{-1}\text{)} = 99.56 \text{ (Pa} \cdot \text{cm}^{-1}\text{)}$$

The pressure for a tree of height 100 m would be:

$$99.56 \text{ (Pa} \cdot \text{cm}^{-1}\text{)} \cdot (100 \text{ (m)}) \cdot 100 \text{ (cm} \cdot \text{m}^{-1}\text{)} = 9.956 \cdot 10^5 \text{ (Pa), or } ca \text{ 1 MPa}$$

The 1 MPa value is an underestimate, because it does not account for constrictions to flow at the junctions of the xylem vessels (resulting in a smaller tube radius). Nor does it account for the counteracting gravitational effect:

$$\rho_{\text{water}} \cdot g \cdot h = 999.8 \text{ (kg} \cdot \text{m}^{-3}\text{)} \cdot 9.78 \text{ (m} \cdot \text{sec}^{-1}\text{)} \cdot 100 \text{ (m)} = 9.778 \cdot 10^5 \text{ (kg} \cdot \text{m}^{-1}\text{} \cdot \text{sec}^{-1}\text{, or Pa), or } ca \text{ 1 MPa}$$

Accounting for these two factors, a required pressure gradient of about 3 MPa for a tree 100 meters high (that is, 0.03 MPa meter⁻¹ for any tree) would be more realistic^[1].

^[1]Source: Nobel PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp.505–513.

A more general summary of pressure gradients, xylem vessel size, and flow rates was compiled by Zimmerman^[1], based on the Poiseuille equation:

$$v = \left(\frac{\Delta p}{l} \right) \left(\frac{1}{4 \cdot \eta} \right) R^2$$

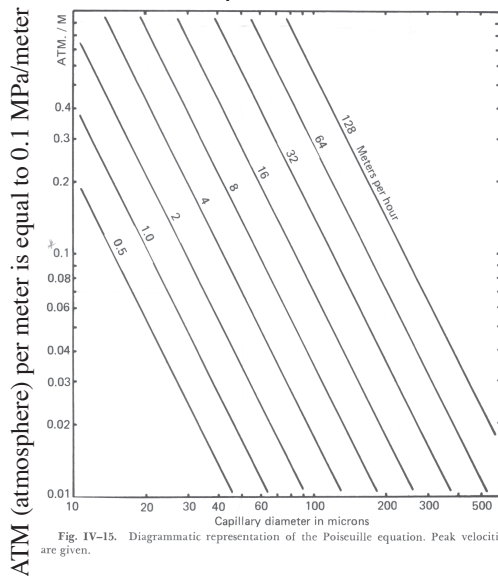
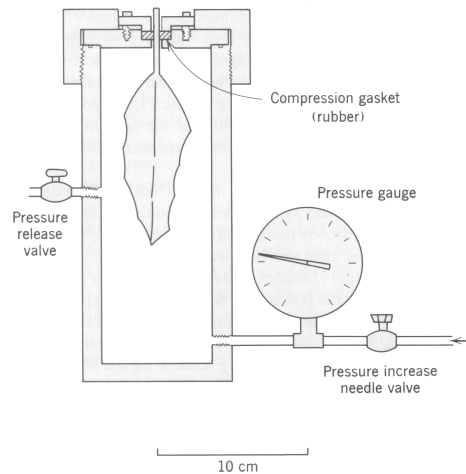


Fig. IV-15. Diagrammatic representation of the Poiseuille equation. Peak velocities are given.

A branch or leaf is cut from the top of the tree (in some instances, if the top is inaccessible, a rifle is used to ‘shoot’ the leaf down). It is placed inside the pressure chamber. Pressure is applied and the cut cross-section is watched to determine the amount of pressure required to force the sap through the cut. This pressure equals the negative pressure inside the leaf. Essentially, when the leaf is cut, the sap ‘snaps’ back into the leaf (since the negative pressure has been alleviated at the cut site). Applying pressure to the leaf gives a measure of the equilibrium pressure that existed in the leaf prior to being cut. The measured negative values will depend to a great extent on factors such as time of day (most negative in the early afternoon); for a Douglas fir tree, -2.2 MPa was observed at the top of the tree (79 meters), -1.7 MPa closer to the base of the tree (30 meters)^[1].

The pressure gradient is not created at the soil/root interface. Although uptake of water into cells due to osmotic potentials can create internal pressures in the range of 0.6 MPa^[2], these are insufficient to push water to the top of a tall tree. Instead, evaporation from the leaves creates a ‘negative’ pressure, which sucks water from the soil. The negative pressures can be measured using a pressure chamber (or pressure bomb)^[3].



The question naturally arises: How can water maintain cohesion under such negative pressures?

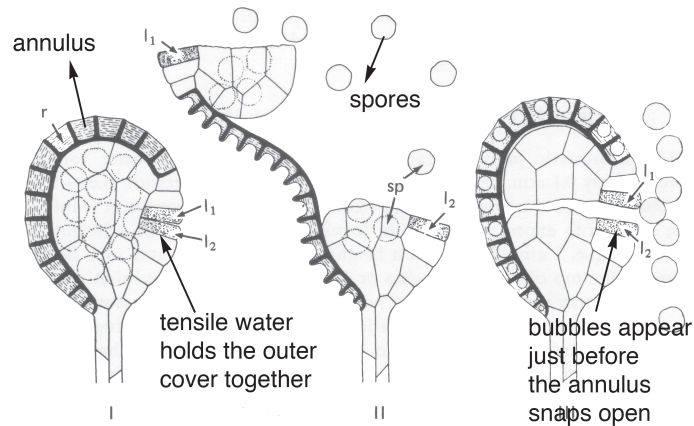
^[1]Zimmerman MH (1974) Transport in Xylem in Zimmerman MH and CL Brown (eds.) Trees. Structure and Function. Springer-Verlag.

^[2]Shabala S and RR Lew (2002) Turgor regulation in osmotically stressed Arabidopsis thaliana epidermal root cells: Direct support for the role of inorganic ion uptake as revealed by concurrent flux and cell turgor measurements. Plant Physiol. 129:290-299.

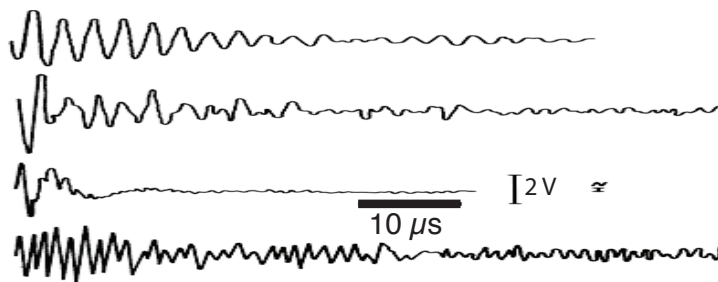
^[3]Kramer, PJ (1983) Water Relations of Plants. Academic Press. pp. 274-275

A variety of techniques have been used to measure the tensile strength of water^[1]. One method was to sandwich a water film between two steel plates and measure the force required to pull the plates apart. The value obtained was about 3.0 MPa. Centrifuging capillary tubes filled with water and determining the internal tension at which the water capillary breaks yields values in the range of 20.0 MPa. Fern sporangia can also be used to measure the tensile strength of water, a system closer to our biological context. The sporangia is enclosed by an annulus which goes halfway around the inside containing the spores. As water evaporates from the annulus cells, the annulus shrinks and eventually breaks to release the spores. The release occurs when the cohesive strength of water is overcome. This can be observed by the appearance of bubbles.

The measurements were made by placing the sporangium in an enclosed chamber in which the relative humidity was controlled. The sporangia would not open unless the solution controlling the relative humidity had an osmotic value of more than 30-50 MPa.



How do these values compare to the tensile force on water, hanging from the top of a tree? To hang from the top of a 100 meter tree, the required tensile strength must be at least 1.0 MPa^[2], but, because of resistance to flow in the xylem, as well as resistance to water uptake from the soil into the roots, undoubtedly greater stresses must develop.



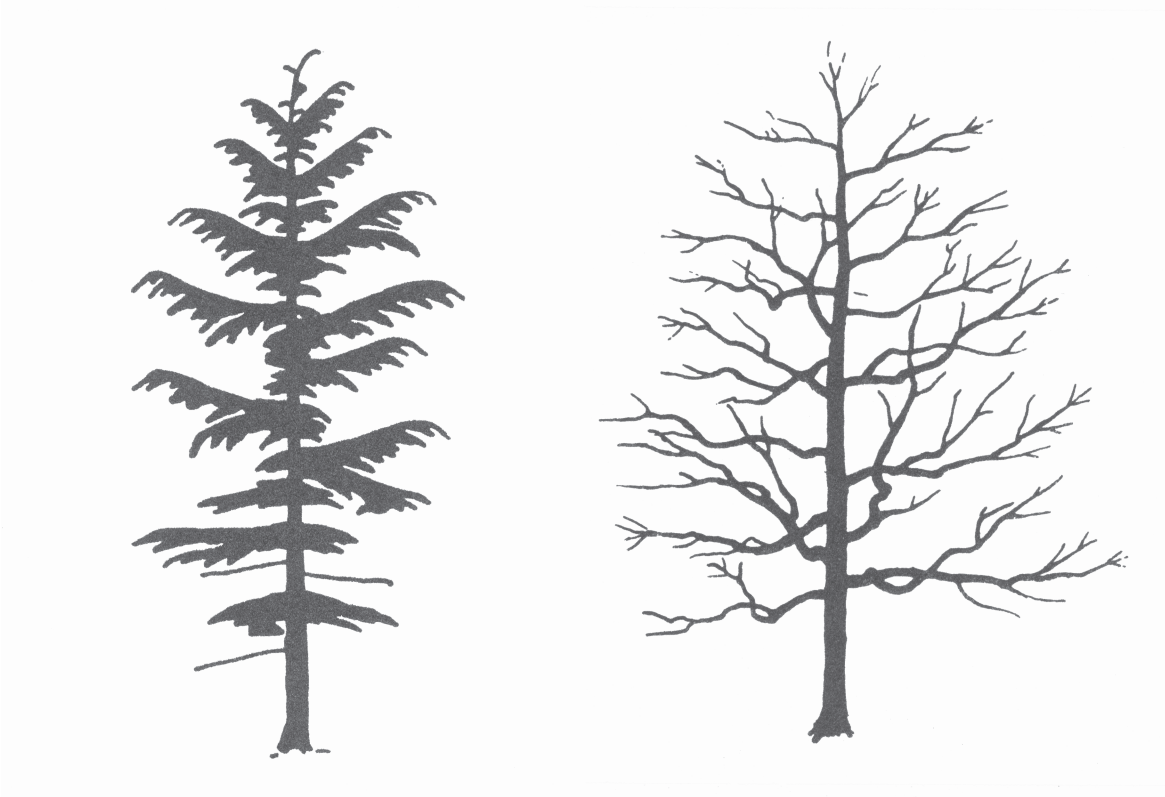
In fact, the sound of water capillaries snapping in the tree can be heard, with a sensitive enough ultrasonic microphone^[3]. So, the tensile strength of water can be limiting.

^[1]Source: Zimmerman MH (1974) Transport in Xylem in Zimmerman MH and CL Brown (eds.) Trees. Structure and Function. Springer-Verlag. pp. 188–190.

^[2]From $\rho \cdot g \cdot h = ca$ 0.996 MPa.

^[3]Tyree MT and MA Dixon (1983) Cavitation events in *Thuja occidentalis* L.? Ultrasonic acoustic emissions from the sapwood can be measured. Plant Physiology 72:1094–1099.

How high can a tree grow? It depends! Although greater height can confer a selective advantage, it comes with a cost, and may be constrained by environmental limitations (such as water availability). Structurally, greater height simply requires a greater diameter (and a well-anchored base); both could be arranged in evolutionary time. More water required? Increase the size of the xylem vessels! Can water be pulled to the top of the tree without breakage? Here, the experimental work points to a significant, real problem with cavitation. That is, in a biological context, maintaining the water columns from the soil to the top of the tree appears to be a challenge. In this case, it is quite likely that a different evolutionary adaptation must appear, could peristaltic pumping or some other mechanism minimize the challenges of maintaining thin strands of water vertically for distances greater than 100 meter? It remains to be seen.

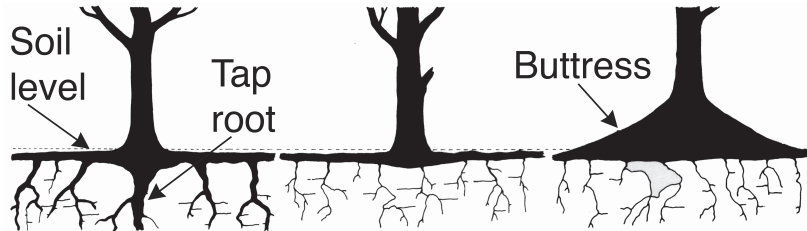


Tsuga canadensis L. (Eastern Hemlock)

Quercus alba L. (White Oak)

Work Problem:

As noted before, a major structural failure in trees is uprooting, and, to a lesser extent breakage due to shear at high wind velocities. Consider the structural impact of shallow, wide-spreading root systems versus large tap roots extending deep into the supporting soil^[1]. Contrast their ability to grow high.



Work Problem:

Many plants do not require a water supply from the soil. They are commonly described as ‘air plants’ (or epiphytes). In some instances, they catch rainwater using vase-like structures. In others, they collect moisture by condensation. The example shown to the left is a lichen (*Usnea* sp.) draped over the branches of a redwood (*Sequoia sempervirens*), one of the tallest trees^[2]. Propose mechanisms by which this would occur.

Work Problem:

Assume, as has been implied, that water tensile strength may limit the height of a tree, based on the observation that the water columns break. On the basis of tensile strength, contrast the possible heights of a tree if alternative liquids were used in place of water. Hint: It may be useful to explore the relation between tensile strength, compressibility, and surface tension.

^[1]Bell AD (1991) Plant Form. An illustrated guide to flowering plant morphology. Oxford University Press. pp.101.

^[2]From Kenneth L. Fisher’s website on Redwood Forest Ecology (www.humboldt.edu/~sillett/redwoods.html)

The physicist and futurist, Freeman Dyson, proposed the possibility of extraterrestrial colonization of comets (“...it is likely that space around the solar system is populated by huge numbers of comets, small worlds a few miles in diameter, rich in water and the other chemicals essential to life.”^[1]) by using genetically engineered trees with modifications suitable for survival in the rigour –cold and vacuum– of space (Dyson trees^[2]). Thus, the leaves would be impermeant to gases but transparent to >400 nm light, and opaque to damaging ultraviolet. Water and CO_2 required for photosynthesis would be extracted from the comet itself, while the O_2 produced as a byproduct of photosynthesis would provide for heterotrophic life forms; for example, humans. The idea of trees growing on comets exists in other forms, such as the Baobab trees out-growing their very small planets in the children’s story, *The Little Prince*^[3].

Dyson considered the height of a tree^[1]: “How high can a tree on a comet grow? The answer is surprising. On any celestial body whose diameter is of the order of ten miles or less, the force of gravity is so weak that a tree can grow infinitely high. Ordinary wood is strong enough to lift its own weight to an arbitrary distance from the center of gravity. This means that from a comet of ten-mile diameter, trees can grow out for hundreds of miles, collecting the energy of sunlight from an area thousands of times as large as the area of the comet itself. Seen from far away, the comet will look like a small potato sprouting an immense growth of stems and foliage. When man comes to live on the comets, he will find himself returning to the arboreal existence of his ancestors.”



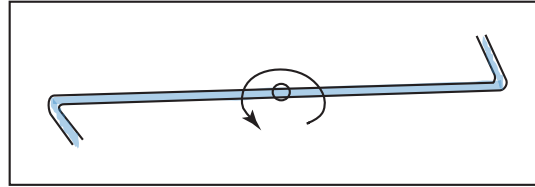
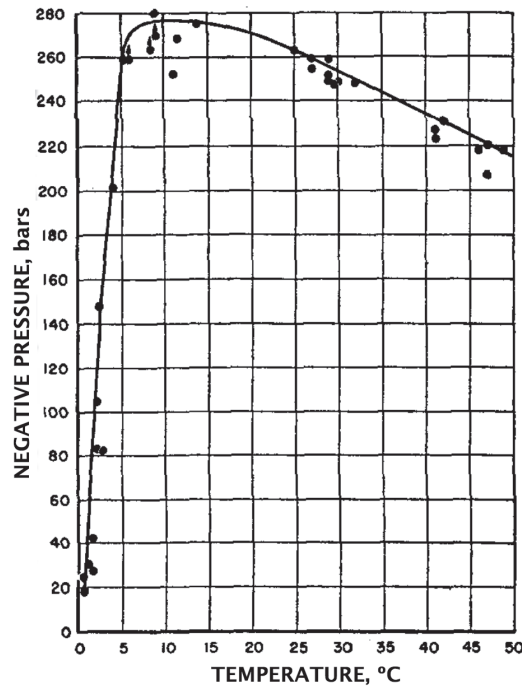
Work Problem:

Is Freeman Dyson right about the height of Dyson trees?

^[1]From Dyson Freeman's essay "The World, The Flesh, and the Devil" republished in *The Scientist as Rebel* (2006) New York Review Books.

^[2]http://en.wikipedia.org/wiki/Dyson_tree

^[3]The Baobab. From *The Little Prince* by Antoine de Saint-Exupery (1943)



One technique used to measure the tensile strength of water was a Z-shaped tube mounted on a rotating plate. The force required to ‘break’ the water column at the center can be calculated from the angular velocity, radius, water density, and the area of the tube lumen. The data are shown in the figure. Maximal tensile strength is about 280 bars, equivalent to 28 MPa. Source: Briggs, LJ (1950) Limiting negative pressure of water. *Journal of Applied Physics* 21:721–722.

Work Problem:

Provide a formal derivation of the equation used to calculate the tensile strength.

Provide explanation(s) for the peculiar temperature dependence of the tensile strength of water.

Explain why the tube is Z-shaped (Briggs used an angle of 140°).

^[1]From Dyson Freeman's essay "The World, The Flesh, and the Devil" republished in *The Scientist as Rebel* (2006) New York Review Books.

^[2]http://en.wikipedia.org/wiki/Dyson_tree

^[3]The Baobab. From *The Little Prince* by Antoine de Saint-Exupery (1943)