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The hierarchical structure and mechanics of plants

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Abstract
The cell walls in plant tissues are made up of just four basic building blocks: cellulose, the main structural fiber of the plant kingdom, hemicellulose, lignin and pectin. Although the microstructure of plant cell walls varies in different types of plants, broadly speaking, cellulose fibers reinforce a matrix of hemicellulose and either pectin or lignin. The cellular structure of plants varies, too, from the honeycomb-like cells of wood to the closed-cell, liquid-filled foam-like parenchyma cells of apples and potatoes and to composites of these two cellular structures, as in arborescent palm stems. The arrangement of the four basic building blocks plant cell walls and the variations in cellular structure give rise to a remarkably wide range of mechanical properties: the Young’s modulus varies from 0.3 MPa in parenchyma to 30 GPa in the densest palm while the compressive strength varies from 0.3 MPa in parenchyma to over 300 MPa in dense palm. The mechanical properties of plants span this entire range. This paper reviews the composition and microstructure of the cell wall as well as the cellular structure in three plant materials, wood, parenchyma and arborescent palm stems, to explain the wide range in mechanical properties in plants as well as their remarkable mechanical efficiency.
Hierarchical structure and mechanics of plants

Introduction

The cell walls of plants are made up of just four basic building blocks: cellulose, hemicellulose, lignin and pectin. Cellulose is the main structural fibre in the plant kingdom and has remarkable mechanical properties for a polymer: its Young’s modulus is roughly 130 GPa and its tensile strength is close to 1 GPa. The properties of hemicellulose and lignin are similar to common engineering polymers: lignin, for instance, has a modulus of roughly 3 GPa and a strength of about 50 MPa. Broadly speaking, the cell walls of plants are made up of cellulose fibers reinforcing a matrix of hemicellulose and either lignin or pectin in one or more layers, with the volume fraction and orientation of the cellulose fibers varying in each layer. The geometrical structure of plant cells also varies, from the honeycomb-like prismatic cells of wood to the foam-like polyhedra in the parenchyma cells of apples and potatoes.

The variations in the hierarchical microstructure of plants gives rise to a remarkably wide range of mechanical properties, illustrated in Fig. 1, which plots, on log-log scales, the strength against the Young’s modulus for three groups of plant materials: woods, parenchyma and arborescent palm stems. The Young’s modulus of parenchyma tissue is as low as 0.3 MPa while that of the densest palm is 30 GPa, a factor of 100,000 higher. The strengths of parenchyma and the densest palm span from 0.3 to 300 MPa, a factor of 1000. Interestingly, there are plants with moduli and strengths spanning nearly this entire range. Here, we explain how the microstructural arrangements of the four basic building blocks in wood, parenchyma and arborescent palm stems, arising from
their different growth patterns, yield the enormous range in the modulus and strength of plants.

*Basic building blocks*

Cellulose is the main structural fiber in the plant kingdom. It is a long-chain polysaccharide made up of 7000-15000 glucose monomer units, which are alternately rotated 180° ([Fig. 2a](#)). Cellulose molecules align to form microfibrils, about 10-30nm in diameter, with crystalline regions (micelles) separated by shorter non-crystalline regions ([Fig. 2b](#)). The cellulose microfibrils themselves are aligned and bound together into macrofibrils, roughly 100-250 nm in diameter, by a matrix of hemicellulose and either pectin or lignin. Hemicellulose is a short chain, amorphous poly-saccharide with 500-3000 monomer units with acidic groups (Bodig and Jayne, 1982; Niklas, 1992). Pectins are a group of polysaccharides rich in galacturonic acid units (Brejnholt, 2010). Lignin is an amorphous, complex phenolic (Dinwoodie, 1981).

Data for the density, Young’s modulus and strength of cellulose and lignin, and the modulus of hemicellulose are given in Table 1; data for the density and strength of hemicellulose and for the properties of native pectin from plant cell wall are not available. Data for the Young’s modulus of cellulose have been obtained from x-ray diffraction measurements on unstrained and strained bleached ramie fibres (Sakurada et al., 1962, 1966; Sakurada and Kaji, 1970). Also included in Table 1 is the theoretical estimate, from lattice dynamics modeling, for the Young’s modulus of crystalline cellulose along the chain axis (Tashiro and Kobayashi, 1991). Data for the Young’s moduli of hemicellulose and lignin have been obtained by isolating powders of each, compressing the powders into a
compact in a mould and then performing unconfined compression tests (Cousins et al. 1975; Cousins 1976, 1978). Data for the tensile strength of cellulose are from tensile tests on bast fibers from hemp, jute, flax and ramie, which all have a high concentration of cellulose.

Plant cell walls

Plant cell walls are secreted by the living protoplast of the cell, external to the plasma membrane that encloses the protoplast (Niklas, 1992). The cell wall is composed of distinct layers, secreted sequentially by the protoplast such that the oldest layer is furthest from the plasma membrane and the youngest layer is closest. As a cell is growing, the primary cell wall layer, composed of cellulose fibers in a matrix of hemicellulose and pectin, is first secreted; hemicellulose binds to the surface of the cellulose microfibrils while pectin cross-links the hemicellulose molecules of adjacent microfibrils (Fig. 2c). Glycoproteins, a minor constituent of the cell wall, are also thought to be involved in the cross-linking. During cell growth, enzymes reduce the yield strength of the primary cell walls, allowing significant deformation under the pressure within the cell. Once growth is complete, the stiffness and strength of the cell wall increases. Adjacent cells are bound together by the middle lamella, which is initially high in pectin.

After cell growth is complete a number of additional processes may occur (Niklas, 1992). In some plants, such as woods and palms, additional secondary layers, with cellulose fibers in a matrix of lignin and hemicellulose, are deposited. The cellulose fibers are typically oriented at different angles in each secondary layer and the layers may differ in thickness. Lignification of the secondary cell wall layers increases their stiffness and strength compared with un lignified
primary layers. In some mature plant tissues, such as wood, the protoplast itself may die but the remaining cell walls continue to provide mechanical support while the lumen allows transport of water and other nutrients. With age, both the middle lamella and the primary cell wall may become lignified and less distinct, so that the middle lamella and its two neighbouring primary cell walls are collectively known as the compound middle lamella. As an example of the hierarchical structure of plant cell walls, a schematic of the structure of wood, showing the primary and secondary cell wall layers, is shown in Fig. 2d.

With this background on the basic building blocks and plant cell wall structure, we now examine three plant materials, wood, parenchyma and arborescent palm stems, in more detail to describe how the basic building blocks are arranged in the cell wall in each case and how the cellular structure varies across different types of plants to give the wide range of mechanical properties seen in Fig. 1.

Wood

Trees increase in diameter as wood cells are added by the cambium, a dividing layer of cells at the periphery of the tree just inside the bark (Dinwoodie, 1981). Outer cells in the cambial zone develop into bark, while inner cells differentiate into wood, with a layer of cambial cells remaining between the two. Over a period of about three weeks as the cells differentiate, they change shape and form the secondary cell wall; once secondary wall formation is complete, the cell dies. The growth process gives a roughly uniform density of wood throughout the tree (with minor variations at the scale of the growth rings and rays).
The cellular structures of a representative softwood (cedar) and a hardwood (oak) are shown in Fig. 3. In softwoods, the bulk of the cells (85-95%) are highly elongated tracheids that provide both structural support and a conduction path for fluids (through small openings, called bordered pits, at their ends) (Bodig and Jayne, 1982). In hardwoods, structural support is provided by fiber cells (which make up 35-70% of the cells) while fluid conduction is through sap channels (also called vessels), enlarged cells with thin walls and large pore spaces (which make up 6-55% of the cells). Both softwoods and hardwoods have ray cells, smaller, more rectangular cells that store sugars; in softwoods, the ray cells make up 5-12% of the cells while in hardwoods, they make up 10-32%. The relative densities of woods (the density of the wood divided by that of the solid cell wall) vary from about 0.05 for balsa to 0.88 for lignum vitae.

The cell walls in wood are made up of a primary layer, with cellulose fibrils randomly distributed in the plane of the layer, and three secondary layers, with cellulose fibrils helically wound in varying patterns in each of the three layers (Fig. 2d). The primary layer is made up of mostly lignin, with a low volume fraction (<20%) of cellulose fibers (Bodig and Jayne, 1982). The S2 layer is typically considerably thicker than the others: for instance, in the spruce Picea abies, the S2 layer makes up 85% of the cell wall thickness (Dinwoodie, 1981). The S2 layer is composed (by volume) of roughly 50% cellulose, 30% hemicellulose and 20% lignin (Bodig and Jayne, 1982), with the cellulose fibrils wound at a slight angle (the microfibrillar angle), typically 10-30º to the vertical (Dinwoodie, 1981). As a result of the thickness of the S2 layer and the high volume fraction and alignment of cellulose fibrils, the mechanical properties of the cell wall largely depend on those of the S2 layer.
While the variations in the microfibrillar angle and details of the composite nature of the wood cell wall lead to some variation in its properties, as a rough approximation, they are similar across different species. Measured values for the density, Young’s modulus and tensile yield strength of the solid cell wall material are summarized in Table 2. For loading along the grain, the compressive strengths of woods are roughly half their tensile strengths (Dinwoodie, 1979). The compressive strength of the cell wall material may also be lower than the tensile strength reported in Table 2 but data to confirm this are unavailable. Detailed models of the mechanical properties of the wood cell wall are available; see, for instance, Bergander and Salmen, 2002; Yamamoto et al., 2002; Fratzl et al., 2004; Hofstetter et al., 2005; Fratzl and Weinkamer, 2007; Neagu and Gamstedt, 2007; and Bader et al., 2011.

Data for the Young’s modulus and compressive strength of woods, plotted against density are shown in Fig. 4. The Young’s modulus and compressive strength along the grain vary roughly linearly with relative density while those across the grain vary roughly with the cube and square of relative density, respectively. The lower axis shows the density normalized by that of the cell wall (1500 kg/m$^3$). That on the left hand side shows the modulus normalized by Cave’s (1968) value for the axial modulus of the cell wall ($E_s = 35$ GPa) or the strength normalized by Cave’s (1969) value for the axial strength of the cell wall in tension ($\sigma_{ys} = 350$MPa). The unnormalized data are shown on the remaining axes. The strength data for loading along the grain are from bending tests, while those for loading across the grain are from uniaxial compression tests. Small clear specimens, such as those used in these tests, fail in compression in bending
tests, as their compressive strength is about one third of their tensile strength (Dinwoodie, 1981). Compressive strength data from uniaxial compression tests are slightly lower than those from bending tests (Wood Handbook, 1999). The data are for a moisture content of 12%.

The cellular structure of wood can be modelled, to first order, as a honeycomb with prismatic cells (Easterling et al., 1982; Gibson and Ashby, 1997). For loading along the grain, the cell walls compress axially and then fail by yield followed by either local plastic buckling or by fracture of the ends of the cells. As a result, both the Young's modulus, $E^*$, and compressive strength, $\sigma^*$, of wood along the grain depend linearly on the relative density, $\rho^*/\rho_s$:

\[
E^*_{\text{along}} = E_s \left(\frac{\rho^*}{\rho_s}\right)
\]

and

\[
\sigma^*_{\text{along}} = C_2 \sigma_{ys} \left(\frac{\rho^*}{\rho_s}\right)
\]

where $E_s$ and $\sigma_{ys}$ are the Young's modulus and strength of the solid cell wall along the grain. The constant $C_2 = 0.34$ is introduced to account for the difference in the measured value of $\sigma_{ys} = 350$ MPa (Cave, 1969) and the value found from extrapolation of the data for the strength of woods along the grain at a relative density of 1, corresponding to the fully dense solid cell wall, of 120 MPa (Fig. 4b).

When loaded across the grain, the wood cell walls bend and, at sufficiently high loads, form plastic hinges. It is relatively straightforward to show, using models for honeycombs, that (Easterling et al., 1982; Gibson and Ashby, 1997):

\[
E^*_{\text{across}} = C_3 E_s \left(\frac{\rho^*}{\rho_s}\right)^3
\]
and

\[ \sigma_{\text{across}}^* = C_4 \sigma_{33} \left( \rho^* / \rho_s \right)^2 \]  

(4)

The modulus and compressive strength of the wood across the grain depend on those of the solid cell wall in the transverse direction. Here, we normalize by the modulus and strength of the solid cell wall in the axial direction to allow a comparison of the normalized data along and across the grain in Fig. 4. The constants \( C_3 = 0.54 \) and \( C_4 = 0.14 \) then incorporate the ratio of the transverse to axial cell wall properties, as well as any differences between the measured cell wall properties and the extrapolated values from Fig. 4 at a relative density of 1 (given in Table 1). When wood is loaded across the grain in the radial direction, the rays act as reinforcement, stiffening and strengthening the wood by a factor of 1.5 or less, relative to loading across the grain in the tangential direction.

The interplay between the influence of the fiber composite cell wall and the cellular structure of wood on modulus and compressive strength is shown in Fig. 5. The figures shows envelopes of modulus and strength for the basic building blocks (cellulose, lignin and hemicellulose), the cell wall and for a number of species of woods. The upper and lower bounds for the moduli of composites made from them can be estimated by simple composites theory; they are plotted with the envelope bounded by the data for cellulose and lignin. The value for the wood cell wall is close to that of cellulose, as a result of the high volume fraction of cellulose in the wall. The moduli and strength of the wood along the grain varies linearly with the density while those across the grain vary with the cube and square of the density, respectively.

The great ranges in the moduli of woods (a factor of over 1000) and the strengths (a factor of over 100) arise primarily from their honeycomb-like
structure. Loading along the grain results in axial deformation of the cell wall, giving rise to a linear dependence of modulus and strength on relative density. Loading across the grain results in bending of the cell wall giving rise to a cubic or squared dependence of modulus and strength, respectively, on relative density. The different mechanisms of deformation and failure for loading along and across the grain, along with the large range in relative densities of woods, from 0.05 to 0.88, then produces the large range of measured moduli and strengths. The fiber composite nature of the cell wall contributes relatively little in comparison, as the moduli and strength of the cell wall differ by a factor of 2 or 3 along and across the grain.

Parenchyma

Fruits such as apples and root vegetables like potato tubers and carrots are largely made up of parenchyma tissue which stores sugars. The microstructures of carrot and potato tuber are shown in Fig. 6. The cells of parenchyma are polyhedral, with thin cell walls. The living protoplasm in the cell consists of water along with the organelles and molecules within it, surrounded by the plasma membrane which secretes the cell wall. In most parenchyma tissues, the cells are densely packed together: they can be thought of as a pressurized, liquid-filled closed-cell foam.

Measurements of cell dimensions for potato tuber parenchyma indicate the cell diameter is 212 µm, the edge length of a polyhedral cell face is 115 µm and the cell wall thickness 1 µm (Hepworth and Bruce, 2000). Assuming a
tetrakaidecahedral cell, the relative density or volume fraction of solid for the potato parenchyma can be estimated from these dimensions to be 0.010.

The thin cell walls consist of only a primary layer; unlike woody plants, they lack lignified secondary wall layers. Within the cell wall, cellulose fibers reinforce a matrix of hemicellulose, pectin and glycoproteins (Niklas, 1992), with pectin making up about a third of the cell wall (Jarvis et al., 1988). Micro-indentation tests on fresh, wet potato tuber parenchyma have been used to estimate the Young’s modulus and tensile strength of the cell wall (Hiller et al., 1996). For cell dimensions in the specimens studied by Hiller and co-workers, as well as by Hepworth and Bruce (2000), the Young’s modulus of the cell wall, $E_s$, is estimated to be 0.5-0.6 GPa. The tensile strength of the wall depends on the geometry of the deformed cell wall. Assuming a conical shape, Hiller and his co-workers calculated a tensile strength of the wall of 114 MPa; using a more realistic paraboloid of revolution, with a sharper angle where the indenter meets the cell wall, gives a tensile strength of 60MPa. This rough estimate suggests that the tensile strength, $\sigma_{ys}$, of the potato tuber cell wall is in the range of 60-100 MPa.

Measured Young’s moduli and compressive strengths of parenchyma from apple, potato and carrot are listed in Table 3. The moduli range from 0.3-14 MPa while the compressive strengths range from 0.25-1.3 MPa.

At normal or high turgor pressures, the cell walls are taut and deformation is dominated by stretching of the cell walls. The Young’s modulus and strength of the parenchyma tissue are then directly proportional to its relative density (Gibson et al., 2010):

$$E^* = E_s \left( \rho^* / \rho_s \right)$$ (5)
where the relative density is equivalent to the volume fraction of solids (i.e. is calculated without the protoplasm filling the cells). At low turgor pressure within the cell, the cell walls are no longer taut and initial deformation is by bending, giving a lower initial modulus. As deformation continues, the cell walls become taut and the slope of the stress-strain curve increases, reaching a value similar to the modulus of the tissue at normal or high turgor pressure.

There is sufficient information for potato tuber parenchyma to allow a comparison between the data of Table 3 and the liquid-filled, closed-cell foam model (eqn 5 and 6). For a relative density of 0.01 (Hepworth and Bruce, 2000), and with $E_s = 0.5$-0.6 GPa and $\sigma_{ys} = 60$-100 MPa (Hiller et al., 1996), the model gives values of the Young’s modulus of potato parenchyma, $E^* = 5$-6 MPa, and the compressive strength, $\sigma^* = 0.6$-1.0 MPa, in good agreement with the measured values of $E^* = 3.5$-5.5 MPa and $\sigma^* = 0.27$-1.3 MPa.

**Palm**

Arborescent palms can grow to heights of 20 to 40 meters, similar to many trees. Unlike trees, palms lack a cambium so that they cannot add cells at their periphery to increase their diameter: arborescent palm stems typically remain roughly constant in diameter throughout their lives. Instead, as the stem grows taller and ages, the increased load is resisted by increasing the thickness of the cell walls. Interestingly, palms do not do this uniformly throughout their cross-section; instead, a radial density distribution develops, with denser tissue at the
base and periphery of the stem, where the bending stresses on the stem are greatest.

The microstructure and mechanical properties of four species of palm have been studied in detail by Rich (1986, 1987a,b). Micrographs of the cross-sections of *Iriartea gigantea* reveal vascular bundles, with their cells aligned along the length of the stem, similar to a honeycomb, separated by ground tissue with more equiaxed parenchyma cells, similar to a closed-cell foam (Fig. 7a,b): the increased cell wall thickness in older vascular bundle tissue can be seen. Higher magnification scanning electron micrographs of a different palm, *Cocos nucifera*, indicate that the thicker cell walls have additional secondary layers (Kuo-Huang et al., 2004) (Fig. 7c,d). The radial density distribution at breast height as well as the vertical density distribution are shown in Fig. 8. There is a remarkable range in density within a single stem: the dry density of the *Iriartea gigantea* tissue varies from less than 100 to over 1000 kg/m$^3$, spanning nearly the entire range of densities of all species of woods, from balsa (75 kg/m$^3$) to lignum vitae (1300 kg/m$^3$).

Data for the cell wall properties of palm are limited. The only available studies are those of Ruggeberg et al. (2008, 2009), who performed tensile tests on small (120 μm x 80 μm x 3 mm), wet specimens taken at varying radial positions within vascular bundles of the Mexican fan palm, *Washingtonia robusta*. The Young’s modulus of both the bulk tissue as well as the solid cell wall were calculated by normalizing the measured load by the cross-sectional area of the entire specimen and by that of the solid cell wall material, respectively. The bulk tissue Young’s moduli ranged from roughly 20 MPa to 1.14 GPa while the solid
cell wall moduli ranged from 0.1-3.0 GPa, with the stiffest tissue corresponding to the highest cell wall modulus. The lowest tissue and cell wall moduli occurred at the periphery of the vascular bundle furthest away from the phloem while the highest values occurred near the phloem. Staining for lignin revealed that the most lignified tissue was nearest the phloem, consistent with the higher measured values of cell wall modulus; lignification of the thinnest wall cells was negligible.

The lower value of the solid cell wall Young’s modulus, 0.1 GPa, is similar to the cell wall modulus of potato tuber parenchyma, 0.5 GPa, reflecting the lack of lignification. The higher value of the solid cell wall modulus, 3 GPa, is substantially less than that of wood (\(E_s = 35 \text{ GPa}\)) with its primary and three secondary cell wall layers; one would expect the cell wall modulus to be lower if the wall had few secondary layers, with less aligned cellulose fibrils.

Measurements of the Young’s modulus, \(E^*\), and bending strength (modulus of rupture), \(\sigma^*\), along the grain of fresh palm tissue indicate that (Fig. 9):

\[
E^* = C_5 \rho^{2.5} \tag{7}
\]

and

\[
\sigma^* = C_6 \rho^{2.2} \tag{8}
\]

where \(\rho^*\) is the dry density of the specimen. The moduli range from 10 MPa to about 30 GPa and the bending strength from 0.3 MPa to 300 MPa; both vary over 3 orders of magnitude. The values of moduli and strength at the lowest densities are similar to those for parenchyma tissue, reflecting their low relative density (about 0.03) and low cell wall properties associated with primary cell walls (Table 3). Those for the highest densities are even greater than the properties of
wood (Fig. 4). Ruggeberg’s data for palm tissue moduli, from 20 MPa to 1.14 GPa, were at the lower range, for lower densities, of Rich’s data.

Palm stems have both vascular bundles, with a honeycomb-like structure, similar to wood, and parenchyma, with foam-like cells. The data in Fig. 9, from Rich’s (1987) study, is based on beam bending tests of 10mm x 10mm x 700mm samples of palm tissue that include numerous vascular bundles as well as parenchyma. Under loading along the grain, both the vascular bundles and the parenchyma cells deform axially, so that the model indicates that tissue modulus is simply:

$$E^* = E_s \left(\frac{\rho^*}{\rho_s}\right)$$  \hspace{1cm} \text{(9)}

where $E_s$ is the Young’s modulus of the solid cell wall at the density, $\rho^*$, of the palm tissue and $\rho_s$ is the density of the solid cell wall. (Unlike wood and parenchyma, the solid cell wall properties vary as the number of layers in the cell wall and the density of the tissue increases.)

The lowest density material tested in Rich’s (1987b) study was roughly 50-100 kg/m$^3$, with tissue moduli, $E^*$, ranging from 10-300 MPa. Vascular bundle tissue of similar modulus in the Ruggeberg (2008) study had a solid cell wall modulus, $E_w$, between 0.1 and 2.1 GPa, within a single vascular bundle. Using these values for $E_w$ along with a tissue density of 50-100 kg/m$^3$ and a solid density, $\rho_s = 1500$ kg/m$^3$, the model gives a value of the tissue modulus, $E^* = 3$-140 MPa, close to the measured range in Rich’s data. Specimens with a density of 100-300 kg/m$^3$ in Rich’s (1987b) study had a tissue modulus of 1 GPa. Specimens with the same tissue modulus in Ruggeberg’s (2009) study had a solid cell wall modulus $E_s$ of 3 GPa. In this case, the tissue modulus estimated from the model is
200-600 MPa, somewhat lower than measured by Rich (1987b). One of the limitations of these estimates is that Rich (1987b) and Ruggeberg et al. (2008, 2009) studied different species of palms and used different testing methods. Rich's data for the Young's modulus of two species, *Welfia georgii* and *Iriartea gigantea*, overlap, suggesting that at least for these two species, the tissue moduli are similar over the same range of densities. There are no measurements of the solid cell wall modulus for higher density palm tissue nor any measurements of solid cell wall strength.

The modulus data for palm give values of $E'$ of roughly 30 GPa at a density of 1000 kg/m$^3$ ([Fig. 9a](#)). Extrapolating linearly, corresponding to axial cell wall deformation, to fully dense material (at about 1500 kg/m$^3$), gives a solid cell wall modulus of $E_s = 45$ GPa, somewhat higher than wood (35 GPa) and bamboo (35-40 GPa, based on linear extrapolation of tensile test data of Nogata and Takahashi, 1995). The high value of $E_s$ for palm reflects the additional secondary layers in the cell wall of the densest tissue. Similarly, a linear extrapolation of strength from 300 MPa at a density of 1000 kg/m$^3$ gives the solid cell wall strength of $\sigma_{ys} = 450$ MPa, between that of wood (120-350 MPa, [Table 1](#)) and bamboo (800 MPa, Nogata and Takahashi, 1995).

This rather simple analysis shows how the large range of density of palm tissue (from 50-1000 kg/m$^3$) and of modulus of the solid cell wall material (from 0.1 to 45 GPa) gives rise to the remarkable range of modulus in palm tissue, which spans over 3 orders of magnitude. The range in density arises from the variation in the number of layers within the cell wall, while the range in the solid cell wall modulus also depends on the degree of lignification of the various
layers and the orientation of the cellulose fibrils within each layer. While there are no measurements of the strength of the solid cell wall in palm, we expect a similar variation, giving rise to the large range in measured tissue strength.

Discussion

The three plant materials described in this paper have exceptionally large ranges of mechanical properties: the Young's moduli span from 0.3 MPa to 30 GPa while the compressive strengths span from about 0.3 MPa to 300 MPa. These large ranges arise from the composition of the cell wall, the number of layers in the cell wall and the volume fraction and arrangement of cellulose fibres in those layers, as well as the cellular structure of the plant tissue. The composition, structure and properties of the cell wall and the cellular structure of wood, parenchyma and arborescent palm are summarized in Fig. 10.

Wood cells form and grow at the cambium layer under the bark. Within a few weeks of cell division, the cells have reached their mature dimensions and three secondary layers are laid down and lignified. The mechanical properties of the cell wall, which are roughly constant across species, are largely determined by the middle secondary layer, which makes up most of the cell wall (~85%) and has roughly 50% cellulose fibers aligned close to the vertical axis of the cell (10-30° off vertical). Wood tissue has a honeycomb-like structure, with densities ranging from about 75 kg/m³ for low-density balsa to 1300 kg/m³ for the densest wood, lignum vitae. Models for the mechanical behaviour of honeycombs indicate that for loading along the grain, the cell walls deform axially and the modulus and strength vary linearly with relative density, while for loading across the grain, the cell walls bend, and the modulus and strength vary with the
cube and square of density, respectively. The large range of density, as well as the different mechanisms of deformation and failure along and across the grain, give rise to the wide range in modulus and strength of wood.

In parenchyma cells, the walls have only a primary layer, with randomly distributed cellulose fibers reinforcing a matrix of hemicellulose, pectin and glycoproteins. The cell wall modulus is much lower than that of wood, due to the lack of lignification, while the cell wall strength is similar, reflecting the role of the cellulose fibers. Parenchyma tissue has roughly equiaxed, polyhedral cells that can be modelled as a liquid-filled closed-cell foam. The cell walls in parenchyma are thin, relative to their length, giving low relative densities, on the order of 1%. Models for liquid-filled closed-cell foams indicate that at normal or high turgor pressures, the cell walls are taut and deform axially, leading to a linear dependence of modulus and strength on relative density. The low modulus of the cell wall, combined with the low relative density, gives rise to low tissue moduli, a few MPa. The tissue modulus and strength are both well described by the model.

Palm tissue is made up of honeycomb-like vascular bundles surrounded by ground tissue. The vascular bundles have honeycomb-like prismatic cells and dense fibres aligned along the length of the stem, while the ground tissue is made up of thin-walled, polyhedral parenchyma. Palms lack a cambium and so cannot increase their radius by cell division at the cambial layer, as woods do. Instead, as the palm stem increases in height, additional layers are added to the cell walls in the vascular bundles, increasing their density and mechanical properties. Within a single palm stem, there is a density gradient that can be as great as from 60 to 1000 kg/m³, with denser material towards the base and
periphery of the stem. The cell wall moduli of palm tissue varies from 0.1 to 45 GPa, with the lower value reflecting the parenchymal tissue with only an unlignified primary layer and the higher value reflecting the modulus of the vascular bundles, with 4 or more lignified secondary layers with highly aligned cellulose fibres in at least some of those layers. The strength of the cell wall is estimated to be similar to that of parenchyma for the ground tissue (60-100 MPa) and 450 MPa for the densest tissue. The combination of low cell wall properties and low relative density of the parenchyma leads to low tissue modulus and strength ($E^\prime < 0.1$ GPa, $\sigma^\prime < 10$ MPa) while the combination of high cell wall properties and high relative density of the vascular bundles gives rise to high mechanical properties ($E^\prime \sim 30$ GPa, $\sigma^\prime \sim 300$ MPa). The range of cell wall properties and densities within a single palm stem produces the vast range in modulus and strength of palm tissue.

The composition, cell wall structure and cellular structure of wood, parenchyma and arborescent palm stems give rise to remarkable mechanical performance in plants.

The trunks and branches of trees are loaded primarily in bending (from the wind or their self-weight). For a beam of given stiffness, span and cross-sectional dimensions, the material that minimizes the weight of a beam is that with the maximum value of $E^{1/2}/\rho$ (Ashby, 1999). For the composite wood cell wall, $E_s = 35$ GPa and $\rho_s = 1.5$ Mg/m$^3$, giving a value of $E_s^{1/2}/\rho_s = 3.94$ GPa$^{1/2}$ m$^3$/Mg. The performance index of woods (for loading along the grain, as is the case in the tree) can be related to that of the solid cell wall material, using eqn (1):
Wood has a value of $E^{1/2}/\rho$ that is higher than that of the solid it is made from, by a factor of $(\rho_s/\rho^*)^{1/2}$. For a typical softwood, such as pine, with a relative density of 0.33, $E^{1/2}/\rho^* \approx 7$ GPa$^{1/2}$ m$^3$/Mg, close to that of the best engineering materials, uniaxially aligned carbon fiber reinforced composites ($E^{1/2}/\rho \approx 8.5$).

Similarly, for a beam of a given strength, span and cross-sectional dimensions, the material that minimizes the weight is that with the maximum value of $\sigma^{2/3}/\rho$. Again, woods have values of $\sigma^{2/3}/\rho^*$ for loading along the grain that are higher than that of the solid cell wall, by a factor of $(\rho_s/\rho^*)^{1/3}$ (from rearranging equation (2)). For loading along the grain, woods have comparable values of $\sigma^{2/3}/\rho^*$ ($\approx 45$ MPa$^{2/3}$ m$^3$/Mg) to those of engineering composites ($\approx 65$ MPa$^{2/3}$ m$^3$/Mg). The performance of woods compared with that of engineering materials is illustrated in Fig. 11.

While the circular cross section of tree trunks and branches allows them to resist loading equally in all directions and to accommodate growth through the circumferential layer of cambium beneath the bark, it is not a highly efficient cross-section for resisting bending. Engineering materials can be fabricated in more efficient shapes (e.g. a circular tube), increasing the performance of engineered components.

In parenchyma cells, the low properties of the cell wall ($E_s \sim 0.5$ GPa; $\sigma_s \sim 60$ MPa) and low relative density ($\rho^*/\rho_s \sim 0.01$) combine to give low mechanical
properties ($E^* = 3-6$ MPa; $\sigma^* = 0.27-1.3$ MPa). In spite of their low mechanical properties, parenchyma tissue can contribute to the mechanical efficiency of plants. For instance, the leaves of monocotyledon plants, such as grasses, irises and maize, have a foam-like core of parenchyma separating two fiber composite-like faces, with dense, stiff, strong sclerenchyma fibers embedded in a matrix of cuticle cells (Fig. 12). The leaves behave mechanically like an engineering sandwich beam: the separation of the faces by the lightweight core increases the moment of inertia of the beam with little increase in weight, making them efficient in resisting bending, the primary mode of loading in monocotyledon leaves. Studies of iris leaves (Gibson et al., 1988; reanalyzed in Gibson et al., 2010) and maize leaves (Moulia and Fournier, 1997) indicate that they do, indeed, behave mechanically like efficient sandwich beams.

The radial density gradient in arborescent palm stems also leads to mechanical efficiencies (Gibson et al., 2010). For Iriartea gigantea, the density data in Fig. 8a can be shown to follow:

$$\frac{\rho^*}{\rho_{\text{max}}} = \left( \frac{r}{r_o} \right)^n$$

where $\rho^*$ is the dry density of the palm tissue at radius, $r$, $\rho_{\text{max}}$ is the maximum dry density of the palm tissue in that cross-section, $r$ is the radial distance from the center of the stem and $r_o$ is the outer radius of the stem and $n$ is a constant. The moduli, $E^*$, and bending strength, $\sigma^*$, data in Fig. 9 can be described by:

$$E^* = C^* \left( \frac{\rho^*}{\rho_{\text{max}}} \right)^m$$

and
The exponents $n$, $m$ and $q$ in eqn (11-13) vary slightly for different species of palm: for *Iriartea gigantea*, $n = 2$, $m = 2.5$ and $q = 2$ (Rich, 1987b). $C'$ and $C''$ are constants.

The flexural rigidity for the palm stem, with the radial density gradient, is then

\[
(EI)_{\text{rad gradient}} = \frac{C'\pi r_o^4}{mn + 4} \tag{14}
\]

The flexural rigidity for a cross section of the same radius and mass, with uniform density across the section, is:

\[
(EI)_{\text{uniform}} = C'\left(\frac{2 + nR}{2 + n}\right)\frac{\pi r_o^4}{4} \tag{15}
\]

For *Iriartea gigantea*, we find that the cross section with the radial density gradient is about 2.5 times as stiff in bending as the equivalent section with uniform density. A similar analysis for another species of palm, *Welfia georgii*, shows that the cross-section with the radial density gradient is about 1.6 times as stiff in bending as the equivalent section with uniform density.

The radial density distribution also gives rise to a non-linear bending stress distribution in the palm stem, under loading in the linear elastic regime. The bending stress, $\sigma$, is:

\[
\sigma(y) = E'\varepsilon = E'kr \tag{16}
\]
where $r$ is the distance from the neutral axis, $E'$ is the Young’s modulus of the palm tissue at $r$, $\varepsilon$ is strain and $\kappa$ is the curvature of the section. Substituting eqn (11) and (12) gives:

$$\sigma(r) \propto r^{m+n+1}$$ (17)

or, for *Iriartea gigantea*, with $m = 2.5$ and $n = 2$, the normal bending stress varies as $r^6$. The bending strength, or modulus of rupture, varies as $r^4$ (eqn 13). A plot of the radial distribution of bending stress and bending strength is shown in Fig. 13: the radial distribution of bending strength closely matches that of bending stress, making efficient use of the material.

Summary

The examples of wood, parenchyma and arborescent palm tissue demonstrate how the 4 basic building blocks in plants, cellulose, hemicellulose, lignin and pectin, are arranged to give an exceptionally wide range of modulus and strength in plant tissues. Trees, the leaves of monocotyledon plants and arborescent palms have all developed remarkable strategies for efficiently resisting bending, their main mode of loading: wood has values of the bending performance indices, $E^{1/2}/\rho$ and $\sigma^{2/3}/\rho$, comparable to engineering fiber composites; monocotyledon leaves are sandwich beams, with a core of low density parenchyma tissue separating dense, stiff strong sclerenchyma fibres in the outer faces; and palm tissue has a radial density gradient which increases the flexural rigidity of the cross section of the palm stem by a factor of roughly 2, compared with that of a section of uniform density. The study of plant tissues
may lead to further insight into the design of engineering materials and structures.

Acknowledgements

I am grateful for helpful discussions with Professors Michael Ashby of Cambridge University, Jacques Dumais of Harvard University and Karl Niklas of Cornell University. Professor Ashby kindly provided a material selection chart that was slightly modified to produce Figures 1 and 11 and Professor Karl Niklas kindly provided Fig. 5c. Don Galler took the scanning electron micrographs in Fig. 6 and Beth Beighlie skillfully assisted in the preparation of the figures. It is a pleasure to acknowledge all their contributions.
References


### Table 1 Mechanical properties of cellulose, lignin and hemicellulose

<table>
<thead>
<tr>
<th>Material</th>
<th>Density (kg/m$^3$)</th>
<th>Young’s modulus (GPa)</th>
<th>Tensile strength (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>167 [6]</td>
<td></td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>5-8 [8]</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>


[2-5] Data for the modulus for crystalline cellulose; [7,8] data at 12% moisture content.

### Table 2 Cell wall properties for wood

<table>
<thead>
<tr>
<th>Property</th>
<th>Literature value</th>
<th>Value inferred from Fig. 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density, $\rho$, kg/m$^3$</td>
<td>1500 [1]</td>
<td>-</td>
</tr>
<tr>
<td>Young’s modulus (axial), $E_s$ (GPa)</td>
<td>35 [2]</td>
<td>28 [3]</td>
</tr>
<tr>
<td>Young’s modulus (transverse) (GPa)</td>
<td>10 [2]</td>
<td>9</td>
</tr>
<tr>
<td>Tensile yield strength (axial), $\sigma_{ys}$ (MPa)</td>
<td>350 [5]</td>
<td>120</td>
</tr>
<tr>
<td>Tensile yield strength (transverse) (MPa)</td>
<td>135 [5]</td>
<td>50</td>
</tr>
</tbody>
</table>

1. Dinwoodie (1981) 2. Cave (1968), from tensile tests on 2mmx2mmx60mm specimens 3. Orso et al. (2006), from cell walls loaded as cantilever beams using an atomic force microscope tip mounted on a micromanipulator 4. Gierlinger et al. (2006) from tensile tests on single tracheids 5. Cave (1969), from tensile tests on 2mm x 2mm x 60mm specimens. Data from [2-5] at ≤ 12% moisture content.
Table 3 Elastic moduli and compressive strengths for parenchyma

<table>
<thead>
<tr>
<th>Plant material</th>
<th>Young's modulus, $E^\ast$ (MPa)</th>
<th>Compressive strength, $\sigma_{\text{comp}}^\ast$ (MPa)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple</td>
<td>$E^\ast = 0.31$-$3.28^1$</td>
<td>0.66</td>
<td>Oye et al., 2007</td>
</tr>
<tr>
<td>Apple</td>
<td>$E^\ast = 2.8$-$5.8$</td>
<td>0.25-0.37</td>
<td>Lin &amp; Pitt, 1986</td>
</tr>
<tr>
<td>Potato</td>
<td>$E^\ast = 3.6$</td>
<td>1.3</td>
<td>Lin &amp; Pitt, 1986</td>
</tr>
<tr>
<td>Potato</td>
<td>$E^\ast = 3.5$</td>
<td></td>
<td>Scanlon et al, 1996</td>
</tr>
<tr>
<td>Potato</td>
<td>$E^\ast = 5.5$</td>
<td>0.27</td>
<td>Hiller &amp; Jeronimides, 1996</td>
</tr>
<tr>
<td>Carrot</td>
<td>$E^\ast = 2$-$14$</td>
<td></td>
<td>Georget et al., 2003</td>
</tr>
</tbody>
</table>

Data for fresh, wet tissue, at normal turgor.

$^1$ The stress-strain curves from the study of Oye et al. (2007) were non-linear, with a long toe region, reflecting initial cell wall deformation by bending followed by a linear portion, reflecting cell wall deformation by stretching. The average initial modulus was 0.31 MPa while the average modulus at 80% of the failure stress was 3.28 MPa.
Figure captions

Fig. 1 Strength plotted against Young’s modulus for selected plant materials. Note the large range in properties produced by varying the arrangement of the four building blocks (cellulose, lignin, hemicellulose and pectin) in the cell wall as well as the cellular structure. The properties of the cellulose and lignin are indicated in red. (adapted from Gibson, Ashby and Harley, 2010, with permission).

Fig. 2 The hierarchical structure of plant cell walls showing: (a) the molecular structure of cellulose, with glucose molecules alternately rotated 180°; (b) the cellulose microfibril, with both crystalline and non-crystalline regions; (c) the cellulose macrofibril; and (d) the plant cell wall (for wood), made up of a primary layer and three secondary layers (S1, S2 and S3), with the cellulose microfibrils arranged in different orientations in each layer. Neighbouring cells are attached to each other by the middle lamella (not indicated). (adapted from Gibson, Ashby and Harley, 2010, based on Dinwoodie, 1979 and Niklas, 1992; requested permission to reproduce).

Fig. 3 Scanning electron micrographs of woods (a) cedar, cross section (b) cedar, longitudinal section (c) oak, cross-section (d) oak, longitudinal section (reproduced from Gibson, Ashby and Harley, 2010, with permission).

Fig. 4 (a) Young's modulus and (b) compressive strength of wood plotted against density. Data from Goodman and Bodig (1970, 1971) Bodig and Goodman (1973); Wood Handbook (1974); Dinwoodie (1981); Bodig and Jayne (1982) and Easterling et al. (1982) (reproduced from Gibson, Ashby and Harley, 2010, with permission).

Fig. 5 (a) Young's modulus and (b) strength plotted against density for woods and their constituents. (a) reproduced from Gibson, Ashby and Harley, 2010, with permission).

Fig. 6 Scanning electron micrographs of (a) carrot and (b) potato showing the relatively thin-walled cells. The ellipsoidal objects within the potato tissue are starch granules (reproduced from Gibson, Ashby and Harley, with permission).

Fig. 7 (a,b) Optical micrographs of cross-sections of Iriartea gigantea showing the peripheral stem tissue of (a) a young individual and (b) an older individual. B = vascular bundle of honeycomb-like cells, including xylem (X) and phloem (P) which conduct water and sap; G = ground tissue, made up of polyhedral parenchyma cells, similar to a closed-cell foam. (c,d) Scanning electron micrographs of cross-sections of coconut palm Cocus nucifera, showing cells near (c) the center of the stem, with a primary layer and one secondary layer and (d) the periphery of the stem, with a primary cell wall and three or four secondary layers. (a,b reproduced from Rich 1987a, Figs 22, 23, with kind permission of American Journal of Botany; c,d reprinted from Kuo-Huang et al., 2004, Figs 1e,f, requested permission of IAWA Journal.)
Fig. 8 Density plotted against (a) radial position (at breast height) and (b) against height above ground in the stem for a 19m tall *Welfia georgii* and for a 17m tall *Iriartea gigantea* (reproduced from Rich, 1987b).

Fig. 9 (a) Young's modulus and (b) modulus of rupture plotted against dry density for two species of palm, *Welfia georgii* and *Iriartea gigantea* (b) Modulus of rupture plotted against dry density for six species of palm: *Welfia georgii, Iriartea gigantea, Socratea durissima, Euterpe macrospadix, Prestoea decurrens* and *Cryosophila albida* (reproduced from Rich, 1987b).

Fig. 10 Comparison of the cell wall and cellular structure of wood, parenchyma and arborescent palm stem. Left: the cell wall composition, microstructure, modulus and strength. Center: schematic showing the structure of each plant material. Right: plant cellular microstructure, and ranges of density, relative density, modulus and strength.

Fig. 11(a) Young’s modulus-density chart for engineering materials, including woods. The performance index $E^{1/2}/\rho$ gives the performance of a material for resisting bending deflections: every point on a single line $E^{1/2}/\rho$ has the same value of $E^{1/2}/\rho$. As the line moves to the upper left, the value of $E^{1/2}/\rho$ increases. Woods loaded along the grain have comparable values to the best engineering materials, fiber composites (adapted from figure from MF Ashby, with permission).

Fig. 11(b) Strength-density chart for engineering materials, including woods. The performance index $\sigma^{2/3}/\rho$ gives the performance of a material for resisting bending stresses: every point on a single line $\sigma^{2/3}/\rho$ has the same value of $\sigma^{2/3}/\rho$. As the line moves to the upper left, the value of $\sigma^{2/3}/\rho$ increases. Woods loaded along the grain have comparable values to the best engineering materials, fiber composites (adapted from figure from MF Ashby, with permission).

Fig. 12 Scanning electron micrograph of the iris leaf, showing the core of foam-like parenchyma tissue and the outer faces of dense sclerenchyma fibres in a matrix of cuticle (reproduced from Gibson et al., 1988; with kind permission of Springer).

Fig. 13 The distribution of bending stress, $\sigma$, (dashed line) and bending strength, $\sigma^*$, (solid line) in the arborescent palm stem, *Iriartea gigantea*, with its radial density gradient. The strength of the palm tissue closely matches the stress distribution (reproduced from Gibson, Ashby and Harley, 2010, with permission).
Figure 1
Figure 2

(a) cellulose molecule

(b) cellulose microfibril

(c) macrofibril

(d) microfibril in amorphous hemicellulose and lignin
Figure 4

(a) Young's modulus, $E^*/E_s$

(b) Compressive strength, $\sigma^*/\sigma_s$
**Modulus - Density**

for woods

(HD), (MD), (LD) = High/Medium/Low Density

- Cellulose: $E = 120-140$ GPa
- Lignin: $E = 2.5-3.7$ GPa
- Hemicellulose: $E = 5-8$ GPa

**Strength - Density**

for woods

- Cellulose: $\sigma = 750 - 1080$ MPa
- Lignin: $\sigma = 25 - 75$ MPa

Solid composites of cellulose, lignin, and hemicellulose lie in this envelope.
Figure 7
**Cell Wall**

Cellulose, hemicellulose, lignin

Primary + 3 secondary layers, added over few weeks as cell grows

$E_s = 35$ GPa

$\sigma_{ys} = 120-350$ MPa

---

**Cellular Structure**

Honeycomb: uniform

$\rho^* = 75-1300$ kg/m$^3$

$\rho^*/\rho_s = 0.05-0.88$

$E^* = 1-30$ GPa (along)

$\sigma^* = 40-100$ MPa (along)

$E^* = 0.01-2$ GPa (across)

$\sigma^* = 0.3-20$ MPa (across)

$\rho^*, E^*$ and $\sigma^*$ vary across species

---

**Parenchyma (Potato)**

Cellulose, hemicellulose, pectin

Primary layer only

$E_s = 0.5-0.6$ GPa

$\sigma_{ys} = 60-100$ MPa

---

**Palm**

Cellulose, hemicellulose, lignin, pectin

Primary + 0 to 4 or more secondary layers, added over years, as the stem grows

$E_s = 0.1-45$ GPa

$\sigma_{ys} = 60-450$ MPa

(estimated from parenchyma + extrapolation)

---

*Figure 10*
Figure 11
Figure 12
$r_0$

$\sigma \alpha r^6$

$\sigma' \alpha r^4$

Figure 13