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A Close-Up View of the Mechanical Design of Arborescent Plants at Different Levels of Hierarchy – Requirements and Structural Solutions[†]

Michaela Eder*, Markus Rüggeberg, Ingo Burgert

*Max-Planck-Institute of Colloids and Interfaces, Department of Biomaterials,
Wissenschaftspark Golm, Am Mühlberg 1, 14476 Potsdam, Germany*

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*Corresponding author: michaela.eder@mpikg.mpg.de

Abstract

Arborescent plants are highly adapted to their terrestrial environment. In competition with other land plants for light, they gain advantage by managing to establish their photosynthesis units at remarkable heights above ground. For this benefit arborescent plants have to transport water over long distances against gravity and internal friction and have to cope with high mechanical loads acting on their stems. Although faced by similar mechanical constraints, the growth strategies of arborescent plants belonging to different species and classes can vary largely. This shows that during evolution different growth concepts with different structural solutions have been successfully established. In this article, we review structure-function relationships of trees and palms. The comparison is made along different levels of hierarchy, starting from the integral level of the stem down to the biochemical composition of the cell walls. Particular attention is paid to the close interdependencies between the structural levels and to the cell wall organisation of the different arborescent plants in terms of adjusting mechanical properties for the specific growth strategy.

Keywords: palm, tree; mechanics; cellulose microfibril orientation; lignification

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Introduction

Plants are sessile organisms, which have to cope with the specific environmental conditions in their habitat. Retaining mechanical stability is a major task, besides maximising photosynthesis, providing water transport and producing and distributing seeds. The optimal trade-off between cost-efficient design and sufficient margins of safety against mechanical failure has to be part of the entire growth strategy of the organism. In this respect, arborescent plants are of particular interest as they represent the tallest living

land organisms. They can reach heights of more than a hundred metres, accumulate masses of several thousands of tonnes and reach ages far more than thousand years. To meet the emerging mechanical requirements, which are given by both external and internal factors, (e. g. wind loads, self-weight, etc) a sophisticated mechanical design is essential.

The arborescent growth form has emerged in several plant species belonging to different families and

classes. In the present article, optimisation strategies with respect to mechanics of large land plants are analysed for trees (conifers and dicotyledonous trees) and monocotyledonous palms. Their comparison can reveal individual growth strategies based on the specific anatomy and morphology to meet the requirements of arborescent growth. Hereby, the organisms are compared at different levels of hierarchical structuring, as the hierarchical organisation from the molecular to the macroscopic scale is believed to be one key issue for the excellent mechanical performance of biological materials (e. g. Aizenberg et al., 2005; Fratzl, 2004; Speck et al., 1996). Already existing comparisons are mainly related to larger length scales, e. g. the stems (Ashby et al., 1995; Niklas, 1994; Rich et al., 1986) or the material performance from a materials science point of view (Ashby et al., 1995). Here we describe the addressed organisms at all hierarchical levels, following the classification by Speck et al. (1996), namely integral level (stem), macroscopic level (tissue structure), microscopic level (cell structure), ultrastructural level (cell wall structure), and biochemical level (cell wall composition).

An intrinsic challenge of such a comparison is that close interdependencies between the different structural levels exist and, consequently, plants manifest a large

variety of structural parameters at the nanoscale to adjust their (macro) mechanical properties. To meet these requirements cross-reference to other levels of hierarchy are inevitable. Moreover, this requires an approach in which the larger scales are presented more in a descriptive manner, but while moving downwards in the hierarchy, the structural adaptations to cope with mechanical loads will be considered more strongly.

Integral Level (stem)

Starting with the largest length scale, often termed the integral level of hierarchy (Speck et al., 1996), straight stems can be simplified viewed as homogeneous, strongly anisotropic porous solids. From a mechanical engineering point of view (Figure 1), the stem can be described as a cantilever beam when loaded in bending due to wind loads and as a column when loaded in axial compression due to the self-weight (Niklas, 1992). In terms of the latter, it is very unlikely that the compressive strength is exceeded, but Euler buckling might be an issue for stems with a high aspect ratio (Niklas, 1994). Hence, the mechanical response to both loading conditions is strongly determined by the geometry of the organ and the flexural stiffness, which is the elastic modulus of a material multiplied by

Figure 1

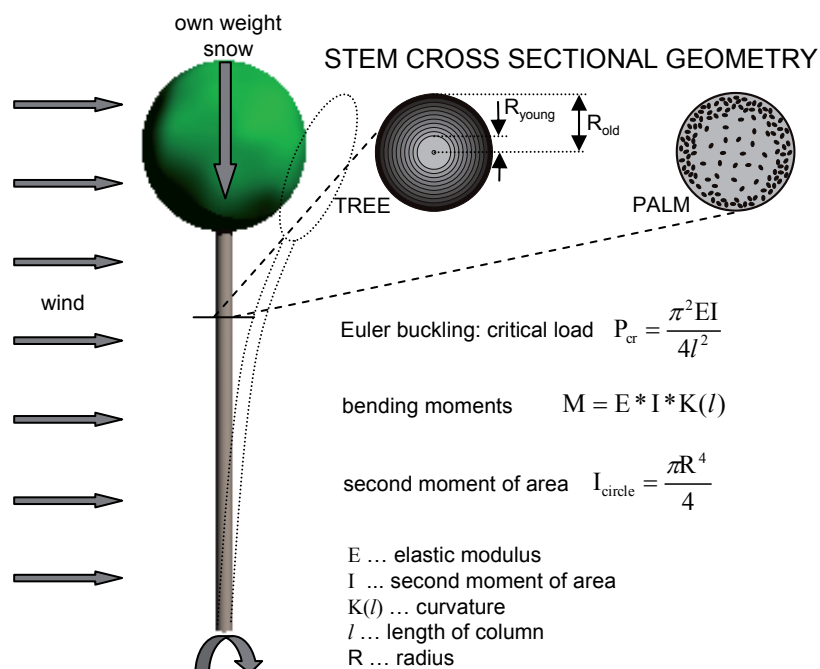


FIGURE 1: Schematic drawing of different loading conditions for an arborescent plant (simplified assumptions considering only static loads). The related equations highlight the crucial role of flexural stiffness at this level of hierarchy. Dark colours in cross sections indicate areas of high density.

the second moment of area. Further aspects regarding stems as “engineering systems” can be found in e. g. Ashby et al., 1995; Lichtenegger et al., 1999; Niklas, 1992.

Although experiencing comparable loads, arborescent plants belonging to different plant families exhibit an almost entirely different anatomy and morphology. Due to differences in growth patterns, considerable differences in geometry of the plant axis arise during ontogeny. The growth of monocotyledonous plants is restricted to primary growth, which means that the cross-section of the stem is more or less pre-defined with limited possibilities of the plant to increase its transverse dimensions. From this it follows that a large stem diameter from the beginning is a prerequisite for the palm to grow tall (Rich et al., 1986). In contrast, trees start with comparably thin and slender shoots and increase their transverse size continuously by secondary growth which results in cone-like shapes.

In young (short) palms, the flexural stiffness of the material is less relevant due to the oversized diameters of the stems. However, an ongoing material adaptation towards higher tissue stiffness is needed during aging and gaining height of the monocotyledonous plant. In contrast, the material properties of trees are adapted to the respective geometry of the stems during ontogeny. Due to their slender shape, the second moment of area is comparably low in young trees (Figure 1). Hence, they have to avoid high wind loads by bending (streamlining) for which a flexible and tough material is needed. Adult, thick and tall trees withstand the wind and support the crown with a high flexural stiffness which is achieved by (i) increasing the second moment of area by secondary growth and (ii) synthesis/deposition of stiffer wood material during ageing. The material-related aspects of these adaptations are described and discussed in the following sections starting with the different tissue structure of arborescent plants at the macroscopic level.

Macroscopic Level (tissue structure)

Besides geometric adaptations during growth, arborescent plants are able to adjust the mechanical properties of their tissues to cope with external and internal loads. With respect to bending moments acting on tall plants, the stiffness and strength of the material should be considerably high, especially at the periphery of the base. To achieve this, different growth concepts are followed by trees and palms.

In trees, ~ 90% of the trunk is made up of secondary xylem. In temperate zones, usually one tree ring is formed by secondary growth in each growth season.

The blocks in Figures 2a and 2b show the secondary xylem of Norway spruce (*Picea abies* [L.]) and poplar (*Populus nigra* [L.]). A layered structure becomes visible, which is a consequence of density variation across tree rings, coming from different amounts of synthesized cell wall material in a given volume (cell wall density ~ 1.5 g/cm³ (Fengel & Wegener, 1989)). The xylem of conifers consists of 90 – 95% fibrous cells (tracheids), which increase their cell wall thickness from earlywood towards latewood across a tree ring (Figure 2a, cross section). In contrast, the evolutionary younger dicotyledonous trees show a more complex xylem structure. The most striking elements are the vessels (Figure 2b) with their large diameters, taking over water transport. Here, density variation across a tree ring is the result of the amount and the particular arrangement of vessels, which are surrounded by the load bearing elements, namely fibre tracheids and libriform fibres. With increasing age, height and stem diameter, the width of tree rings becomes smaller. This trend is often accompanied by an increase in density (Niemz, 1993).

Palm stems control their macroscopic properties by the number (and type) of vascular bundles dispersed in parenchymatous tissue (Ashby et al., 1995; Rich, 1987b). An example (Mexican Fanpalm *Washingtonia robusta* [H.Wendl.]) is shown in Figure 2c. Although different types of vascular bundles exist (described in more detail in the section on Microscopic Level) they have in common that their density is much higher compared to the surrounding parenchymatous tissue. The fibre caps of the vascular bundles possess a high density and reach diameters of more than 2 mm (Waterhouse & Quinn, 1978) and are the main stiffening elements of the trunk (Rich, 1987a). The amount of vascular bundles is typically high at the periphery of the stem (Figure 1), resulting in a higher density of the bulk material.

As indicated in Figure 1, the main loading direction of plant stems is parallel to the longitudinal axis. Consequently, the material properties in longitudinal direction are adapted to higher loads resulting in 10 – 20 times higher stiffness compared to radial and tangential direction. Besides the loading direction, the type of load also influences the material response. The tensile strength of wood parallel to the longitudinal axis is twice as high as its compressive strength (e. g. Bodig & Jayne, 1993; Eberhardsteiner, 2002; Niemz, 1993). Trees are able to compensate for the low compressive strength by pre-stressing the outer parts of trunks in tension (Boyd, 1950; Dinwoodie, 1966; Kübler, 1987). In contrast, in terms of palms, Abasolo et al. (1999) and Huang et al. (2002) reported about longitudinal compressive stresses at the periphery of the stem.

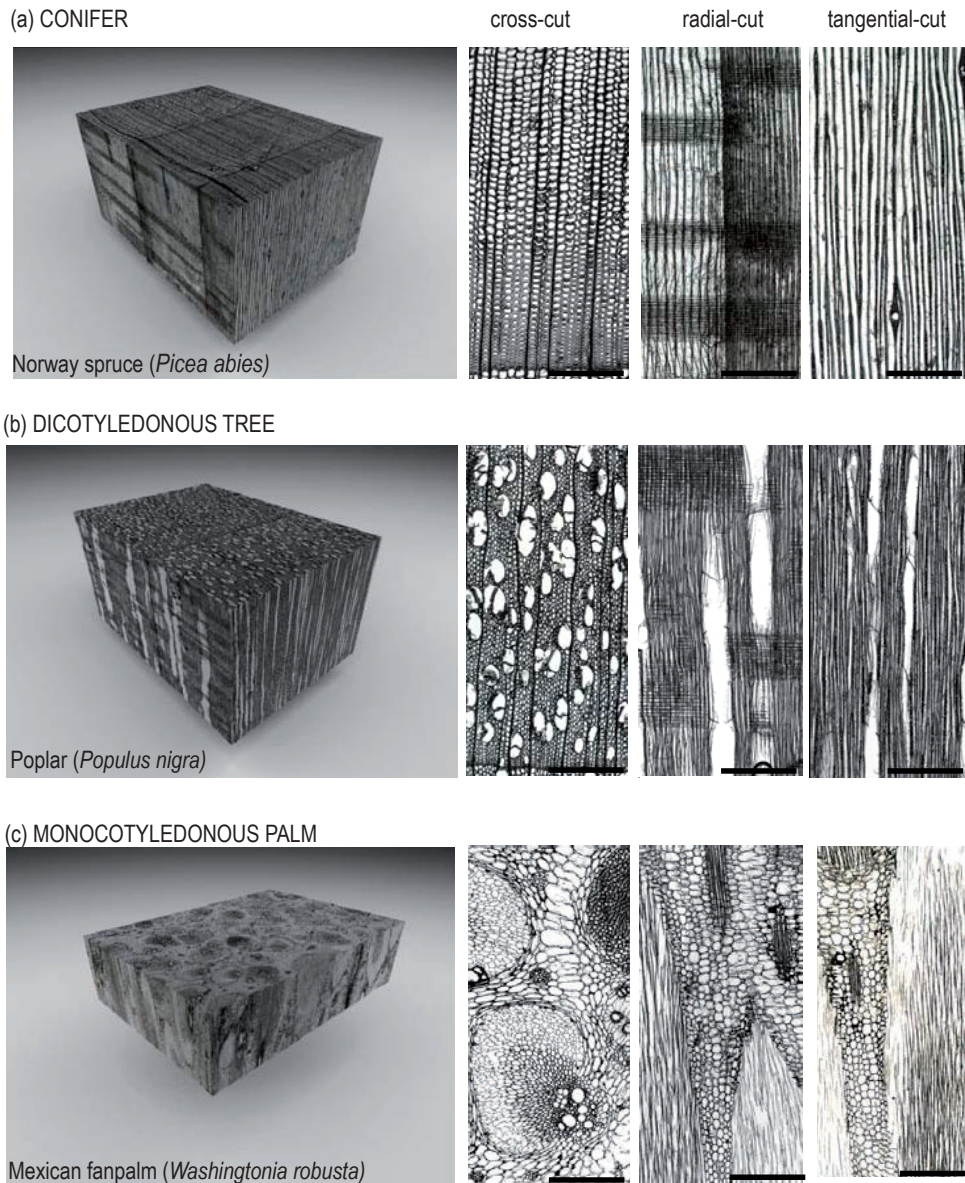


FIGURE 2: Blocks and thin sections showing the anatomy of (a) conifer wood (*Picea abies*); (b) dicotyledonous wood (*Populus nigra*); and (c) palm (*Washingtonia robusta*). Scale Bar 250 μm

Macroscopic material properties are strongly correlated with density, (e. g. Kollmann, 1951; Niemz, 1993). Provided that the mechanical properties of a solid phase in a cellular material are constant, a higher density at a given architecture is accompanied by an increase in stiffness and strength (Gibson & Ashby, 1999). The schematics in Figure 3 show wood of dicotyledonous trees and palms as simplified composite structures of high and low density materials. Wood of trees can be considered as a laminated structure composed of layers with different densities (early- and late-wood), whereas a block of palm “wood” consists of long, dense cylinders (vascular bundles)

embedded in a relatively soft parenchymatous matrix. The stiffness $E_{composite}$ of such structures can be roughly estimated by the following relationship:

$$E_{composite} = V_{hd}E_{hd} + V_{ld}E_{ld} \quad [1]$$

where $V_{ld} = (1 - V_{hd})$ [2]

V_{hd} is the volume fraction and E_{hd} is the corresponding stiffness of the high-density material (latewood and fibre caps of vascular bundles, respectively), while V_{ld} is the volume fraction and E_{ld} is the corresponding stiffness of the low-density material (earlywood, parenchyma). There are two possible mechanisms

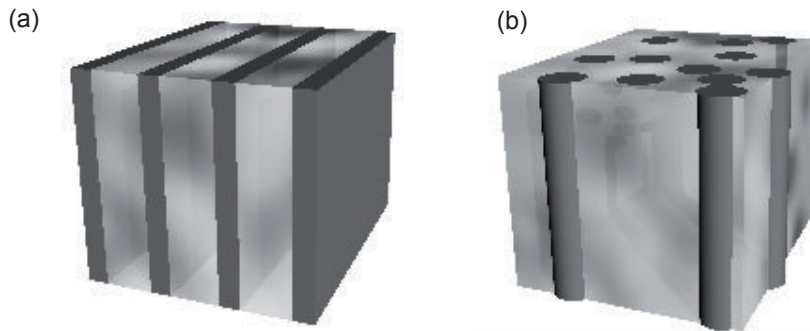


FIGURE 3: schematics of laminated composite (wood) and fibre reinforce composite (palm). Light gray portions depict earlywood (a) and parenchymatous tissue (b); dark gray areas depict latewood (a) and vascular bundles (b), respectively.

to increase $E_{composite}$, either the proportion of the high-density material can be increased or the stiffness of the materials can be increased by increasing their density. Both mechanisms can be observed in trees as the volume fraction of latewood (V_{hd}) may be increased as well as E_{hd} and/or E_{ld} . In palms, V_{hd} remains constant due to the lack of secondary growth. An increase in $E_{composite}$ can be achieved by increasing density, hence stiffness of the materials (E_{hd} and/or E_{ld}) only.

It is noteworthy that, for both trees and palms, an increase in density to optimise the mechanical stability is cost-intensive by means of additional synthesis of material and increases the own-weight. Moreover, other important functions of the material such as the water-transport are repressed by a lower porosity due to higher density. Hence, the density of the plant material needs to be balanced for an optimised growth of the organism. However, plants manifest various density-neutral parameters to increase the stiffness at the ultrastructural and biochemical level which are discussed in the following.

Microscopic Level (cell structure)

Zooming further into the macroscopic structures reveals an assembly of porous and fibrous elements (Figure 2) which are described with a particular focus on the main load bearing elements. Hereby, in analogy to fibre composites the aspect ratio of the plant fibres is a crucial parameter of cell structure. The final length of a fibre is strongly dependent on the length of the meristematic initials. Derived from the cambium, subsequent elongation of wood cells is not higher than $\sim 10\%$ in conifers (Brändström, 2001), in dicotyledonous trees up to a two-fold increase in length was reported (Ridoutt & Sands, 1993). In the case of oil palms, Kahlil et al. (2008) reported fibres five times longer than the cambium initials they were derived from.

The dominating cell type of conifer xylem, the tracheids (90 – 95 %), are $\sim 10 - 50 \mu\text{m}$ wide and up to $\sim 4 - 5 \text{ mm}$ long. Their geometry is not only influenced by the particular position in the tree ring (Figure 2a, cross section), but also by the location in the tree. Tracheids of juvenile wood differ both in width and length from adult cells: Brändström (2001) reported in an excellent review article about a fibre length of 1.3 – 2.7 mm for juvenile and 2.8 – 4.3 mm for adult cells of Norway spruce. The width of juvenile wood cells ranges from 15.0 – 28.5 μm and that of adult wood cells from 29.3 – 39.7 μm . These datasets point to a rather constant aspect ratio of ~ 100 . Compared to the tracheid geometry in conifers, the fibre tracheids and libriform fibres of dicotyledonous trees are shorter with a length of 0.5 – 1.5 mm. Considering their widths, ranging from 10 – 30 μm (Bodig & Jayne, 1993), again an aspect ratio of ~ 100 is a rough estimate. Analogous to conifers, the fibre geometry is dependent on the particular location in the tree (e. g. Bonham & Barnett, 2001; Ridoutt & Sands, 1993).

In contrast to the xylem of trees which is composed mainly of dead cells, most of the cells (not only parenchyma cells) in palm trunks remain alive throughout the entire life time of the plant (Rich, 1987a). The anatomy of vascular bundles with phloem, xylem and fibre cap varies with the specific function and location in the trunk (Tomlinson, 1990; Waterhouse and Quinn, 1978). In *Washingtonia robusta*, bundles with uniformly thick-walled cells can be differentiated from bundles where the thickness of the fibre cell walls is variable (Rueggeberg et al., 2008). The former type, shown in Figure 2c, is the almost exclusive type in the central cylinder, the latter one is dominant in the subcortical zone of the central cylinder. The available data describing fibre geometries are sparse. Khalil et al. (2008) studied fibres of Malaysian oil palm and reported lengths of 0.66 mm and diameters

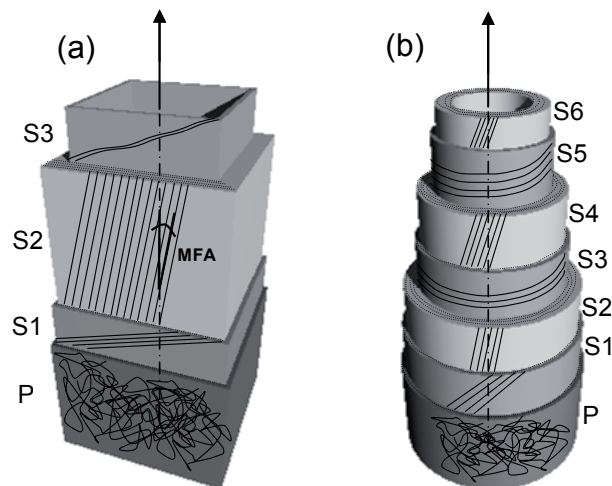


FIGURE 4: Schematic drawing of the cell wall organisation in (a) trees; and (b) a monocotyledonous plant (bamboo; after Parameswaran & Liese, 1976). Black lines indicate orientation of cellulose microfibrils.

of 16.6 μm , resulting in an aspect ratio of ~ 40 which is much lower when compared to tree fibres.

Ultrastructural Level (cell wall structure)

Plant cell walls consist of different layers, which vary in thickness and are characterised by both their specific biochemical composition and the orientation of the cellulose microfibrils (see section below). Cells in a tissue are glued together by the middle lamella. The primary cell wall is laid down during the growing phase of the cell, giving mechanical support whilst allowing the expansion of the cell. At the completion of growth, a much thicker and more rigid secondary cell wall is deposited, which represents the main mechanically supportive element of the plant cell wall. The schematics in Figure 4 show the organisation of the cell wall with primary and secondary wall of (a) trees and (b) palms.

In conifers and dicotyledonous trees, the secondary cell wall is usually composed of three layers (S1-S3), with a predominance of the S2 layer ($\sim 80\%$ of the whole cell wall). Hence, composition and structure of this cell wall layer set up to a large extent the mechanical properties of the whole cell wall. The fibre cells of the secondary xylem die after the completion of cell wall synthesis including lignification. By contrast, the fibre cells of the monocotyledonous palms stay alive throughout the life time of the plant (Tomlinson, 2006). While ageing, cell wall thickness is continuously increased as consecutive secondary cell wall layers are deposited which results in a multilamellar structure of the secondary wall. For rattans (climbing palms) and bamboo it has been shown that thick and thin layers alternate (Bhat et al., 1990; Liese, 1987; Parameswaran & Liese, 1976). The continuous deposition of additional cell wall layers

during ontogeny leads to a considerable increase in tissue density and hence, tissue stiffness (see also section on Macroscopic Level). In the absence of secondary thickening growth, the deposition of additional stiffening material within a given trunk is the only way to increase flexural stiffness of the trunk during height growth.

Biochemical Level (cell wall composition)

In the plant cell wall, cellulose chains are aggregated to stiff microfibrils of 2 – 4 nm diameter and several micrometres in length, which are embedded in a rather compliant matrix of hemicelluloses, pectins and /or lignins (Fahlen & Salmén, 2005; Hepworth & Vincent, 1998; Kerr & Goring, 1977; Salmén & Olsson, 1998). Hereby, the volume fraction of the different polymers varies considerably, depending on the particular cell wall layer (Fengel & Wegener, 1989). Due to the very high tensile stiffness of cellulose compared to that of hemicelluloses and lignin (Bergander & Salmén, 2002; Salmén, 2004), the cellulose fibrils are the main load bearing elements within the cell wall. Consequently, their structural arrangement within the cell wall layers has a prevalent influence on the mechanical properties (e.g. stiffness and toughness). The cellulose fibrils are less orientated in the primary cell wall, allowing for cell expansion and providing the cell with sufficient resistance (against osmotic pressure). The fibrils run parallel to each other within the secondary cell wall. Their inclination to the longitudinal axis of the cell is termed microfibril angle and varies considerably in the different cell wall layers (Figure 4). Both biochemical composition and cellulose orientation influence the mechanical properties of the cell wall.

For wood, numerous datasets of microfibril angles of the predominant S2 layer in different tissue types exist. A comprehensive review of microfibril angles in wood and appropriate experimental methods was given by Barnett and Bonham (2004). Comparisons with data from mechanical tests revealed a strong correlation between microfibril angle and stiffness. Barnett and Bonham found microfibril angles of 5 – 10° for normal adult wood in conifers and dicotyledonous trees. The axial cell wall stiffness in tension was reported to be 20 – 35 GPa (Burgert et al., 2005; Eder et al., 2008; Mott et al., 2002). In juvenile wood, microfibril angles of ~ 15 – 25° and a corresponding cell wall stiffness of 9 GPa were found (Burgert et al., 2007)

Investigations by various groups on the microfibril orientation of different palm species have revealed rather high microfibril angles. For example, Abasolo et al. (1999) observed a wide range of angles (23 – 34°) for fibre cells across the trunks of the climbing palm (rattan) *Calamus merrillii* [Becc.]. Bhat et al. (1990) observed angles of ~ 40° for the thick cell wall layers of fibre cells for *Calamus* species by transmission electron microscopy (TEM). In the arborescent Mexican Fanpalm (*Washingtonia robusta*), high resolution measurements of microfibril orientation across individual fibre caps revealed angles between 15° and 40°. Despite the considerable high scattering of values, no trend in microfibril orientation was visible. Corresponding microtensile tests, performed on thin

consecutive fibre strips of these fibre caps revealed values for the cell wall stiffness between 450 MPa and 2 GPa (Rueggeberg et al., 2008). These values are in the same order of magnitude compared to thin wood tissue slices with very high microfibril angles (Burgert et al., 2004; Reiterer et al., 1999).

The curves in Figure 5a summarise the above described findings concerning the correlation of microfibril angle and mechanical properties in schematic drawings of the cell wall response. When the microfibrils are aligned almost parallel to the fibre axis (upper cylinder in Figure 5a), axial loads are directly transferred to the very stiff cellulose fibrils. The shape of the corresponding stress-strain curve reveals high stiffness and rather low extensibility. The amount of stress transferred to the matrix increases with increasing microfibril angle. In this case, the mechanical properties of the softer matrix contribute more to the overall stiffness. This is seen in the stress-strain curves by the lower slope of the initial, elastic region. The yield point indicates the point when the critical shear stress of the matrix is reached. Beyond the yield point, plastic flow occurs with the cellulose fibrils gliding past each other (Fratzl et al., 2004a; Fratzl et al., 2004b; Keckes et al., 2003; Köhler & Spatz, 2002; Page & El-Hosseiny, 1983). For higher microfibril angles the yield point is shifted towards lower stress levels. Yet, the cell wall gains in extensibility and toughness when loaded in tension (Cave, 1969; Lichtenegger et al., 1999; Reiterer et al., 1999).

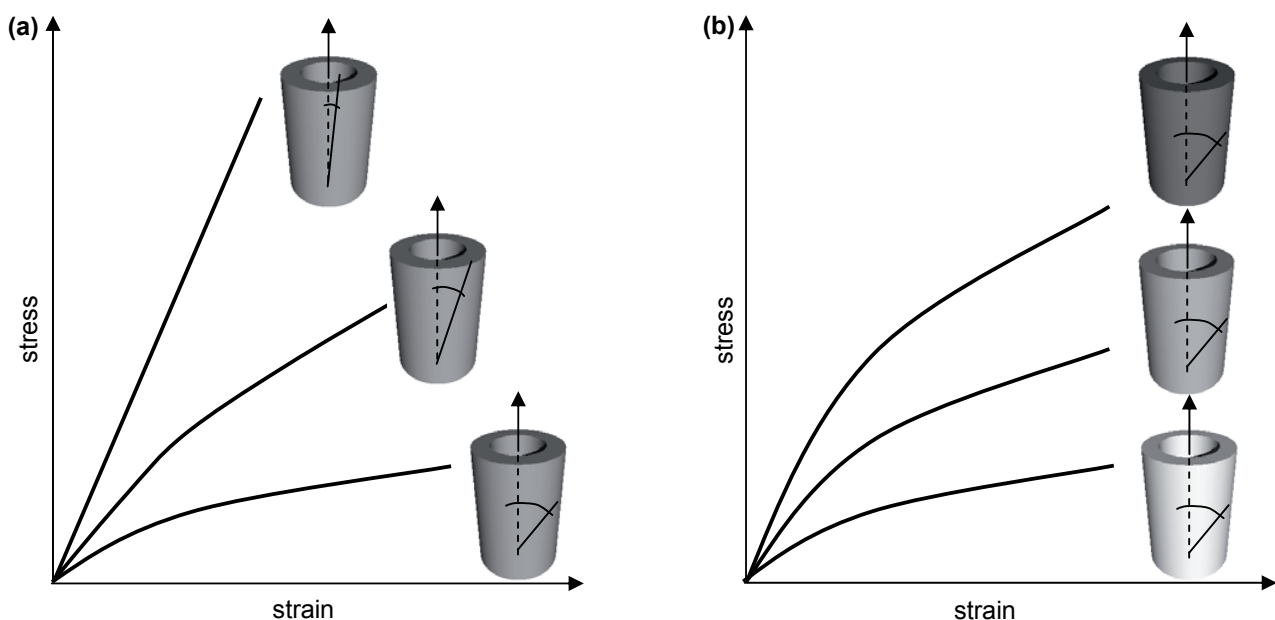


FIGURE 5: (a) Schematic stress-strain curves of cell walls which show the influence of the microfibril orientation, which is indicated in the cylindric cells. (b) Stress-strain curves at a high microfibril angle, exhibiting different levels of lignification, which are indicated by the grey levels of the cells.

The investigations on the fibre caps of *Washingtonia robusta* have revealed variations in cell wall stiffness which did not correlate with the microfibril orientation but with the degree of lignification. The model suggested by Fratzl et al. (2004a; 2004b) is also appropriate to interpret this relationship. As already described for wood cell walls, at high microfibril angles the axial cell wall stiffness is strongly influenced by the shear modulus of the matrix. It is very likely that lignification can increase the shear modulus of the matrix and, hence, the axial stiffness of the cell wall. This is shown in Figure 5b for different levels of lignification. In many palm species the entire stem (both vascular bundles and parenchyma) becomes lignified during ageing which results in an increase in cell wall stiffness.

Both experimental results and theoretical considerations on trees and palms point to an adjustment of the mechanical properties of cell walls by at least two alternative concepts: (i) stiffness and toughness can be adjusted by the orientation of the cellulose microfibrils; and (ii) given that microfibril angles are high, stiffness can be tuned by the level of lignification. The former concept seems to be predominant in trees whereas the latter concept appears to be the favoured strategy converted in palms.

Concluding remarks

In all arborescent plants, the progressive height growth continuously increases the mechanical stresses at the periphery of the base when the stems are bent under wind loads. The crucial factor, flexural stiffness ($E \cdot I$; see equation in Figure 1) can be adjusted by either increasing the elastic modulus of the material or by increasing the second moment of area due to secondary growth, or by changing both parameters simultaneously. The comparison of structural features and mechanical properties of trees and palms at all levels of hierarchy revealed the close interrelation between a given growth strategy and required structural adaptation processes to meet the resulting mechanical requirements.

Trees, either softwoods or hardwoods, are able to adjust both parameters during their ontogeny. The secondary growth results in a geometrical adaptation by increasing the second moment of area. A high stiffness of the wood at the periphery of the base is either achieved at the tissue/cell level by means of a high tissue density (high cell wall fraction), at the biochemical level by a small cellulose microfibril angle and a sufficient lignification or by adaptations at both levels of hierarchy. This exceptionally high structural and geometrical flexibility of the organisms combined with a highly efficient water transport strategy are the

bases for the tremendous heights trees can reach.

The palms, lacking secondary growth, are not able to form new material along the stem. Hence, required adaptation processes during ontogeny are restricted to the already-built material. This makes it essential to keep the parenchyma cells and the sclerenchymatous fibres alive. Ongoing formation of new cell wall layers and the lignification of existing cell walls result in a further accumulation of material and an increase of its elastic modulus. However, since these adaptation processes are restricted to a given stem diameter, palms are limited by their growth strategy to increase flexural stiffness compared to trees. This could be one important reason why palms do not reach the exceptional heights to which trees grow.

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