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Wood and the Activity of Dead Tissue

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Wood is a prototypical biological material, which adapts to mechanical requirements. The microarchitecture of cellulose fibrils determines the mechanical properties of woody materials, as well as their actuation properties, based on absorption and desorption of water. Herein it is argued that cellulose fiber orientation corresponds to an analog code that determines the response of wood to humidity as an active material. Examples for the harvesting of wood activity, as well as bioinspiration, are given.

1. Introduction

One of the hallmarks of wood and of most biological materials is the intrinsic variability of their physical properties. There is a deep history of human usage of this variability of wood from fire hardened stiff wooden sticks and flexible bows, to wooden planks or crocked timber for shipbuilding or large-size wooden logs in architecture. Engineering materials in contrast, such as polymers, steel, or ceramics, are characterized by well-defined specifications and properties that allow for material selection for specific applications in standardized industrial processes,[1] which provides stability, predictability, and reliability to facilitate product design processes. Based on this principle, the intrinsic variability and susceptibility of wood and other biobased materials might be considered a serious drawback. This progress report reverses the standpoint by considering the activity of wood and wood-based materials as an opportunity rather than a weakness. The perspectives taken are historical (Section 2) and biological (Section 3); materials development is discussed based on harvesting the activity of wood (Section 4) and on drawing inspiration from it (Section 5).

Traditional engineering approaches are based on the perception that passive and inert matter needs to be transformed into technology with the aid of motors by the external input of fuel-based and/or electric energy and the input of human or artificial intelligence (information). This general approach is increasingly challenged by the advance of smart or responsive materials, which change their properties, such as color, form, dimensions, or conductivity in response to the environment but without direct external control. Many of these materials are inspired by biology.[2,3] To respond in an appropriate way to the environment, the material structure often requires structural complexity over several length scales.[3] Processes for successful synthesis of responsive materials exist;[4] however, the application of adaptive materials that can actively change their properties upon changing needs is still in its infancy.

Natural materials are for the most part responsive and adaptive to the environment, and wood is a prime example. Indeed, wood and other plant tissues with secondary cell walls are prototypic examples that adapt to their environment. Although being part of organisms they are at the same time material and consist to a large extent of nonliving cells. They immediately react upon environmental stimuli and adapt to injuries or changing loading conditions by growth and are able to synthesize material with a wide range of properties fulfilling the new needs of the organism. Prominent examples would be the formation of reaction wood, which generates stresses to upright leaning stems or branches.[5] The adaptation occurs on several length scales, ranging from that of the biomolecular composition to the cell wall structure, cell shape, growth ring thickness, and up to the overall organism geometry. Many natural materials such as wood show this adaptation capability as they carry the information about the interaction with the environment within their internal structure. Disciplines such as dendrochronology use the storage/representation of climatic conditions in growth rings to date wood pieces and historic artifacts and to locate their origin.[6] A consequence of the high adaptability to changing environments is that the properties of this important renewable resource are highly variable and are thus not "normalized" such as standard engineering materials or synthetically developed smart materials. Even long time after harvest, when all metabolic processes have stopped, wood is still an active material that changes shape and properties upon environmental stimuli.

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It has been a long-lasting wood engineering tradition to "silence" the activity of wood. Already in ancient Egypt and Greece unwanted movements were prevented by crosswise gluing thin wood strips or planks. Later this practice fell in oblivion and was rediscovered in the mid of the 19th century with the first industrial production processes of plywood, which becomes more dimensionally stable and less anisotropic by a crosswise assembly of wood veneers. In each geometrical direction of the plywood, the high-dimensional stability of veneer layers in their longitudinal direction (orientation of fibers) impedes the by far larger dimensional changes upon swelling and shrinking in the transverse direction of conjoined veneer layers. The gain in dimensional stability is at the cost of mechanical performance in the main loading direction, but in general a more homogenous, determined, and reliable wood product is produced.

Instead of silencing the activity of wood, recent engineering approaches are coming back to taking advantage of it, in architecture, in wood-based smart composites or as inspiration for soft robotic systems. Our goal here is to advocate a change in paradigm, increasingly working with the intrinsic activity of materials rather than against them.

2. Active Materials: Definition and Historical Perspective

Focusing on wood and its inner material activity has to be regarded as an unconventional view of modern technology, since a material is generally regarded as mere substance being a passive carrier of informed components and forces that make special functions or activities possible. Whereas in antiquity wood was considered an active material, in modern times activity is usually externally added and directed toward a passive material substrate, be it in the case of "living" thoughts stored as material "dead" letters on paper, or be it in the case of a tool or a machine by energy that must be supplied to activate the material device against its own inertia.

This fundamental antagonism between material and activity is omnipresent within the dichotomies of digital versus material, operative code versus material carrier and it exemplifies the classical philosophical dichotomy of mind and matter: For the early modern philosopher René Descartes, the sphere of *res cogitans* of human thought is opposed to *res extensa* of physical and material reality.[7] This classical distinction between living spirit and dead matter refers not only to an epistemological model but also to a fundamental technological principle that established and materialized this epistemology in our technology in a radical way.[8] Material in this sense is thought as a passive, rigid, and reliable means that executes externally added structured activity: This is the basis of modern machinery and this is why all internal material activity that could disturb the functioning of machine gears is excluded.

In Vitruvius's *Ten Books of Architecture*, a machine is still "a combination of timbers (materia) fastened together, chiefly efficacious in moving great weights."[9] The many types of wood are essential for construction and material for machines such as hoisting machines, engines for raising water, water mills, water screws, or catapults. And even more: since the Greek concept ὕλη (hylé) that originally (e.g., in Homer) meant wood (construction wood, firewood) was taken by Aristotle in the more general sense of matter and finally translated into Latin

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as “materia” or “materies” (for both wood and matter), in an etymological sense wood can be seen as the paradigm of matter and material in general.

This older history of wood as matter makes evident that the idea of passive materials is quite recent. Since ancient history a much larger scope of active and passive material properties was exploited. Within this context wood plays an extraordinary role since its inner activity as well as its rigidity in terms of strong beams were long since known and widely used. In the case of ancient shipbuilding and barreling with the swelling of wood, wood carving, turning, planing, and tilling, and the wear of wooden teeth of gear wheels the activity of wood was productively applied. Timber was used as one of the most important construction materials. As a consequence, large deforestation occurred in the Mediterranean area and the usage as fuel was restricted for saving construction material.[10]

Above all, since industrialization wood was widely replaced by iron, steel, and concrete thus taking advantage of their rigid and passive character. The mill as the paradigmatic wooden machine until the 18th century and the steam engine as the emblematic machine of industrialization show the material shift from wood to metal mechanisms: The manufactured wood gear wheels depended on a constant process of fitness, abrasion, and finally dysfunction. Therefore, the production of identical components for machines as exchangeable elements changed to metal. In gun production, Honoré Blanc was one of the pioneers for the production of modular standardized elements, identical in terms of position, form, and dimension.[11] The fundamental basis of these identical elements consists primarily in rigid, passive, and therefore reliable materials: metal turned out to be the decisive medium of precision and normalization. The comparison of ancient and early modern textbooks on machines such as Heron[12] or Ramelli[13] with 19th century textbooks on machinery design such as Reuleaux[14] makes this shift from wood to iron and steel quite obvious.

But wood was not only replaced due to its material activity in machinery but also in architecture: iron is celebrated in building construction as a material that does not contain any formal constraints. In contrast to stone or wood where the material structure defines the possible shape as block or beam, using iron allows great freedom in the construction process.[15] Thus, being a completely malleable material iron is seen as passive carrier that makes the implementation of any preconceived form possible: it can be taken as a physical representation of the mind–matter relation. In this way, wood of half-timbered building construction was widely replaced by metal structures or concrete.

The reinvention of plywood in the 19th century makes this shift to passive materials in mass production evident. The active wood layers are oriented against each other for antagonistically neutralizing the activity and thus generating a stable and passive material: This shows how materials are conceived and finally designed as essentially passive. In the case of wood, the obvious inner activity is strategically silenced. Ancient bending of wood steves for barrels by heat and humidity[16] was used for bentwood furniture mass production of Thonet chairs.[17] The mind and matter relation—implicit in construction processes of implementing preconceived ideas into shape or function—requires the most malleable and passive material possible that does not disturb the building process. Thus, the very structure and the activity that is realized within the artifact are externally added. This dichotomy of energy and information versus material defines modern technology in all its forms, and it becomes especially visible in cybernetic and digitalized robotic machines that not only need external energy supply but also information input for performing the desired functions.

The shift to electrical energy and subsequently to electrical information technology had enormous consequences for the relationship of matter, energy, and information and their mutual interplay and emphasized the gap between passive material and activity. As a result, the symbolic control operations were separated from the mechanical operations of the working machinery in its classical cybernetic manner. To put it in Norbert Wiener’s words: “Information is information: not matter or energy.”[18] The physical movement is produced by a motor fed by the input of external electrical energy, whereas the material is considered the neutral carrier for transmitting both external energy and external information. Classical information theory[19] exactly corresponds this idea when there is a sender and a receiver: the receiver is some sort of neutral, passive, and empty box that depends completely on the transmission of the external electrical code. Thus, the very concept of material is reshaped in information theory: material as a substance empty of energy, information, or activity.

Looking at woody material, one easily recognizes that—in a paradigmatic way for any kind of material—it does not obey this idea of neutral matter. Wood shows an intrinsic activity triggered by humidity, which changes the fundamental relationship of matter, energy, and information in a decisive way: in seed awns one can perceive strong active torsion by drying or elongation through humidity as a reversible operation.[20–22] This plant device acts according to its inner structure as a sort of intrinsically coded matter. No external cable of energy or code is necessary to perform this activity. This situation makes a completely different version of relating matter, energy, and information visible (**Figure 1**). All the three are integrated in one and the same material structure and no longer separated by the fundamental mind and matter dichotomy. This different and necessarily triple relationship is based on material that is no longer passive, rigid, and dry, but a dynamic structure that takes its kinetic energy from the humidity changes of its environment. In this natural material, electricity is replaced by the activity of water; the code of the movement is also not transmitted from outside, it is inherent within the structure of the material, similar to the gears of a classical machine. Wood presents in an exemplary fashion an integrated unity where the material generates an energetic potential, contains in its geometry its inherent code, and is the machine that performs its very function.

The shift from passive to active material intertwines matter and information as mechanical hardware that stores, retains, and eventually releases the potential energy: it is the intrinsic code of the materials structure that defines the proper activity. Thus, the material’s structure is the geometric code of its operation, the sensor for transforming the changing humidity conditions of the environment into signals, and the motor of the activity. This integrated machine goes far beyond our mechanical and informational machines. There is no cybernetic separation of information processing from the mechanical work, this

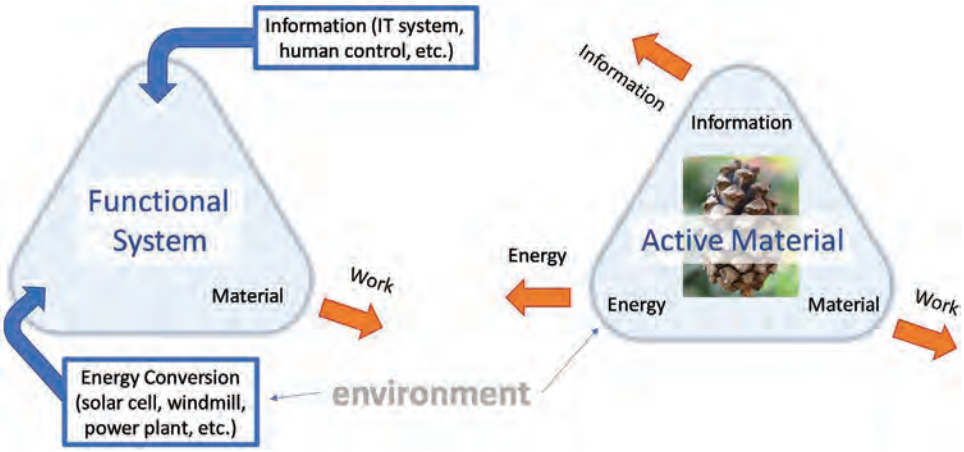

Figure 1. Removing the dichotomy between information/energy and material in an active material: A functional system (left), such as a robotic arm, is based on passive material (e.g., steel or aluminum) that is activated through the import of information from an IT-system (e.g., a digital processor) and through the import of energy (previously converted from environmental or fossil sources). An active material (right) is a functional system in its own right. It is not just a passive material but carries information for the function (such as the cellulose fiber arrangement that encodes the opening movement of the pine cone) and takes the required energy directly from the environment (such as humidity changes to actuate the pine cone scales). The orange arrows symbolize potential outputs (e.g., work). Active materials may also convert environmental gradients into information (and, thus, work as sensors) or even into (electrical) energy, for example, by coupling to a piezo-element.[23]

machine is integrated, it is active matter: wood as biological material is a machine.[24] This new notion of active matter and active materials changes the classical understanding of material. The active material structures as being paradigmatically described in the following sections, represent from a technical point of view a new integrated system of material, energy, and information which can be understood and studied as a new type of hardware. Wood is today perhaps in the process of becoming the *materia* par excellence of the future—as it was in ancient times—the paradigmatic model for active material that makes a new art of building and engineering necessary and possible and opens up a new relationship between technology and nature.

3. Structure of Plant Cell Walls and the Storage of Information

Wood is known to adapt its structure to counterbalance asymmetric forces, such as side winds or gravity on branches. Plants also grow seed capsules that open on demand and move to help disseminating the seeds. All this implies a wide local heterogeneity of the wood structure that provides functionality to the tree even when the wood tissue is not anymore living. The structure itself can be finely tuned on various length scale. The main macromolecules cellulose, hemicelluloses, and lignin are assembled into different cell wall patterns with pronounced effects on mechanical and swelling properties. Cell wall thicknesses ranging from 0.5 to 10 µm effect water transport, local densities, and mechanics and the arrangement of different cell types into tissues at the mm-scale creates laminated macroscopic material with various densities and a wide range of properties.

All hierarchical levels of the wood structure (**Figure 2**) also contribute to its activity.[25] Particularly important is the wood cell wall that is able to provide actuation through the absorption of water.[26] Cellulose fiber orientations in the cell wall convert isotropic swelling into a directed movement. Structures at the next higher level, e.g., in the cell lumina are discussed next to provide additional activity in reaction wood. Finally, macroscopic tree shapes, such as trunk cross sections, are known to adapt to challenging environmental conditions through adaptive growth.[27]

3.1. Cell Wall Architecture Programmed by Living Cells for Function after Death

Plant cells are characterized by the presence of cell walls. Growing cells are encased by thin, strong, and pliant primary cell walls, which provide sufficient mechanical stability while simultaneously allowing cell expansion. Primary cell walls are mainly composed of cellulose, hemicelluloses, and pectins, which dynamically change during development by expansion, changes in water content, and synthesis.[33] Cell shape and geometry is determined through the complex interplay of turgor pressure, mechanical anisotropy, local variations in wall properties, different growth rates, and external restrictions, e.g., by neighboring cells.[34] After cessation of growth, many cells start to synthesize secondary cell walls, especially those with mechanically relevant functions. Secondary cell walls are much thicker and more rigid than primary walls and are important building blocks for mechanically stable plant structures such as stems, branches, roots, or seed pods. They contribute to a large proportion of the available plant biomass and as such they are relevant for applications and human use with bamboo and wood being prominent examples. A drawback in application is the inherently large variability in material properties since it complicates predictions related to material performance. If one takes the "materials" perspective of a sessile plant it becomes clear that the large variability is simply a consequence of resource limitation translated to the organisms need to fulfill a function in a given environment. Therefore, exploring the

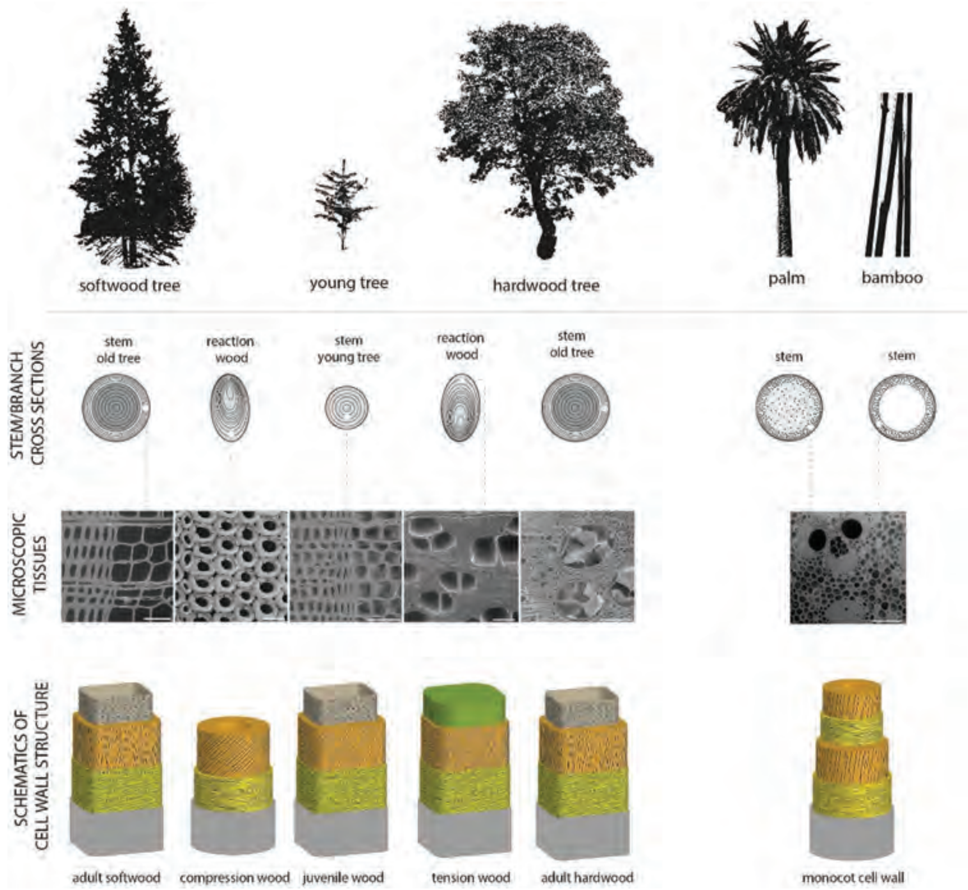

Figure 2. Structure of arboreal plants. Cartoons of stem and branch cross sections with year rings as black lines for softwood and hardwood trees. Dark gray area in the middle of old stems indicates heartwood, eccentric cross sections depict compression wood for softwoods and tension wood for hardwoods. Dark dots in the cross sections of palm and bamboo indicate the distribution of vascular bundles. Microscopic tissues from left to right: adult spruce wood (bar 50 µm), spruce compression wood (bar 20 µm), juvenile spruce wood (bar 50 µm), poplar tension wood (50 µm), adult oak wood showing vessels with thylosis (bar 200 µm), and vascular bundle of bamboo (bar 200 µm). Last row showing schematics of cell wall structures. Light gray indicates the compound middle lamella (0.5–1.5 µm) and primary cell wall (≈0.1 µm), yellow S1 layer with a thickness of 0.1–0.35 µm and a cellulose microfibril angle of 60°–80°, orange S2 layer, 1–10 µm thick and a cellulose microfibril angle of ≈10° for normal adult wood and monocots, 30°–55° for compression wood, ≈15°–30° for juvenile wood, ≈35° for tension wood; inner light gray layer shows the 0.5–1.1 µm thin S3 layer with a cellulose orientation of 60°–90°; the green G-layer in tension wood fibers can fill the whole lumen and the cellulose fibrils are oriented along the longitudinal cell axis. Values for cell wall thicknesses and cellulose angles from refs. [28,29–32].

interactions between plant material and environment inside and outside the organism, contributes substantially to a deeper understanding of the natural material and might pave the way to an efficient and at the same time sustainable material use.

Although trees and arboreal monocots, such as bamboo and palm trees (Figure 2), have to cope with similar loading conditions, there are remarkable differences in the way the problem is solved. While bamboo grows a hollow and lightweight tube, trees have a solid core and must, therefore cope with a much higher weight at identical dimensions of the stem. This is the consequence of the fact that trees are capable of secondary growth, which makes the stem grow thicker over time, whereas bamboo or palm trees, without a cambium layer, can only grow taller. This means that trees have a much higher capacity of geometrical adaptation and can react to bending forces with an increased secondary wood growth, which increases the moment of inertia.[35] This may also be related to the generally longer lifetime of trees as compared to monocotyledons (e.g., bamboo or palms). In consequences, trees can afford to have a relatively fast cell death (2–3 weeks for earlywood cells and ≈2 months for latewood cells)[36] as information can be incorporated in cell walls of newly formed tissues. On the contrary, bamboo or palm trees can react to changing mechanical loading conditions exclusively with the already existing and still living cells in the stem and increase the thickness of their cell walls to cope with increasing mechanical forces.[37] This means that they need to be able to incorporate information in their cell walls over a much longer time span compared to wood fibers. While this may explain, why trees do not need to keep newly formed fibers alive, it does not elucidate why fibers in trees have to die so quickly. For water conducting elements like vessels or earlywood tracheids, a by far more efficient water transport in the remaining hollow tubes after cell death is a strong argument, however this is not of particular relevance for fibers. It appears more plausible that the energy efficiency of trees as long-lasting organisms is a decisive driving force. In the wood tissue of a stem only a comparably small fraction of so-called parenchyma cells remain alive. Since most of them are located in the wood rays, which are arranged like spokes in the radial direction of the stem, they connect the outer living part (cambium, young phloem) with the almost entirely dead inner part. These living parenchyma cells are mainly responsible for storage and radial transport,[38] which provides trees still access and control of the inner wood tissues. Hence, trees manage to reduce the number of living cells in the stem to a minimum, which decreases the energy demand to retain cell metabolism. Since newly formed cells can cover the required information incorporation, older tissues do not need to retain this capability.

3.2. Structure and Properties of Wood Cells and Adaptation to Environmental Conditions

The growth of plants is not only a developmental process, which increases the size of the plant. Simultaneously, growth allows the adjustment of the organism to changing needs. Since remodeling processes are absent, the plant material can be seen as a mirror of developmental and environmental conditions during a plant's life and the material serves as an analogue long-term storage system for information related to changes in environmental conditions, both inside and outside the plant.

Visible with the naked eye, tree rings reflect climatic conditions of growth seasons. Ideal growing conditions (light, water, nutrients, temperatures, length of growth season) lead to increased growth, whereas a "bad year" will result in reduced growth and/or even in the formation of "abnormal" rings.[6] The discipline of dendrochronology uses tree ring patterns as year-by-year records, which allows dating of wood to the years of formation. The determination of precise ages and origins of wood and artifacts is possible, solely based on the growth ring pattern.[6] Years with extreme weather conditions facilitate the dating process. In a recent study, the accuracy of dating growth rings has been confirmed by a global study, comprising dendrochronological samples from five continents. Tree rings formed from 770 to 780 and 990 to 998 CE were radiocarbon dated. A higher ^{14}C content is globally detectable in the rings formed in 774 and 993 due to cosmogenic radiocarbon events and it has been shown that all previously performed dating based on tree ring patterns was correct.[39]

However, wood does not only carry information related to past climatic conditions. Exposure to mechanical challenges, such as a frequent side wind for a slim stem in young plants or a landslide, affect the pattern of cell formation. Plants possess a range of sensors which induce reactions to changing mechanical conditions. Small inclinations are, e.g., detected by statoliths a type of gravisensor that allows a fast response of plants to deviations from the vertical direction.[40] Various mechanosensors in meristematic cells trigger cell responses which change the expression of transcription factors resulting in altered growth rates. As a consequence, the distribution of mechanical loads changes in the plant. These feedback loops involve multiple complex processes, are only partly understood and modeling plays an important role for a deeper understanding.[41]

As a consequence, plant materials record the whole history of growth. For instance, growth rings are wider in young trees and wood density is typically lower (Figure 2). Strong wind loads can result in reaction wood formation (see Section 3.4). But not only the growth rings thickness is able to adapt to these challenges. Additional active stresses can also be generated in the cells to counteract forces from the environment through changes in cell geometry and the internal structure of the secondary cell wall.

It is obvious that the macro- and microscopic density of wood is relevant for mechanical stability of the organism and determines mechanical properties of wood material to a large extent, which is reflected in the availability of a wide range of wood material properties. In general, the density is strongly determined by the growth ring formation and pattern, leading to a combination of cell arrangements with cells of different geometries and wall thicknesses (Figure 2, microscopy images). When normalizing for density some of the specific properties of "normal wood," particularly along the fiber direction, are very similar for a wide range of species (**Figure 3**).

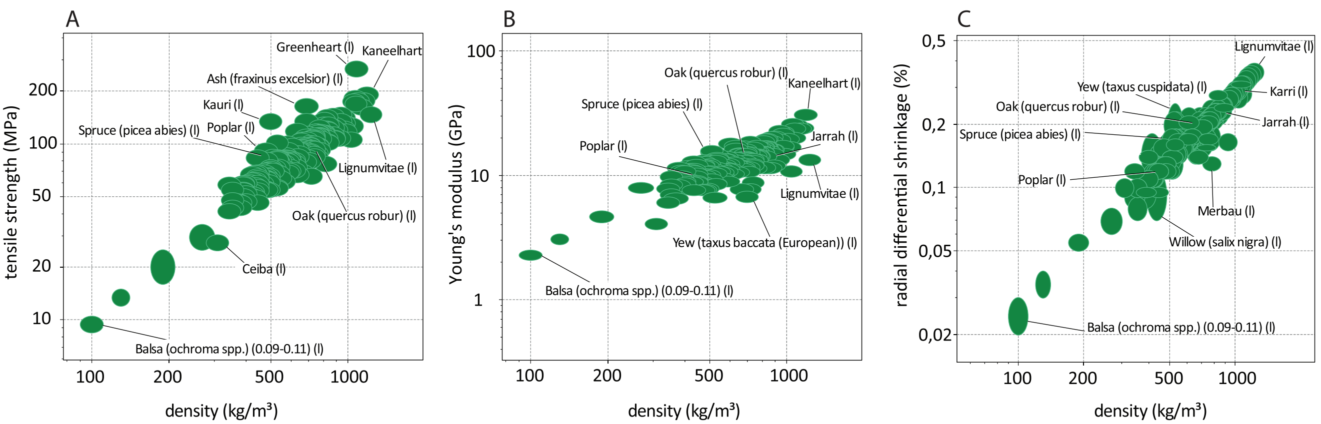

Figure 3. Specific mechanical properties and radial shrinkage of "normal" macroscopic wood of various tree species. A) Tensile strength along the fiber direction plotted versus density, B) Young's modulus along the fiber direction plotted versus density, and C) radial differential shrinkage (dimensional change upon 1% change in wood moisture content) plotted versus density. For the location of wood in materials properties charts with respect to other natural materials and the effect of loading directions, we refer to ref. [42]. A–C) Prepared using CES EduPack 2019, Granta Design Limited, Cambridge, UK 2019.[43]

However, wood material properties can be drastically different without any effect on density if the cellulose orientation in secondary cell walls changes. Secondary wood cell walls are usually composed of three layers, S1, S2, and S3 with the S2 layer being the thickest and most dominant (Figure 2, orange layers in cartoons). The stiff (≈130 GPa)[44] cellulose fibrils (indicated by parallel black lines in the cell wall schematics of Figure 2) run approximately parallel to each other at the so-called cellulose microfibril angle (MFA) to the longitudinal axis. The fibrils are embedded in a softer matrix of hemicelluloses and lignin (20 MPa and 2 GPa in wet condition)[44] with lignin being the macromolecule which completes cell wall formation.[32] Similar to other fiber-reinforced composites, the mechanical properties strongly depend on the orientation of stiff and strong elements with respect to the loading direction. Cell walls of cells with a low MFA can reach stiffness values of ≈30 GPa when the cell is strained in tension[45] and the values go down to 0.5 GPa for cells with a MFA of ≈45° such as those found in compression wood.[29] Trees fine-tune their material properties with both density and cellulose orientation to ensure functionality. Juvenile wood of young stems and tree tops are less dense and possess a rather high MFA, providing a sufficiently flexible material to cope with loads, e.g., caused by wind.[46] As the tree grows, stiffer material at the stem periphery is needed to support the crown. The density increases and the MFA decreases. Density and MFA ensure needed flexibility and stiffness and with specific spatial arrangement even stress generation both in tension and compression is realized.[47]

3.3. Biochemical Composition and Postmortem Changes

Besides the cellulose orientation, the macromolecular composition effects the specific properties. In a recent experiment on transgenic poplars with reduced lignin content but very similar cellulose microfibril angle and crystallinity index as in wild type poplar, it has been shown that not only higher cellulose angles but also a reduced lignin content lead to a decrease in tensile stiffness.[48] In naturally grown trees, different degrees of lignification are found in reaction wood but also—very rarely—in latewood, when early and severe frost events take place and the lignification of the latewood cells is incomplete.[49] More frequently, less lignified latewood is found in trees growing at the tree line.[36] Extreme cases of woody plants are found in the arctic with tiny growth rings and almost completely missing lignification.[50]

Even though all the water conducting cells and fibers of trees are dead cells, many cell walls experience changes and incorporation of substances years after their formation. This phenomenon can be observed for the so-called "heartwood" formation[51] which frequently leads to a darker coloration of the inner stem parts (adult stem cross sections, Figure 2). Wood cells (fibers, vessels, tracheids) that had served for water transport or mechanical stability for several years in dead state are further modified in this process. The wood cell walls are impregnated or cell lumina are filled with chemical substances that can lead to a higher hydrophobicity and even toxicity to microorganisms. Furthermore, the water transport in vessels is interrupted by so-called thylosis, which are balloon-like structure that grow into the large diameter lumina (microscopy image of adult hardwood in Figure 2). This information incorporation in dead cells is only possible by cooperative processes at the tissue level. The abovementioned parenchyma cells, which kept alive in the wood body synthesize the chemical substances (so-called extractives) that impregnate the cell walls of the wood cells and those parenchyma cells that surround vessels grow as thylosis in the vessel lumina. The parenchyma cells also die during the heartwood formation, which finally results in an entirely dead inner wood core.

3.4. Reaction Wood: Structures Designed to Generate Tensile and Compressive Forces

Reaction wood formation leads frequently to asymmetric growth rings (Figure 2) with wider rings and a high density on the bottom of the leaning stem or branch for softwoods and wider rings on the top for hardwoods to generate the required forces to re-orient the particular organs. Like discussed above a change from regular wood formation to reaction wood formation comprises all levels of the hierarchical wood structure. Since the required stress generation is not based on the activity of living cells but on the active properties of the (nonliving) cell wall, the stresses need to be implemented in the cell wall during the cell differentiation process. Although the underlying mechanisms of tensile and compressive generation in reaction tissues are not fully understood yet, the crucial impact of the microfibril angle in the cell walls is widely accepted.

In terms of compression wood formation in softwoods, Yamamoto has shown that tracheids with a microfibril angle below ≈30° generate axial tensile stresses and tangential compressive stresses,[52] which is in accordance with the regular growth stress generation in trees.[35] However, tracheids taken from the compression wood region with a microfibril angle above 30° generate axial compressive stresses and tangential tensile stresses.[52] Based on the "lignin swelling hypothesis" by Boyd[53] the stresses are generated during the cell differentiation process by lignin insertion into the cell wall and hence the cellulose orientation dictates whether tensile or compressive stresses are formed in the axial direction (**Figure 4**A). If one assumes that the cell wall matrix swells, but the partially crystalline cellulose fibrils embedded into the matrix expand only elastically and very marginally, the geometrical model predicts cells to contract for $\mu < 45°$ and expand for $\mu > 45°$ in case torsion is completely impeded.[47] However, compression wood tracheids differ from regular tracheids not only in microfibril angle, but also in terms of cell geometry, secondary cell wall layer structure or lignin content.[54] These structural and chemical features may provide the compression wood tracheids with a torsional freedom that facilitates axial extension/compressive stress generation even at lower microfibril angles.

For extended axial tensile stress generation, most hardwoods form tension wood fibers, which possess a characteristic G-layer, which can be structurally very diverse, as recently investigated for tropical tree species.[57] The G-layer is an additional layer, which can fill the entire lumen of the tension wood fiber (Figure 2 tension wood microscopy image and schematics and Figure 4E) and consists in many trees of almost

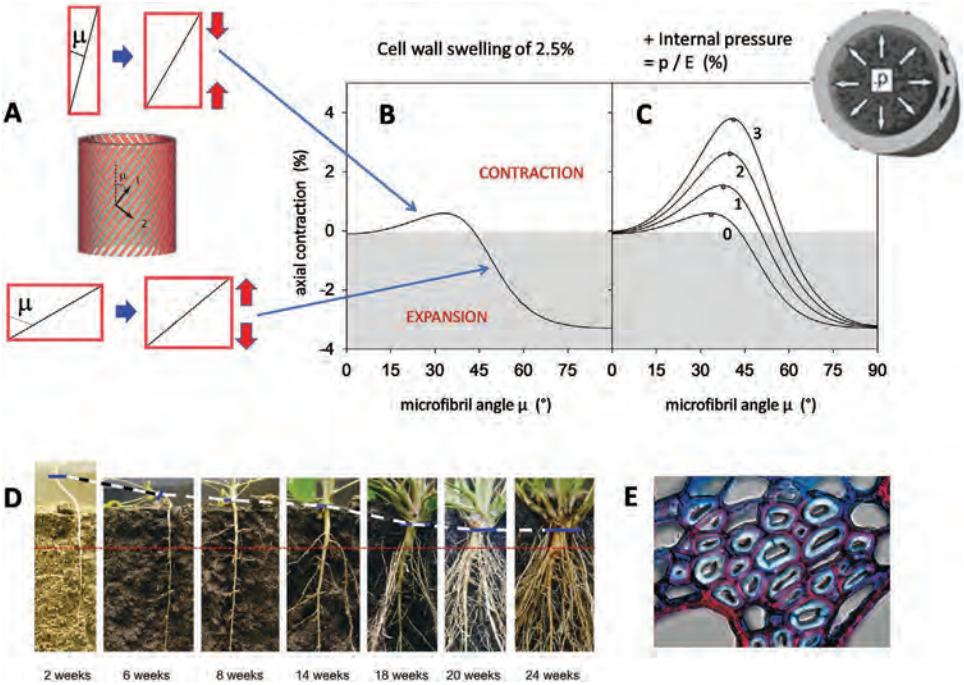

Figure 4. Tensile or compressive forces generated by cell wall swelling: A) In spruce wood, the main cell wall layer has cellulose oriented with a microfibril angle μ with respect to the cell axis. When the cell wall matrix swells (but the partially crystalline cellulose fibrils embedded into the matrix expand only elastically), the cell contracts for $\mu < 45°$ and expands for $\mu > 45°$ (A and B). B) The axial contraction was calculated for a matrix swelling of 2.5%.[55] C) In tension wood of many hardwoods (e.g., poplar), the cell lumen is filled with a strongly swellable cellulose gel (G-layer) that may lead to internal pressure that enhances the contraction of the cell. The graph in (C) shows the contraction for several values of the internal pressure p given in percent of the cell wall Young's modulus E.[31] D) A similar principle may be used for contractile roots of clover that gradually pull the foliage buds into the ground.[56] E) The G-layer in the cell lumina of the roots is visualized by histology. D,E) Reproduced with permission.[56] Copyright 2010, The Authors, published by John Wiley and Sons.

pure cellulose with a microfibril angle of ≈0°. This results in an extremely high axial stiffness, which is beneficial for high tensile stresses, but only if a certain contractibility is allowed at the same time. This may be achieved by a highly directional honeycomb structure in the G-layer,[58] which could result in an axial contraction upon G-layer swelling or by matrix swelling in the honeycomb like cellulose network.[59] Alternatively, a swelling of the G-layer in the transverse direction (in accordance with a microfibril angle of ≈0°) may exert a radial force on the surrounding secondary cell wall. Based on a mechanical model of the cell wall, this causes a maximal axial contraction of the secondary cell wall, if its cellulose orientation is in the range of 35°–40° (Figure 4C), which was in accordance with the experimentally measured microfibril angle.[31] Interestingly, tension wood fibers for axial tensile stress generation do not only occur in wood, but also in tendrils[60] or contractile roots.[56] For the latter, a similar mechanism of extended tension wood fiber contraction would allow for pulling foliage buds of red clover deeper into the soil.

3.5. Seed Pods as Material-Machines Fuelled by Humidity Changes

In the living tree, wood (xylem) cell walls are permanently in the fully hydrated state. The situation is somewhat different in other tree organs, e.g., in seed pods. During seed and pod development cells and cell walls are in the fully hydrated state. Later, seed release is often accompanied with a drying step causing a pod to open. The underlying mechanisms are typically found in the cell wall properties. Upon drying, the mechanical properties of the hemicelluloses in the matrix drastically change from 20 MPa in the water saturated state to ≈2 GPa in the dry condition,[44] leading to changes in cell wall mechanics. Depending on the MFA stiffness increases up to 50% for cells with a high MFA.[30] Simultaneously, these changes in water content lead to shrinkage, with the dimensional changes taking place mainly perpendicular to the longitudinal direction of the dimensionally stable and stiff cellulose fibrils.[61] Some seed pods and seed dispersal units contain bilayer structures, which are composed of two layers with different cellulose orientation. Upon drying one layer shrinks more in a particular direction and the other layer retains its dimensions. The differential shrinking results in a movement, leading to seed release and dispersal. In pine cones or the dispersal unit of wheat seeds, the bending movements which lead to scale opening and the swimming movement of the awns are based on a resistance- and active-layer assembly with their main orientations often being 0° and 90° to the longitudinal axis (**Figure 5**). By varying the orientations of two layers with respect to the longitudinal directions other types of movement are possible such as the chiral movement of Bauhinia seed pods[21] where the two layers run at ≈45° (Figure 5). With a tilted cellulose helix in the cells the awn of Erodium coils upon humidity changes to propel the

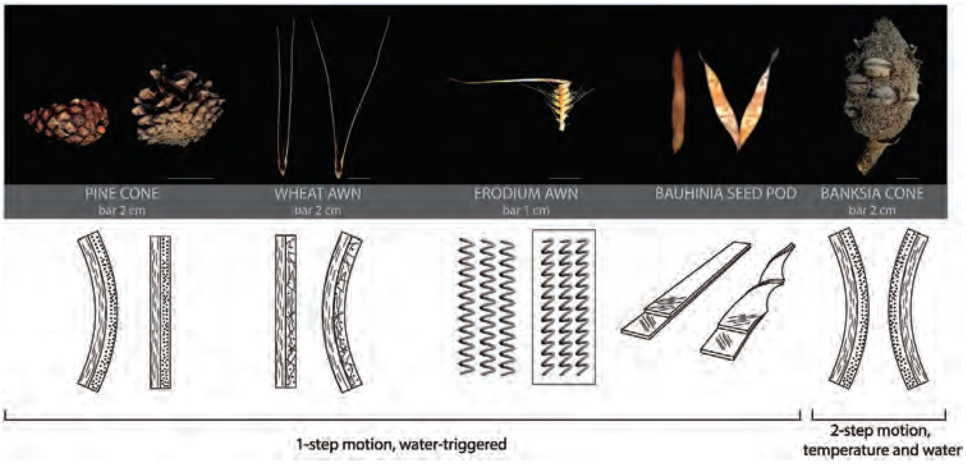

Figure 5. Seed pods and seed dispersal structures and their humidity and temperature triggered movements. The movement of pine cone scales and Banksia seed pod valves is based on a bilayer with the main swelling directions along and across the scale and valve axis. In wheat awns one of the layers has no preferential cellulose orientation. Erodium awns coil upon the tilted helical orientation of the cellulose; the left cartoon shows an untilted and the right cartoon the tilted helix. The chiral twist of Bauhinia seed pods is based on a 45° orientation of the main swelling directions to the longitudinal pod axis. Bauhinia photograph: Reproduced with permission.[22] Copyright 2007, American Association for the Advancement of Science.

seeds forward[20] (Figure 5). For seed release, the environmental trigger is not limited to changes in humidity and can even be a two-step process. The seed pods of some plants growing in Mediterranean climates, e.g., Banksias open upon elevated temperatures caused by bushfires (Figure 5). This initial opening is not sufficient for seed release. The seeds are kept in the pod until sufficient water exposure leads to further opening and finally seed release. By this two-step opening process the structure senses temperature and humidity changes that are good indicators for proper conditions for germination: the availability of nutrients after fire and water.[3,62]

3.6. Technological Consequences of Cell-Wall Drying

Less important for the tree as a living organism but needed for a technical use of wood by humans are drying processes, taking place after harvest. Currently, there are almost no applications in which wood is used in its natural wet state. Recent research activities have tried to exploit the liquid transport potential of wet wood and used wood as filter or membrane, but these studies are still far from implementation.[63,64] The reasons to use wood in a dried state are manifold and the most obvious one is that wood as a hygroscopic material naturally starts to dry at ambient conditions until an equilibrium moisture content is reached. Hence, it would be difficult and energy-intense to remain wood in a wet state in particular for larger constructions or furniture. However, one can imagine a use of wet wood in specific applications in the future, based on the fact that several limitations of wood as an engineering material are connected with the drying. If wood is kept entirely wet, like in the living tree, there are no issues with dimensional instabilities and low durability. Sorption does not play a role and brown rot and white rot fungi could not degrade the fully saturated wood as they need oxygen for respiration. Additionally, fire resistance, an important factor for wooden buildings would be much higher compared to dry wood. However, drying of wood has also technical advantages. The processability is strongly facilitated and the great majority of mechanical properties is improved.[65] For instance, the elastic modulus of wet wood increases by ≈30% with drying,[65] at the same time its density decreases. However, shrinkage of the cell walls often leads to crack formation. Due to its importance in wood use, wood–water relations have been extensively studied in the past,[66] still many open questions remain, particularly related to mechanosorptive creep[67] or to differences in swelling of isolated cell walls, cells, tissues, and tissue compounds. Currently, modern 3D imaging tools such as microcomputed tomography (μCT) allow to even study swelling and shrinkage of wood cell walls in three dimensions. On micropillars prepared out of latewood cell walls it has been shown that swelling strains are anisotropic at the cell wall level in the transverse plane.[68] Furthermore, it has been shown that the volumetric swelling of the isolated cell wall exceeds the one of cells (and possibly cell walls) in intact small wood samples, especially when both early and latewood are present.[69]

4. Harvesting the Activity of Wood

The informed understanding of the material wood and its characteristics that inherently depend on environmental interactions makes wood an extremely versatile but challenging raw material. Due to enhanced characterization techniques, information on composition, structure, and active properties is now available down to the nano- and molecular scale. This not only allows to better understand wood use, crafts, and wood processing of the past, but also opens up opportunities for new and innovative uses of this active material.

4.1. Unmodified Wood

In the design of wooden constructions, inherent dimensional changes upon water uptake and drying need to be considered.

Expansion joints are integrated to avoid stresses on neighboring elements. A prominent example is the gap between wooden floor boards and walls to prevent the floor from wrapping and the walls from cracking. Unsurprisingly, wood craftsmen, engineers, designers, and industries consider the hygroscopicity of wood and the associated changes in dimensions and mechanical properties as problematic. However, with a different mindset and approach the movement potential of native wood is worthwhile harvesting. An early example dates back to ancient Egypt: they used simple wood blocks and dowels to split rocks. Dry wooden wedges were inserted into cavities and wedge gaps of the rock (e.g., granite) and then wetted with water. The expansion and swelling pressure of wood was sufficiently high to fracture the rock.[70]

Despite the simple volumetric expansion of wood, biological systems like pine cones[71] or wheat awns,[22] which rely on simple bending movements based on the uptake or release of water from the cell walls are highly capable sources of bioinspiration for a transfer for wood elements in architecture.[72]

A prominent example is the hygroscope, a permanent exhibit in the Centre Pompidou in Paris.[73] It consists of 4000 surface responsive wood veneer elements (**Figure 6**A, left photograph), which were designed in such a way that they open upon an increase in moisture. In the project Hygroskin,[73] a meteorosensitive pavilion, the elements are completely open in the dry state—on sunny days (Figure 6A, right photograph). When exposed to moisture the skin closes completely and creates a tight boundary between inside and outside. In both hygroscope and hygroskin, the geometry and assembly of the triangular elements play a crucial role for the reversible movement of the wooden elements.[74]

An example for a rectangular shape changing structure upon hydration are wood layers (veneers) with crosswise fiber directionality assembled to bilayer structures.[76] This principle has been used for reversible systems, for instance, for shading systems at building envelopes (Figure 6B).[75,77] The diffusion-based bending response strongly depends on the change in relative humidity, the layer dimensions, and layer thickness ratios and the selected wood species. For an informative basis on the order of magnitude, an immediate relative humidity change from 85% to 35% results in a curvature of $\approx 5 \times 10^{-3}$ mm^{-1} after 6 h for a thin bilayer specimen of a length of 120 mm, consisting of a 1 mm thick "passive" spruce layer and a 4 mm thick "active" beech layer.[76] However, the diffusion-based response times of self-moving structures slow down enormously with increasing size[78] and for dynamic structures a current design challenge is to find the right trade-off between mechanical stability and speed of movement. For operating shading elements, a reasonable size is required which results in slow deformation speeds that impede the respective utilization. Grooved elements or coupled elements can be an improvement, but in particular the latter results in rather complex installations (Figure 6B).[75,77] By eliminating the principle of reversibility, recently, the shape changing potential of wooden bilayers upon humidity changes was utilized to develop curved cross-laminated timber (CLT) in an elegant way.[79] Since wood has to be dried during processing from the saw mill to the timber product, one can utilize this processing step to implement information into the elements. Flat wood bilayer structures were fabricated in the green state. During the drying process they bent (self-shaped) into predetermined geometries (Figure 6C, drawing). Afterward, these bent bilayers were assembled and glued to a CLT element, which locked the deformation and impeded reversible movement upon possible humidity changes. Hence, in the production process the activity of wood was first utilized and then silenced.[79] The process was successfully upscaled by producing a 14 m tall wooden tower for a garden exhibition in the south of Germany (Figure 6C).

4.2. Functionalized Wood

An emerging research field is to embed functionality into the wood structure and thereby generating wood materials with new property profiles and responsiveness. This goes beyond classical wood modification treatments, which usually treat wood to improve the dimensional stability and durability for technical applications.[80] By using wood as a scaffold and adding inorganic or organic matter with high nano- and microstructural control, naturally inherent features, can be enhanced or modified to create entirely new functionalities.[81] Examples for the latter are wood materials with magnetic properties or transparent wood. The precipitation of iron oxide nanoparticles in wood as well as partly or fully delignified wood scaffolds results in directional magnetic properties dictated by the anisotropic hierarchical wood structure.[82–84] In natural wood samples, the nanoparticles of a size of ≈20 nm are not formed in the cell wall but are deposited as thin layer aggregates onto the internal cell wall surfaces facing to the cell lumina. Since the shape of the wood cells dictates the layer formation one can make use of the directionality of wood in combination with additionally incorporated sensitivity and responsiveness. Measurements on the degree of magnetic anisotropy based on the ratio of the maximum to minimum principal susceptibilities in longitudinal and transverse direction revealed a ratio of 1.70 for beech wood at an intermediate precursor concentration.[84] Hence, hybrid wood materials can be manipulated and positioned in a magnetic field, but more interestingly, they are capable to interact with the environment and carry information even beyond the natural smartness of wood. A second example for entirely new properties and functionality is transparent wood, which can be achieved by a two-step process consisting of a delignification or modification of lignin and a subsequent infiltration with a polymer with a refractive index matching the refractive index of cellulose.[83,85] Such wood-derived materials are limited to a certain thickness, but have implementation potential in application fields that go far beyond the common use of wood.

In recent years, several research approaches have exploited the water transport function of wood in the living tree to develop smart wood materials by functionalization treatments that particularly utilize the directionality of transport channels in the hierarchical wood structure. By a decoration of the inner surface of the cell lumina with suitable substances, a certain chemical selectivity can be implemented into the wood scaffolds, which allows, for instance, for using wood as a filter for waste

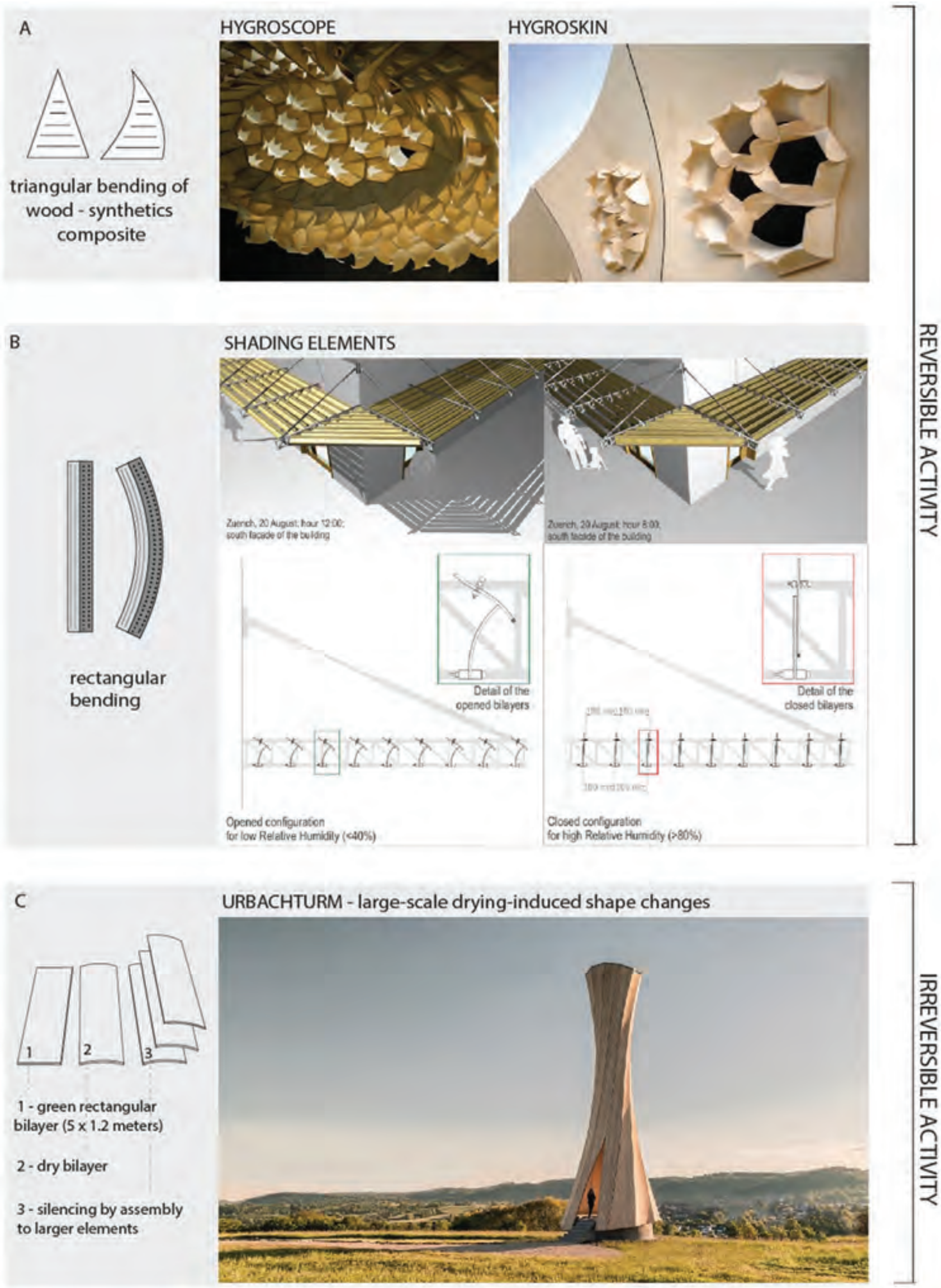

Figure 6. Activity of wood in architecture. A) Hygroscope and hygroskin, photographs reproduced with permission.[73] Copyright 2015, John Wiley and Sons. B) Façade elements moving with changing humidity Reproduced with permission.[75] Copyright 2017, Elsevier. C) Urbachturm, on the left 5×1.2 m large bilayered elements that bend upon drying and are glued together to silence their activity. Photograph copyright ICD/ITKE, University of Stuttgart 2019, reproduced with kind permission from Achim Menges, University of Stuttgart.

water treatments.[64] Other approaches aim at implementing electrical properties to create wood-derived systems with a high directionality of properties. Trey et al. added polyaniline to the wood structure in an in situ polymerization process, which was mainly incorporated in the middle lamella.[86] An alternative method from Wang et al. filled the wood pores with a metal to achieve directional electrical conductivity.[87] By specifically utilizing the large inner surface area of wood and in particular of cellulose scaffolds more sophisticated wood-derived electrical devices for various functions can be utilized.[88] Wood-based sensors, energy harvest systems, or sophisticated wood-derived materials for energy savings can be foreseen, ideally in combination with smart building solutions that fully exploit the opportunities that come along with the embedding of novel functionalities in a sustainable scaffold with large-scale application potential.

5. Drawing Inspiration from the Activity of Wood

The plant kingdom provides a great diversity of secondary cell wall based structures. While the material properties of wood have been of interest since a long time, only a few other plant structures were studied with the aim to understand their material. However, many of the studied plant examples (e.g., pine cone scales, Bauhinia seed pods) turned out to be of interest for bioinspired materials and served as inspiration for the development of composite actuators[89] with different sizes, some of them reaching ultrafast response times.[90] The spectrum of materials used for such actuators is manifold, e.g., polyionic liquids, hydrogels, mineral platelets, carbon nanotubes, or cellulose whiskers, just to name a few.

A rather new technique to design and fabricate actuators is 3D and 4D printing. In some sense, the printing process is comparable to plant growth processes and living wood has recently been considered as additively manufactured by cell division and expansion.[91] This perception might even better apply for the cell walls where cellulose and the other polymers are immediately after synthesis deposited as extracellular matrix. The fourth dimension arrives from the fact that the cell walls and wood as a composite are able to generate forces, mainly at the periphery of the stem in the form of growth stresses.

With current additive manufacturing techniques, controlled assembly of multiple materials is possible at multiple length scales. The technology is a platform to design and experiment with novel inks but also to fabricate active functional materials and structures: plant-inspired moving structures have been produced in a one-step process with an ink consisting of stiff cellulose fibrils embedded in a acrylamide matrix.[92] With the printing process the cellulose fibrils were oriented by the print path and in analogy to the examples of the bilayer from the plant world twisting and bending bilayers were produced just by combining layers with different print path orientations. Recently, 3D-printed cellulose-containing scaffolds were wet densified, resulting in composites with highly aligned cellulose and a volume fraction of more than 27% cellulose.[93] This is a promising direction toward the designed assembly of cellulose for structural materials requiring good mechanical properties. The printing of materials with anisotropic composition is also of interest for 3D wood printing. Correa et al.[94] use mono- and multimaterial printing methods to design and fabricate hygroscopically fueled self-moving structures for buildings. In recent work, they were able to 4D print structures which perform consecutive motions, inspired by the Bhutan pine cone scales.[95] Markstedt et al.[96] follow a different goal with 3D wood printing. Inspired by wood being grown into the shape of chairs, which is a slow natural process they sped up the manufacturing process by 3D printing to fabricate artificial cellular wood-like structures that mimic biogenesis.

Interestingly, the soft robotics community does not only make use of smart and other materials but also takes inspiration directly from the plant kingdom. A root-inspired soft robot with sensorized robotic roots mimics the sensing capability of natural roots and performs differential bending.[97] Equipped with a 3D printing head and a heater at the tip the robot is able to grow and bend by (differential) circular deposition of material from the filament while the mechanical properties of the printed material are controlled by temperature and feeding speed.[98] The material deposition and its properties are based on the sensed environment and the whole process can be described as an adaptive construction of a material—a process close to what we see in plant growth: a "metabolic structure"—the printhead or the cell—synthesizes dead material which assembles into a functional structure in close interaction with the environment.

A different perspective on bioinspiration and wood is the potential that findings on nonwood plant structures provide for the development of new environmentally friendly and tailor-made wood-based materials such as the examples where the analogy to the bilayered seed pod structures (Figure 5) and the moving elements in the constructions (Figure 6) can be seen. However, the biomimetic potential is by far not exhausted yet. Nonwood plant structures exist in diverse shapes, sizes, and geometries, however only a few systems have been studied so far and the majority is still unexplored. Therefore, only little is known about how structural features relate to functions or motions and natures diversity might provide simple solutions for complex movements. Despite the shape changing potential, many plant materials possess outstanding long-term stability and are resistant against degradation or dimensional changes, such as the physically dormant seed coats of *Stylobasium spathulatum*. Even when incubated on moist substrates for years, the seed coat stays intact and prevents water absorption and as a consequence germination. Only physical damage of the seed coat, e.g., by high temperatures during bushfires, allow the seeds to imbibe and germinate.[99] Some of the properties of such plant materials seem to be desirable for wood use. We speculate that the transfer of mechanisms found in one plant material into another one (which is available in large quantities) is possibly not too difficult since the basic building blocks are at least similar.

6. Conclusion: Toward a Materials Information Technology

Wood is the prototype of the Latin *materia*, but does not have the attributes of passivity that one usually confers to materials. The plant is adaptive to the environment and synthesizes cell wall structures that confer activity to wood materials even when the corresponding plant cells are not anymore living. This activity subsists when wood materials are collected for technical use.

On the one hand, the intrinsic activity of wood may be seen as challenge that needs to be overcome by proper treatment of the wood to reduce its susceptibility to humidity or by creating plywood structures where potential intrinsic forces would compensate each other. Thus, by silencing the inner activity a more rigid and passive material can be obtained.

On the other hand, the intrinsic activity of wood may represent an opportunity. The condition, however, is that we fully understand this activity and consider it in the design phase of engineering devices. This seems challenging, as every plant will have imprinted a different microstructure into the wood, depending on the environmental conditions it faced during life. But in times where on-demand and on-time fabrication becomes routine in engineering processes, it might well be possible to deal with the uniqueness of every wood log.

The most exciting perspective is that material microstructure may actually be considered as materially programmed information. In seed pods, the cellulose architecture encodes a complex set of movements triggered by humidity changes. Wood and most biological materials are active by hosting the information required for a specific function (in the form of a specific fiber architecture) and by directly using environmental gradients as energy sources. In our digital age, this provides interesting concepts for a better balance between analog information stored directly in the material (and, thus, not requiring energy for processing) and external (digital) information to control the overall process. In the case of seed pods, this external (digital) information produced by its sensor capacity may be just one bit, namely, the humidity level, or—for the Banksia capsules—two bits: sudden temperature rise due to bushfire and humidity change due to rain. These small bits of information are acting like switches and trigger an activity with a much greater complexity by using the information stored in the material structure. Of course, one can easily imagine other kinds of switches based on a variety of signals, such electrical, optical, or magnetic. This provides inspiration for a new approach to engineering where smart materials with analog information would be designed to interact with digital systems. In fact, wood and woody materials, such as seed capsules, are examples for the fusion of material and code, rather than just serving as passive material support for externally implemented intelligence.

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Conflict of Interest

The authors declare no conflict of interest.

Keywords

active materials, analog codes, cellulose fibrils, physical intelligence, wood materials, wood microarchitecture

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