Scope and Extent of Wood Biology

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Abstract

Over the last two decades, major advances have been made in the field of wood biology. This chapter reviews these advances in the major thematic areas within the field. First, the diversity of wood structure of tropical trees is presented, starting with growth rings and climate-growth relationships, which are important for climate reconstructions. In addition, by describing the cellular wood structure of characteristic tree species from various tropical growth zones, multiple anatomical structures correlating with environmental conditions become obvious. The large diversity in wood structure could have developed over millions of

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years because no ice ages occurred in equatorial zones. Second, an overview is given of the three main functions of wood in the living tree. Of special interest is the long-distance transport of water, since very efficient transport systems with large vessels have evolved in the tropics (e.g., as in lianas). Besides water transport, mechanical stability also plays a key role in tropical trees, which often reach heights of 60 m and have to be stable against mechanical loads such as wind. As a consequence, buttresses providing mechanical support have been developed only in tropical tree species, and their characteristics and functions are described here. Finally, emphasis is given to the third physiological function of wood: the storage of reserve materials such as carbohydrates, fats, and proteins, and the current state of knowledge on this topic is summarized.

Introduction

At present, wood has taken on an increased significance as the most important renewable raw material. More than half of worldwide-harvested wood is being used as fuel; however, the excellent properties of wood allow it to be processed into widely differing products. The largest woodlands on earth are the boreal woods of the northern hemisphere and the tropical rain forests. The latter, especially, fulfill various significant functions such as production of fuel and the provision of materials for construction, paper and non-wood forest products, as well as social functions for local people and environmental benefits. Furthermore, tropical forests are the most species-rich land ecosystems on earth and comprise about 47 % of total global forest area. Half of all described species live in tropical forests, which also makes them of great interest from a wood biological point of view. In previous studies it was thought that tropical trees grow continuously throughout the year because temperature and humidity are more or less constant in equatorial zones. Since the 1980s, however, researchers studying trees in various tropical regions found that each species has its own growth rhythm due to diverse climates in the various tropical regions.

A large number of papers and reports on the periodicity of growth in tropical trees have been published over the last hundred years. Due to the great heterogeneity of tree species, however, the influence of soil conditions and climate on the growth of tropical trees is still not completely understood. Nevertheless, significant findings and achievements have been made in the field of tropical dendroecology during the last decade. For instance, chronologies have been constructed for tropical tree species allowing climate reconstructions and analysis of climate-growth relationships (Rozendaal and Zuidema 2011). Studies of the width of tree rings and of their stable isotope fractions offer the potential to investigate the responses of various tree species to climate change. For instance, studies from

stable carbon isotopes from tropical tree rings indicate a precipitation signal (Fichtler et al. 2010). Such studies are of great importance because tropical trees play a key role in the global carbon cycle. They account for more than 30 % of net terrestrial carbon stocks. Also anatomical variables of wood, such as vessel diameter, have been shown to make valuable contributions to dendrochronology in the tropics (Fichtler and Worbes 2012). Furthermore, long-term growth patterns of trees throughout their life have yielded new estimates of tree ages. It is generally presumed that very old trees occur rarely in tropical forests. Moreover, model tree longevity value is reported to be between 200 and 400 years (Martinez-Ramos and Alvarez-Buylla 1998), and reports that millennia-old trees grow in the Amazon (Chambers et al. 1998) have provoked controversy in the literature. Reliable age estimates are nonetheless required to assist the ecological management of tropical forests. An accurate and direct method for tree age determination is tree-ring analysis (Martinez-Ramos and Alvarez-Buylla 1998). Rozendaal and Zuidema (2011) summarized ages from tree ring counts for numerous tropical tree species and found an average age of 101 years and maximum ages of 241 years. Interestingly, tree-ring analysis has shown that tree ages to reach the minimum cutting diameter were rather high for numerous commercial tree species. For instance, in deciduous woodlands in tropical Africa *Pterocarpus angolensis* needed more than 100 years to reach the minimum cutting diameter of 35 cm (Therell et al. 2007).

The present review focuses on current progress on structural and physiological aspects of tropical wood biology. For each of these topics, we emphasize the new insights contributed by recent scholarship.

Structure of Tropical Wood

Growth Rings

As long-living species, trees record important environmental information in their growth rings. It is well known that ring width is a predictor of tree performance in a changing environment. Climate conditions as well as abiotic (e.g., nutrient status) and biotic (e.g., pathogen attack) conditions affect the width and structure of growth rings. In order to respond to a changing environment, trees have the capacity dynamically to adjust the process of wood formation, for instance, by changing vessel size and density. As a result, such variables imprint ecological information within single tree rings (e.g., Garcia Gonzales and Eckstein 2003) which can be used in dendrochronology to reconstruct environmental scenarios of the past with sub-annual resolution in trees of temperate zones (Fonti et al. 2010). Numerous studies deal with the relationship between different vessel variables and their function, as well as their significance for ecological strategies in trees (e.g., Preston et al. 2006; Rana et al. 2009; McCulloh et al. 2010). On the other hand, species-specific differences in vessel variables can be related to precipitation or aridity (Choat et al. 2007; Martinez-Cabrera et al. 2009). Furthermore, wood density is an

important parameter in investigations on life history strategy in tropical trees (Müller-Landau 2004). Although previous studies have denied the occurrence of annual growth rings in the tropics (e.g., Lieberman et al. 1985), annual growth rings have been described by other researchers, such as Worbes (2002). They are generated when tropical trees undergo cambial dormancy once a year due to inauspicious external conditions such as dry seasons (e.g., Worbes 2002), flooding periods in floodplain forests (e.g., Schöngart et al. 2002), or variations in salinity in mangrove forests (Chowdhury et al. 2008). In almost all tropical zones, some kind of seasonality occurs by various external influences. Anatomically, the boundaries of tropical tree rings are often less marked than in trees of the temperate zone, and often wedging rings occur (Worbes 2002). Furthermore, tropical tree-ring boundaries can vary significantly within a species and among individuals and can sometimes disappear completely. In addition, non-annual ring formation has also been found, e.g., in trees of the central Amazon (Dünisch et al. 2003). Nevertheless, in many tropical regions, annual tree rings have been shown in numerous species (e.g., Worbes 2002; Dezzeo et al. 2003; Brienen and Zuidema 2005), either caused by reduced radial growth or by changes in wood structure. Worbes and Fichtler described four basic types of growth zone structures in tropical trees. First, several rows of fibers with reduced diameter and thickened walls cause density variations that mark the growth-ring boundaries, as shown in *Annona* sp.. Second, marginal parenchyma bands (e.g., in *Swartzia argentea*) mark the ring boundaries. Third, patterns of parenchyma and fiber bands (e.g., in *Pouteria glomerata*) provide a characteristic change at the boundaries. Fourth, variation in vessel density and size can occur in certain areas within a single ring (e.g., *Pseudobombax munguba*).

Various techniques have been used to detect the annual character of tropical tree rings. One method involves the measurement of periodic tree growth with dendrometers (Bräuning et al. 2009). Another method analyzes structural changes and counts the number of tree rings after wounding the cambium (e.g., Lisi et al. 2008), while an additional method that is able to assist in the structural identification of ring boundaries is radiocarbon dating (Fichtler et al. 2003). This method makes it possible to date trees younger than 50 years old because nuclear tests in the 1960s raised the content of ^{14}C in atmospheric CO_2 (Hua et al. 1999). A different method is based on the cross dating of ring widths from a tree population to evaluate whether synchronous ring generation occurs, in order to relate tree growth to climate factors (e.g., Wils et al. 2010). For instance, rainfall correlates with wood growth in various tree species (e.g., Baker et al. 2008). Methods also exist to detect rings in tree species without differentiable ring boundaries. For example, in Kenyan mangrove trees, vessel density reveals a link with climate (Verheyden et al. 2005).

In general, tree ring formation is affected by climatic factors. Seasonally dry forest species respond to rainfall differently, for example. Relationships between radial growth and total annual rainfall, total rainfall in the rainy season, rainfall in the dry season, and rainfall in the transition have been observed (Rozendaal and Zuidema 2011). For instance, the seasonal cambial activity of tropical tree species in Central Thailand showed that the cambium of *Tetrameles nudiflora* and

Magnolia baillonii was most active when rainfall reached its maximum amount in June (mid-rainy season), while the cambium of *Canarium euphyllum*, *Toona ciliata*, and *Spondias axillaris* was most active in March during the transition from the dry to the wet season (Pumijumnong and Buajan 2013). In addition to rainfall, tree growth can be correlated to the water level in the non-flooded period in Amazonian floodplain forests (Dezzeo et al. 2003) or with the length of the non-flooded phase (Schöngart et al. 2005). Because of the relationship between growth and precipitation, climate reconstructions based on tree rings became possible. So far, for some species, chronologies with a length varying from 150 to 400 years have been set up (Schöngart et al. 2005, Therell et al. 2006, Sass-Klaassen et al. 2008). Generally, climate reconstructions from Asia, tropical Africa, and South America have shown large-scale climatic fluctuations toward drier conditions recently. According to the Monsoon Asia Drought Atlas (MADA), developed by Cook et al. (2010), several intense droughts occurred in Asia during the past millennium. Based on preceding climate fluctuations, therefore, the response of tropical trees to future climate variations could be predicted. For instance, a climate-growth analysis for a Mexican dry forest tree showed the strong impact of sea surface temperatures and predicts a future decline in growth (Brienen et al. 2010).

There are, however, still gaps in knowledge regarding the effect of increasing atmospheric CO_2 and rising temperature. On the one hand, data from permanent sample plots in tropical forests have shown an increase in aboveground biomass, tree growth, and stem turnover during recent decades (Lewis et al. 2009), presumably due to increasing atmospheric CO_2. In addition, studies indicate that rising concentrations of atmospheric CO_2 outweigh negative temperature effects (Lewis et al. 2004). Similar to temperate forests, tree-ring analysis of tropical trees can also show the response of trees to rising atmospheric CO_2. Rozendaal et al. (2010) found a historical growth increase in Bolivian tree species which corresponds with expected responses to increased atmospheric CO_2 (Lloyd and Farquhar 2008). In contrast, Nock et al. (2010) found that growth has decreased in recent years in tree species from a tropical dry forest in Thailand, which might be caused by increased water stress induced by temperature increases. Such contradictions need to be cleared up in the future, because measurements of growth rate are important to predict global carbon budgets. Since tropical trees play a significant role in the global carbon cycle, it is important that the responses of these trees to climate changes are untangled.

Cellular Structure of Wood

The richness of species in tropical forests has been the topic of numerous publications (e.g., Wheeler et al. 2007) and is mirrored in various cellular wood structures. Together with subcellular features, wood structure often allows the determination of family and genus, although wood structure can vary within a species or even a single tree. For a living tree, wood serves as a long-distance water transport,

nutrient transport and storage, as well as a source of mechanical stability. As a consequence, changes in frequency, size, and distribution of the various cell types can produce a high variability in wood structure in order to perform different functions within a large range of ecological settings (Chave et al. 2009).

In general, tropical forests consist of moist broadleaf, dry broadleaf, coniferous, and mangrove forests (Olsen et al. 2001). Alternatively, they can also be divided into near-equatorial humid lowland forests, tropical montane forests, half-evergreen tropical forests, and finally savannah regions.

Near-equatorial humid lowland forests are not uniform, but show distinct edaphic and floristic differences. The three humid tropical regions are northern South America and Amazonia, western Central Africa, and Southeast Asia. The tropics are frost-free and form the largest climate and vegetation zone on earth. The annual mean temperature lies between 24 °C and 30 °C and the annual rainfall between 2,000 and 4,000 mm. In principle, short periods without rain can affect wood formation in a climate without seasons. Due to the warm and humid climate, the turnover of substances is favored within the soil; therefore, humus is not accumulated and the soil is depleted. This means that mineral nutrients are located mainly within the trees, while nutrients from plant waste are taken up by mycorrhizal fungi and supplied to the roots. The structure of the stand consists of 30–70 m high trees and epiphytes, which form the rutted highest storey; below it grow younger trees and below them shrubs, herbaceous perennials, and ground-cover plants. Due to the lack of drought and frost, there is high biodiversity, with approximately 60–100 tree species per hectare, and competition for light is therefore the main ecological factor between species. For instance, *Afzelia bella* (Fabaceae-Caesalpinioideae) growing in West and Central Africa is a characteristic tree species of the hot humid lowlands. The wood structure of this species is characteristic for this growth zone: macroporic vessels (>100 μm in diameter) are surrounded by paratracheal-aliform parenchyma sheaths and distributed equally across the growth ring (Fig. 1a, b). From a radial and tangential perspective, numerous rays can be observed, most of them two cells wide (Fig. 1c, d). *Afzelia* heartwood is very durable, and due to a relatively high wood density (0.78 g/cm^3), it is popular for construction purposes. Typical pantropic families are Bignoniaceae and Lauraceae, while Dipterocarpaceae and Pandanaceae are typical Palaeotropical families. Lianas (e.g., *Bignonia aequinoctialis*, Fig. 2) are among the most important species in tropical forests and generally grow through all storeys. They have very deep and efficient root systems which allow them to absorb water and nutrients deep in the soil (Holbrook and Putz 1996). These species show interesting structural characteristics linked to their climbing habit, predominantly a high vessel density (Fig. 2). Also, since they have lost large amounts of supporting tissue compared to trees, they need external supporting objects. During their evolution, they have developed additional conductive and storage tissues (Angyalossy et al. 2012). In general, wood of lianas shows wider vessels (Fig. 2), larger amounts of axial parenchyma as well as rays, and longer fibers compared to trees. Rattan palms also occur within the climbing plants, and there are over 370 species within the genus *Calamus*, all growing in the Palaeotropics. Most of them are leaf climbers
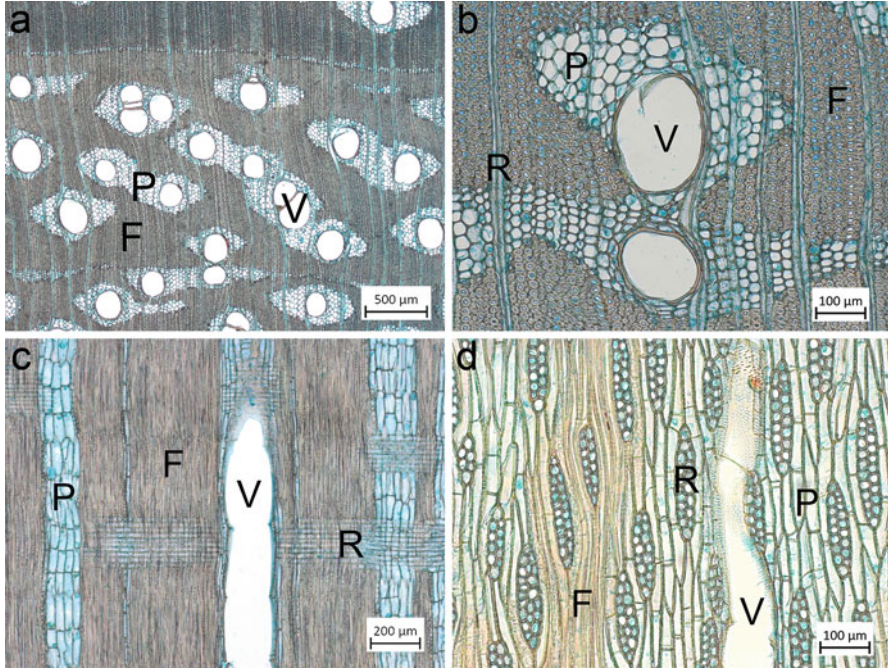
Fig. 1 Wood structure of *Afzelia bella*. (**a**, **b**) Transverse view showing large vessels (*V*) surrounded by paratracheal-aliform parenchyma (*P*). (**c**) Radial section indicating storied axial parenchyma cells (*P*), ray cells (*R*), and elongated fibers (*F*) with narrow lumina. (**d**) Tangential section showing rays, vessels, fibers, and axial parenchyma

with slender stems reaching a height of 30–40 m. The stem shows a typical monocotyledonous structure and consists of numerous vascular bundles surrounded by a crescentic fiber sheath and embedded in parenchymatic tissue (Fig. 3). One large vessel occurs within each bundle, enabling efficient water transport. Also coniferous trees occur in humid lowland forests. Regarding *Podocarpus elatus*, a species growing in tropical rain forests of East Australia up to an altitude of 1,000 m, a typically coniferous wood structure is conspicuous, consisting of 90–95 % axial tracheids serving for both water transportation and mechanical stability (Fig. 4). In addition, uniseriate rays and axial parenchyma occur in *Podocarpus*, whereas resin ducts are lacking (Fig. 4).

Between 1,000 and 4,000 m above sea level, *tropical montane forests* appear. Annual rainfall exceeds 2,000 mm significantly, and above 1,800 m fog occurs from midmorning to late afternoon. The height of these forests varies from 3 to 5 m at the forest boundary (3,600–4,000 m) to 45 m at lower altitudes. The annual mean temperature is approximately 17 °C at 2,000 m and 11 °C at 3,000 m, and frost occurs above 2,500 m. With increasing altitude, more and more humus accumulates because the cool and wet climate retards the biodegradation of litter. The stand structure of the lower montane forests is similar to that of tropical lowland forests,
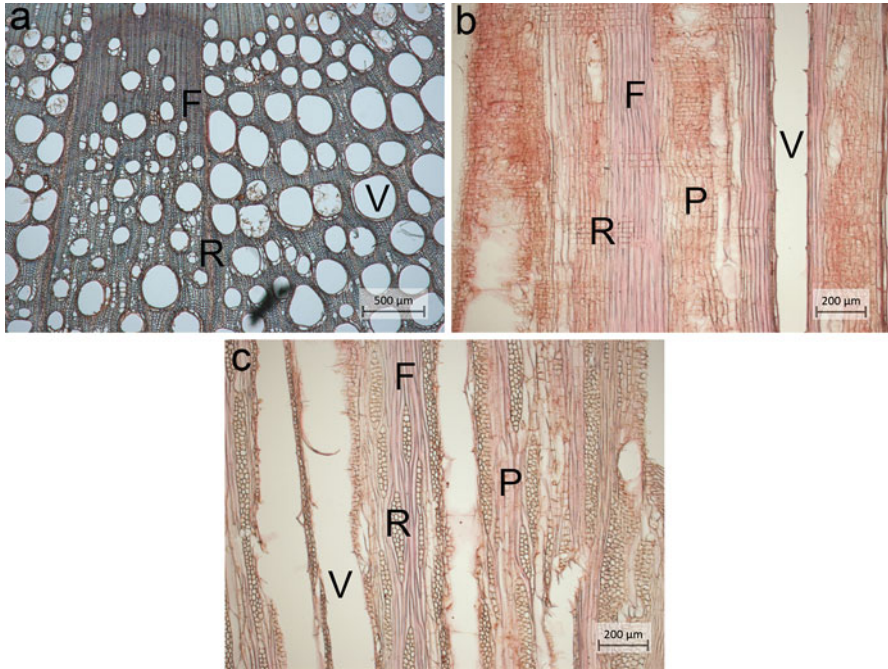
Fig. 2 Xylem structure of *Bignonia aequinoctialis*. (**a**) Transverse view showing a high density of large vessels (*V*). (**b**) Radial view with elongating fibers (*F*), rays (*R*), parenchyma (*P*), and vessels (*V*). (**c**) Tangential view with large vessels (*V*)
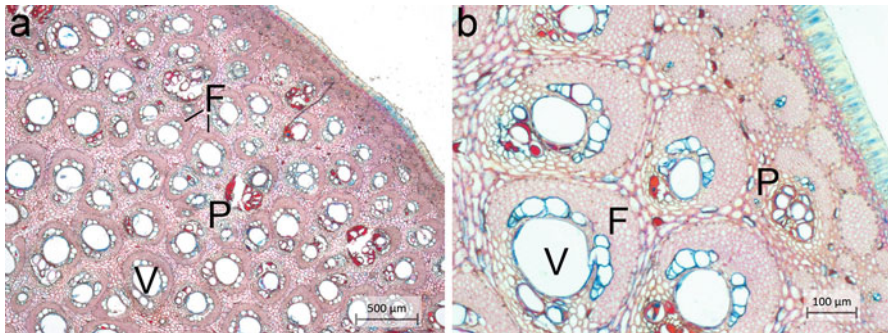

Fig. 3 Stem structure of *Calamus densiflorus*. (**a, b**) Transverse view showing numerous vascular bundles, each with one large vessel (*V*). The bundles are surrounded by a crescentic fiber sheath (*F*) and embedded in parenchyma tissue (*P*)

with increasing altitude; however, the storey organization disappears to leave low trees and shrubs. At lower elevations, families such as Moraceae and Rubiaceae typically dominate, but with increasing elevation, trees of the Fagaceae, Nothofagaceae, and Lauraceae become more important. Also coniferous trees
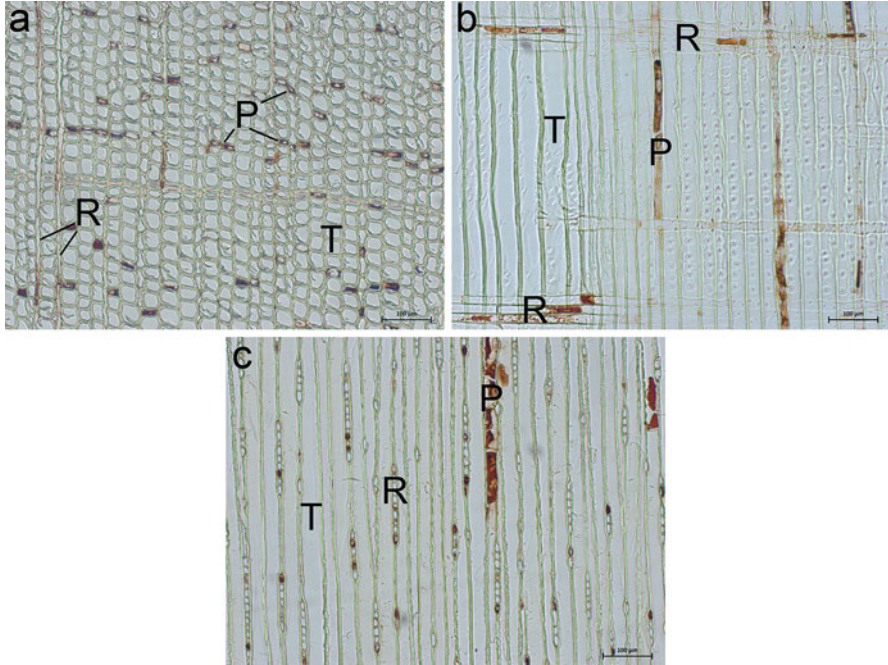
Fig. 4 Wood structure of *Podocarpus elatus*. (**a**) Transverse view showing mainly tracheids (*T*). Axial parenchyma cells (*P*) with red-brown extractives appear frequently. (**b**) Radial view showing horizontally oriented ray cells (*R*), tracheids (*T*), and axial parenchyma cells (*P*). (**c**) Tangential section showing exclusively uniseriate rays (*R*)

such as Podocarpaceae and tree ferns like *Cyathea* increase with rising altitude, although they are not dominating. In general, in tropical montane forests the number of woody species decreases with rising elevation, with only a few species occurring at the forest boundary, conspicuously Rosaceae in Africa and South America and Ericaceae in Africa and Southeast Asia. In the tropical Andes, for instance, *Polylepis* forests appear at the forest boundary. Due to the high elevation and the possible occurrence of frost, *Polylepis racemosa* trees have very small vessels in order to establish vascular safety (Fig. 5).

Along the edge of the tropical forests, *half-evergreen tropical forests* affiliate. In this region seasonal rainfall occurs, leading to seasonal characteristics within the vegetation as manifested in monsoon forests or tropical dry broadleaf forests. The changes between dry and wet seasons result in periodic foliage. The annual mean temperature is similar to tropical humid lowland forests (24–30 °C), although with increasing distance from the equator, the dry season becomes cooler and the rainy season warmer. The character of the forests is determined by both the length of the dry season and the amount of precipitation. With increasing drought tree height is reduced and the number of epiphytes as well as lianas decreases. Half-evergreen tropical forests are strongly threatened by humans because of their easy
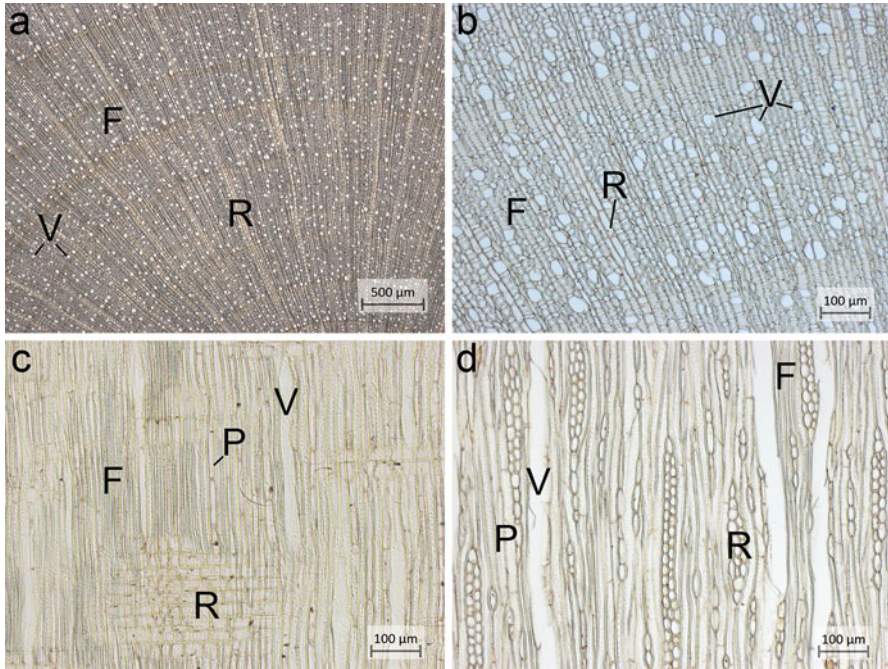
Fig. 5 Wood anatomy of *Polylepis racemosa* from Peru. (**a**, **b**) Transverse view showing diffuse-porous wood with small vessels (*V*), large amounts of fibers (*F*), and rays (*R*). (**c**) Radial view indicating also the occurrence of axial parenchyma (*P*). (**d**) Tangential view indicating that rays are mainly two cells wide

combustibility during the dry season, which facilitates clearing. The biological diversity of such forests is enormous; important families are the Malvaceae (e.g., *Chorisia*) and Anacardiaceae (e.g., *Schinopsis*) in South America, Verbenaceae (e.g., *Tectona grandis*) and Dipterocarpaceae (e.g., *Shorea robusta*) in the monsoon forests of Southeast Asia, and Fabaceae (e.g., *Brachystegia*) in Africa. Teak (*Tectona grandis*) is one of the most valuable kinds of timber because of its high durability against pathogens and its favorable properties. It has a ring-porous structure with wide vessels and axial parenchyma marking the ring boundaries (Fig. 6). Recently, the seasonality of ring formation was examined in mature teak trees growing in Ivory Coast (Die et al. 2012), showing that a three-month dry season resulted in cambial dormancy and formation of annual growth rings. Cambium thickness was significantly correlated with monthly rainfall and xylem growth zones were formed during the seasonal development of new foliage, indicating that such growth zones can be used as proxies for analysis of the tree history and climate (Die et al. 2012).

Similar to half-evergreen tropical forests, *savannah regions* depend on the seasonal rhythm of the amount of precipitation. In the savannah characteristic grasslands develop through the interaction of climate, soil, fire, and wild animals,
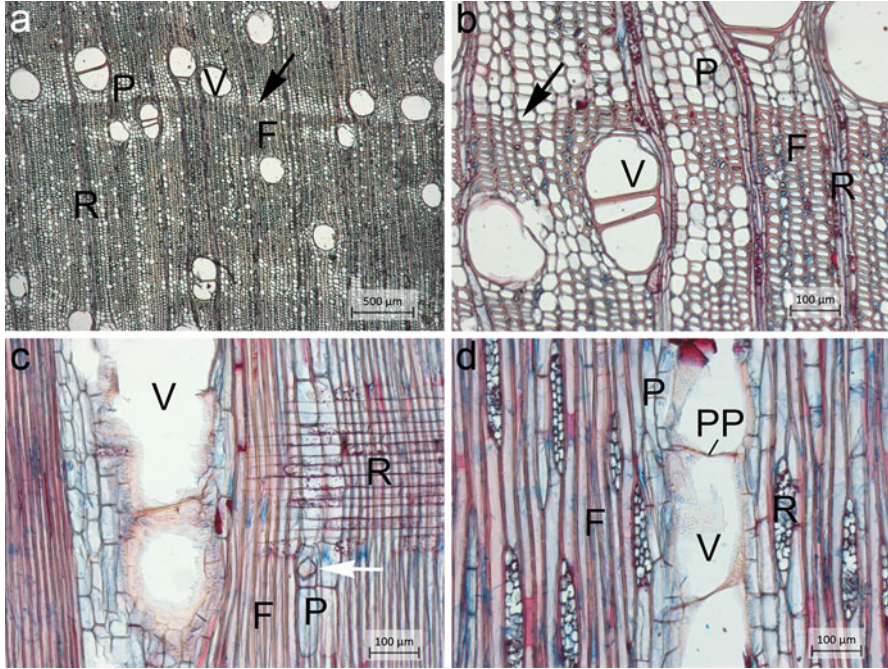
Fig. 6 Wood structure of *Tectona grandis*. (**a, b**) Transverse view showing ring-porous orientation of vessels (*V*) with large amounts of banded axial parenchyma (*P*) at the ring boundary (*arrow*). (**c**) Radial view with horizontally oriented ray cells (*R*), axial parenchyma (*P*) with crystals (*open arrow*), and elongated fibers (*F*). (**d**) Tangential view showing vessel elements with perforation plates (*PP*)

interrupted by forestland and riparian forests at watercourses. The savannah climate is characterized by annual precipitation below 1,500 mm and night temperatures below 10 °C in high-lying areas. The African savannah is an open woodland with elephants and hoofed animals which prevent the regeneration of forestland. The acanthaceous genus *Acacia* (Fabaceae-Mimosoideae) occurs in lowland areas of African savannahs, while shrubs of the Combretaceae grow on hills. For instance, the wood of *Acacia senegal* shows relatively small vessels fulfilling the conditions of vascular safety under drought stress (Fig. 7). Important species of the Llanos in the northern parts of South America are *Curatella* and *Byrsonima*. In the Chaco region of inner South America, *Prosopis* species as well as *Schinopsis lorentzii* (Quebracho) occur, while in northern Australia, evergreen *Eucalyptus* and thornless *Acacia* with phylloids are characteristic species.

   Apart from these growth zones, mangrove forests occur at tropical coasts, growing in seawater and having important ecological functions. A characteristic mangrove species is *Rhizophora mangle* from Cuba. Its wood structure is characterized by numerous, relatively small vessels and a large amount of fiber tissue
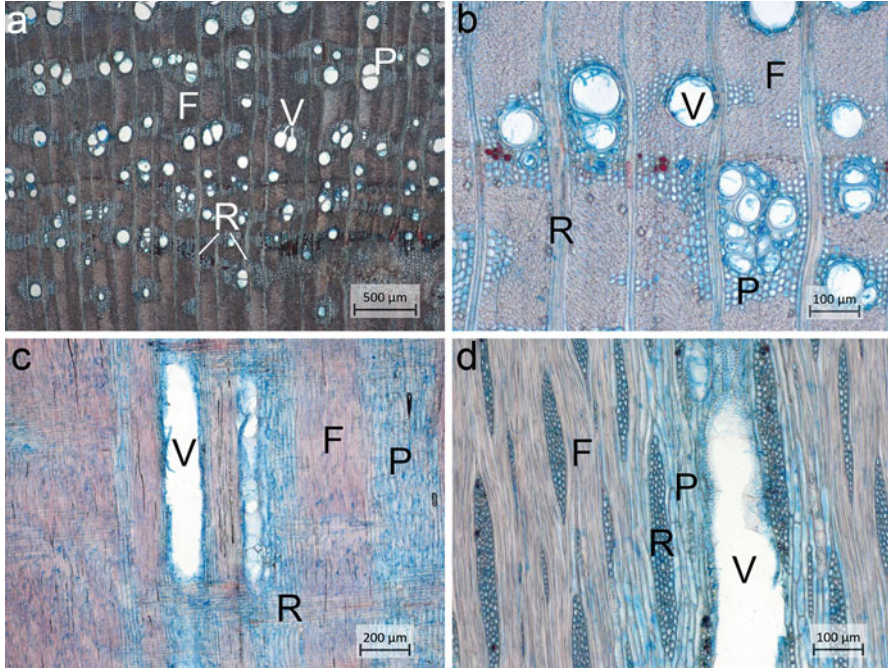
Fig. 7 Wood anatomy of *Acacia senegal*. (**a**, **b**) Transverse view with relatively small vessels (*V*) surrounded by paratracheal-aliform parenchyma (*P*). (**c**) Radial section showing large amounts of fibers (*F*) and (**d**) tangential view indicating the occurrence of mainly multiseriate rays (*R*)

which provide physical stability (Fig. 8). Interestingly, axial parenchyma only rarely occurs in this species, indicating that storage of reserve materials plays a lesser role. However, numerous crystals appear in ray parenchyma cells.

Physiological Functions of Wood

Three main functions are performed by wood in the living tree: (1) long-distance transport of water and mineral elements from the roots to transpiring leaves in tracheids and vessels; (2) mechanical stability through tracheids and fibers allowing trees to reach heights of up to about 115 m; and (3) transport and storage of carbohydrates, lipids, and proteins in living axial and ray parenchyma cells. Parenchyma cells have also developed mechanisms of defense against pathogens (e.g., fungi, insects) by wound responses and by the generation of secondary metabolites in the transition zone between the sap- and heartwood. Taken together, these three functions, and their associated structural attributes, show important trade-offs, and each tree species reveals a specific balance for its site of growth. For example, if wood shows numerous wide vessels, mechanical strength may decrease, as in many lianas. However, an increase in fiber wall thickness can compensate for large
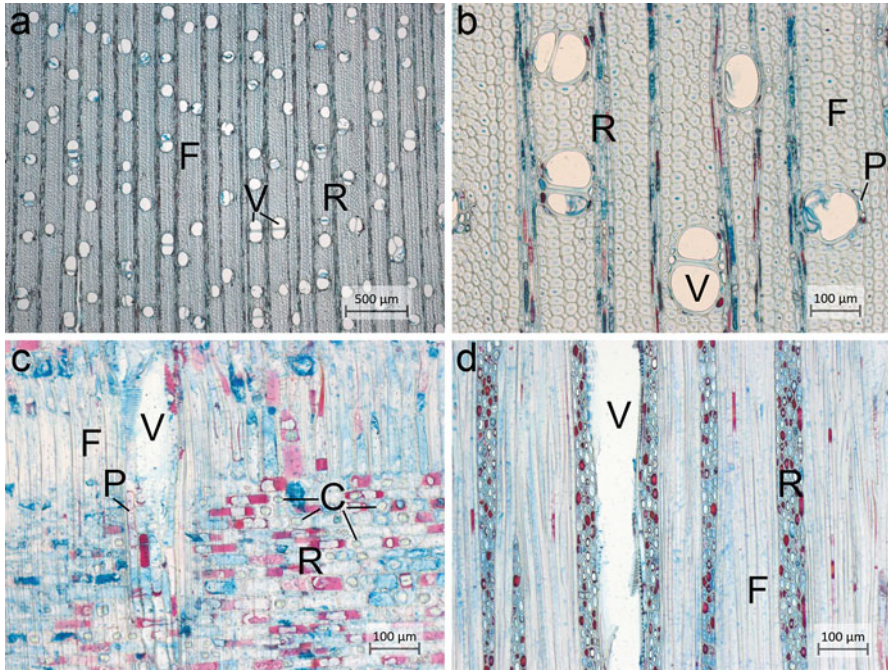
Fig. 8 Wood structure of *Rhizophora mangle*. (**a**, **b**) Transverse view showing diffuse-porous wood where all vessels are contacted by rays (*R*), also large amounts of fibers (*F*) occur but axial parenchyma (*P*) is sparse. (**c**) Radial view with horizontally oriented ray cells (*R*) with numerous crystals (*C*). (**d**) Tangential view indicating that rays are very high with numerous cells (*R*)

proportions of vessels and parenchyma cells. Therefore, in most species (especially in tall trees), a close correlation between water conductivity and mechanical strength exists. In particular, tree organs with most negative water potentials, such as small twigs and leaves, need sufficient amounts of fiber for structural support.

Long-Distance Transport of Water and Mineral Elements

Long-distance water transport in trees is mainly driven by transpiration and occurs in the lumina of nonliving tracheids and vessels. Moreover, hydraulic conductivity of the xylem depends on vessel size and frequency as well as vessel arrangement, type of perforation plate, and pit membrane porosity (Sperry 2003). Especially under stress conditions, these parameters play a key role in determining tree growth. Under different climate conditions hydraulic demands are different; for instance, ring porosity is a hydraulic strategy in seasonal climates. In the tropics, some highly monsoonal species are also ring-porous, e.g., teak. Ring porosity is characterized by earlywood vessels which are much wider than latewood vessels and which show

little flow resistance in comparison to narrow latewood vessels that are more resistant to water flow (Fromm et al. 2001; Fromm 2013). Since water conductivity increases with the fourth power of vessel diameter and only with the first power of vessel frequency (Tyree and Zimmermann 2002), large vessels are the most efficient cell types for water flow. Besides efficiency, however, the safety of the xylem conduits is significant for tree growth and survival. Larger vessels are more vulnerable to cavitation than smaller ones, and therefore earlywood vessels become embolized relatively soon in the growing season. On the other hand, it is now known that embolism is not always a disastrous event for the tree, as had previously been assumed. The generation of embolism and its disappearance can happen daily under high evaporation (e.g., Johnson et al. 2009; Zufferey et al. 2011), with the dissolution of embolism occurring both by internal pressure imbalances (Domec et al. 2006) and by active sugar importation from nearby parenchyma cells into empty vessels followed by passive water fluxes (Zwieniecki and Holbrook 2009). Regarding the complex network of water-conducting cells in trees, it could be advantageous to confine embolism to regions where repair is easily possible, for instance, in roots, which are near the water source, or leaves and petioles, which are close to assimilate sources. In terms of vulnerability, narrow vessels are much safer. Moreover, the vulnerability to cavitation also depends on the mechanical strength of the xylem cells. Trees with higher wood density are able to tolerate a higher negative pressure compared to species with low wood density (Hacke et al. 2001). Furthermore, some deciduous species (e.g., *Quercus robur* in temperate forests) still have tracheids to compensate embolized vessels and guarantee vascular safety. Generally, vessel size and frequency are negatively correlated, and the relationship between both mirrors a trade-off between vascular efficiency and safety.

Recently, an analysis of tree water use parameters from trees across species in 23 diverse geographic regions representing all continents showed that trees were most efficient in water transport when the wood density was between 0.51 and 0.65 g/cm^3 (Kallarackal et al. 2013). The water transport rate (as indicated by daily sap flow density) was reduced when wood density increased or decreased from this range. Presumably, the reduction in water flow with decreasing wood density is a precaution taken by the tree to avoid cavitation in the larger conducting cells that are typical of low density wood. Kallarackal et al. (2013) conclude that the occurrence of a high number of tree species with wood density in the range of 0.51–0.65 g/cm^3 points toward the importance of wood density for the efficient functioning of water transport. Roderick and Berry (2001), meanwhile, assumed that sap velocity might also be strongly related to wood density. They concluded that both parameters are closely correlated in conifers because of the uniform wood structure. Studies on angiosperms have also revealed good correlations between wood density and other plant physiological parameters, such as sap flow (Bucci et al. 2004; Meinzer 2003; Phillips et al. 1996), indicating that wood density can be a predictive parameter for potential water use by tree species. In addition, an analysis across plant families and a wide climatic gradient of 139 tropical trees showed that vessel diameter correlated closely to other wood anatomical variables and tree morphology (Fichtler and Worbes 2012). Moreover, tree size and crown

exposure to light showed the strongest positive impact on vessel size, whereas the general climatic site conditions strongly affected fiber and parenchyma tissue. Remarkably, vessel diameter varied strongly within families but also between some families; e.g., the vessels of the Malvaceae were significantly larger while the Myrtaceae and Annonaceae showed smaller vessel diameters than other families (Fichtler and Worbes 2012).

Wood anatomy and hydraulic properties also change along the root-to-shoot flow path. It is presumed that vessel diameter and hydraulic conductance decrease acropetally from roots to leaves. Recently, however, Schuldt et al. (2013), working on the tree species of a perhumid tropical rain forest in Indonesia, showed that vessel diameter and sapwood area-specific conductivity attained a maximum in the trunk and strong roots and a minimum in both small roots and twigs, indicating that vessel size depends on the diameter of the organ. Such a variation could be an adaption to the perhumid climate where there is a low risk of hydraulic failure. Interestingly, the specific conductivity at the roots, trunk, or twigs increased with the aboveground biomass, which was closely related to both specific conductivity and mean sap flux density in the trunk sapwood (Schuldt et al. 2013), demonstrating the significance of hydraulic efficiency for tree productivity. These observations therefore confirm the postulation by Tyree (2003) that a high plant hydraulic efficiency is a prerequisite for the high productivity of trees. In contrast to Kallarackal et al. (2013), Schuldt et al. (2013) could find no correlation between wood density and xylem anatomy and related hydraulic properties. From the above summary it is clear that these relationships need to be analyzed more deeply in future studies.

Furthermore, a wood anatomic analysis of five dipterocarp species endemic to the Philippines has shown that, despite very similar vessel lumen cross-sectional areas, their cumulative predicted conductance varied widely (Rana et al. 2009). Wood density, meanwhile, was shown to be negatively correlated with the abundance of axial parenchyma cells. For instance, in *Dipterocarpus kerrii* high density correlated with high predicted conductance (Rana et al. 2009). Since this species has been reported to attain heights of more than 30 m, a combination of wide vessels, high conductivity, and thick-walled fibers might be required in emergent large trees and broad crowns.

Recently, the functional relationship between cell types performing each of the xylem functions, wood density, and theoretical conductivity was analyzed in approximately 800 tree species from China (Zheng and Martinez-Cabrera 2013). An interesting evolutionary link was found between high conduction capacity and larger amounts of axial parenchyma, presumably related to water storage and embolism repair. In contrast, larger amounts of ray tissue have evolved with increased mechanical support and reduced hydraulic capacity (Zheng and Martinez-Cabrera 2013). In another study of a tropical dry karst forest in southwest China, hydraulic conductivity, vulnerability curves, wood anatomy, leaf parameters, and photosynthetic capacity were compared between evergreen and deciduous tree species (Fu et al. 2012). It was shown that the deciduous trees had higher stem hydraulic efficiency, larger vessel diameter, and a higher photosynthetic rate, while the evergreen species revealed higher xylem-cavitation resistance.

It is also important to understand the ecophysiological characteristics of trees in the process of plant succession. Hydraulics and photosynthesis in numerous woody species from different successional stages of subtropical Chinese forests were studied recently by Zhu et al. (2013). In contrast to late-successional species, early-successional species had the highest hydraulic conductivity, net photosynthetic rates, photosynthetic nitrogen, and phosphorus use efficiencies but the lowest photosynthetic water use efficiency. These results suggest that hydraulic efficiency and photosynthetic function play a significant role in species distributions along plant succession (Zhu et al. 2013).

The prototypes of hydraulic conductivity in tropical rain forests are lianas which have at least twofold wider xylem vessels than trees (Angyalossy et al. 2012). The wide vessels allow these plants to transport water to a large leaf area (Fig. 2). Liana species also have longer vessels in comparison to tree or shrub species (Jacobsen et al. 2012). In addition, the axial vessel elements of lianas can be connected by radial conducting cells called perforated ray cells (PRC) through perforation plates (Angyalossy et al. 2012). The PRCs may function to produce an osmotic force in embolism repair of empty vessels. Surprisingly, PRCs have a strategic position within the xylem rays, forming a connection between wide and narrow vessels in order to function as bypasses for embolized vessels (Angyalossy et al. 2012). The phloem rays can also show specialized conducting cells called sieve ray cells (SRC, Angyalossy et al. 2012), which are connected with the axial sieve elements through sieve plates. In tropical forests, lianas represent approximately 25 % of woody plant species. They decline with increasing elevation, indicating that these types of plants function less well in cold climates. The very efficient vascular network of lianas enables them to climb and overgrow host trees. Their relatively thin stems play only a minor role in mechanical support, and most of the assimilates produced by the leaves can be transported to young sinks like fine roots and young leaves, allowing faster growth.

Mechanical Support

Among the various functions of wood, mechanical support is very important, especially for trees. While in conifers tracheids fulfill both functions, water transport and mechanical stability, in angiosperms the fibers in the wood matrix contribute directly to biomechanical strength and act against implosion (Baas et al. 2004). In addition, the thickness of fiber walls also contributes to mechanical strength and can compensate for high tissue proportions of vessels and parenchyma cells. Especially under stress conditions such as drought, fiber walls are usually thicker and vessels are narrow and more frequent than under normal conditions (Arend and Fromm 2007; Lautner 2013). Interestingly, larger amounts of ray tissue have evolved with increased mechanical support, as analyzed in numerous trees growing in China (Zheng and Martinez-Cabrera 2013).

An important parameter that affects mechanical support is wood density. This has been the focus of extensive research in recent years and describes the amount of carbon invested in mechanical support (King et al. 2006). In general, wood density is

inversely related to growth rates (e.g., Müller-Landau 2004). Trees with low wood density are comparatively short-lived, fast-growing, pioneer trees, whereas trees with high wood density are mostly long-lived climax trees (Wiemann and Williamson 1988, 1989; Saldarriagga et al. 1988). Thin-walled fibers are more characteristic of rapidly growing, early-successional trees, while thick-walled fibers mainly occur in climax species (Swaine and Whitmore 1988). A high wood density promotes cavitation resistance by increasing the strength of the fibers surrounding vessels (e.g., Pratt et al. 2007). Wood density, as well as nonconducting cell types such as fibers, can vary a lot between species, with tropical trees, for example, exhibiting a broad range of wood densities from 0.3 to 1.2 g/cm^3. Regarding the relationship between wood density and vessels, however, research has revealed contradictory results. While some papers have showed a close relationship (Preston et al. 2006; Fan et al. 2012), other studies have not (Russo et al. 2010; Zanne et al. 2010). Many authors have found that water storage or capacitance decreases with increasing wood density (Pratt et al. 2007; Chave et al. 2009). Wood density also varies strongly in a radial direction from the center of the stem to the cambium. In two Neotropical rain forests, Hietz et al. (2013) showed that wood density tended to increase toward the outside in trees with low initial density and to decrease toward the outside in trees with high initial density, which is important for tree mechanics. Apart from these observations, drought and decay resistance increases with wood density.

One fascinating phenomenon in tropical trees is buttresses, which are the result of secondary growth of surface roots (Richards 1996). Numerous species show buttresses, with most of these growing into the canopy of tropical rain forests. Undoubtedly, buttresses provide physical support and stabilization for larger trees, especially when loads are asymmetrical or strong winds occur (Smith 1972; Ennos 1993). For instance, it has been reported that more than 50 % of the 468 tree species in tropical dipterocarp rain forests produced buttresses (He et al. 2013), mostly in large species. Buttresses also promote nutrient acquisition, however, although mainly in smaller trees where surface roots spread out laterally to get soil nutrients (Richards 1996). For instance, the central African rain forest tree, *Microberlinia bisulcata*, has quite distinctive buttressing with a strong lateral extension of surface roots in juvenile trees (Newbery et al. 2009). Generally it is suggested that in soils with very low nutrient status, buttresses can aid nutrient acquisition, and indeed, buttresses seem to increase as nutrient availability decreases. In this context, a study of a tropical rain forest in India has shown that buttresses induced habitat heterogeneity and increased nitrogen availability (Pandey et al. 2011). Buttresses, therefore, are a distinctive feature of tropical rain forests and play two main roles: as sources of physical support and as a means of promoting nutrient acquisition.

Transport and Storage of Carbohydrates, Lipids, and Proteins

Storage of reserve substances in living parenchyma cells in the rays and the axial system is the third main function of wood. In contrast to all other cell types of the wood body, which die after wood formation has finished, parenchyma cells can stay

alive for a substantial time. Within the physiologically active sapwood, water transport takes place in vessels and tracheids, while storage of reserve materials occurs in the living parenchyma cells. In general, carbon can be stored as nonstructural carbohydrates such as starch and soluble sugars as well as fat (Höll 2000; Sauter and Witt 1997), while proteins can also be accumulated in certain species. With regard to the predominant carbon storage material, trees can be classified as starch trees (e.g., most ring-porous species) or fat trees (e.g., most diffuse-porous angiosperms). The dominating carbohydrates in trees are starch and sucrose, glucose, fructose, and, in few species (e.g., *Araucaria*, *Populus*), maltose. In trees of the temperate hemisphere, soluble carbohydrates (glucose, fructose, sucrose and its galactosides) act as effective cryoprotectants in winter (Guy et al. 1992), while starch is deposited in summer (Magel 2001). The interconversion of starch-sugar and sugar-starch is enabled by enzymes of starch and sucrose turnover (Magel 2001). Regarding the so-called fat trees, triacylglycerols (TAG) are the dominant food reserves. While in the sapwood of softwoods TAG pools do not change significantly from spring to autumn, clear changes in the amount of storage lipids are found in linden trees from the dormant to the growing period (Magel 2001). The third group of storage materials within the sapwood is proteins, which were first discovered in fruit trees (Tromp and Ovaa 1973) and later in other angiosperm and gymnosperm species as well. In summer, protein levels are low in the sapwood, with their formation starting within the yellowing of leaves (Sauter and Witt 1997), initiated by rising levels of nitrogenous components (Magel 2001). Apart from carbohydrates, fats, and proteins, numerous tropical tree species store crystals in ray and/or axial parenchyma cells: a feature which can be used to determine the tree species. To summarize, the major storage substances of starch, fats, and proteins are accumulated in parenchyma cells of the sapwood during favorable periods to be used up at times of demand.

Conclusions

The evolution of life in the primeval forest at the equator has neither been disturbed by ice ages nor by land subsidence and flooding; hence, plants, including trees, have been able to develop an extraordinary and unique diversity of species. Distinctions between species can be highly developed, but also variations within the same species can be pronounced. In their phenotype, tropical tree species are very often specialized for their exceptional habitat, resulting in high, branchless stems, due to the competition for light, and extensive buttresses, due to the competition for nutrients as well as for enhanced stability.

Along with the diversity of tree species, tropical wood also varies greatly in its appearance. The term "tropical wood" in everyday language describes the heartwood of tropical broadleaf species. Many of those feature excellent mechanical properties based, for example, on high density as well as excellent durability, based on their broad range of heartwood extractives. The outstanding colorings of tropical wood, in combination with its distinct textures, make it very sought-after in international markets.

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