

Many of these, as happened with crop domestication, represent dramatic changes in the structure of a tree and how that structure functions. Our ability to visualize this 'new' tree is extraordinarily difficult as we are so used to incremental changes. Modeling, including the use of 'virtual plants,' offers one approach. However, there are large segments of society who, for one reason or another, will find such a transformation of a tree unacceptable. Relying on either conventional silviculture or further increases in a CO₂ fertilizing effect to meet future fiber and fuel needs may not be realistic. Given continued population growth, increased consumption, the relatively low carbon costs of using wood and wood products (vs. other products for construction, for heating, for chemicals), it would seem unwise not to explore this opportunity. Had the same constraints been placed on the original progenitors for our current agricultural crops, I would not be writing and you would not be reading.

Summary and Conclusions

Understanding how the whole organism functions, and that it is not merely the sum of its parts, that it can be represented as an 'extended phenotype,' and that an untapped potential for change in its phenotype exists are the key messages developed within this article. It is also clear that there are very large unknowns: what are the controls on age- and size-related declines in productivity, how is 'information' transmitted through an organism, and how is transport in the phloem and the xylem controlled and integrated? Finally, what changes in structure and function would accompany domestication and how does our current understanding of whole tree physiology aid or impede domestication?

See also: **Ecology:** Forest Canopies. **Environment:** Carbon Cycle. **Hydrology:** Hydrological Cycle. **Soil Biology and Tree Growth:** Tree Roots and their Interaction with Soil. **Tree Physiology:** Canopy Processes; Mycorrhizae; Nutritional Physiology of Trees; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Tropical Tree Seed Physiology; Xylem Physiology.

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Xylem Physiology

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Introduction

Secondary xylem, or wood, is a product of the activity of a secondary meristem, the vascular cambium. Those plants which possess one can be very long-lived, their life span being only limited by catastrophic events such as gales and lightning strikes or disease. More wood is added each season, with the result that it is the most abundant natural product on earth. The cambium and xylem differentiation have been the subjects of a number of monographs and it is not the purpose of this chapter to précis these works. Rather, some important aspects of the way the structure of wood is related to its behavior and

properties postdifferentiation will be considered. Only a brief overview can be presented here and the reader is recommended to the list of further reading for more comprehensive reviews.

The structure of wood differs between tree species as a result of local evolutionary pressures and each has its own wood properties. This was exploited intuitively early in human history and is one of the factors that make wood such a variable and useful raw material. The long life span and generation times of trees meant that many also developed the ability to survive the significant changes in environmental conditions which occur from time to time. This is evidenced by the fact that arboreta, botanic and private gardens, city parks, and streets are furnished with tree species which evolved in regions whose climate and range of day lengths were markedly different from those in which they are now growing successfully. Sometimes the trees are more successful in terms of growth in an alien environment than in their native home. *Pinus radiata*, a native of the Monterey peninsula, where it is slow-growing and of poor form (from a forester's viewpoint), has become the linchpin of the New Zealand forest industry, where it is fast-growing and of good form (see **Tree Breeding, Practices: *Pinus radiata* Genetics**).

The evolutionary process has thus resulted in selection of trees which may be considered over-designed for survival in their environment as it is today. A 500-year-old oak tree growing in the UK will have experienced the mini ice ages of the seventeenth and nineteenth centuries, and periods of global warming in between. It is often only when trees are growing at the limits of their geographical range where environmental conditions are limiting that the value of some morphological and anatomical adaptations can be understood.

The Biological Functions of Wood

Wood has two major functions: firstly, to support the crown of the tree, enabling the leaves to compete for light, and secondly, to provide a conduit for water and nutrients between the roots and the crown. It also incidentally supports the phloem which comprises the inner bark and conducts nutrients from the leaves to other parts of the tree. As the crown moves higher and enlarges, the stem must thicken to support the extra mass. Eventually the wood at the base of the stem may support hundreds of tonnes. The wood must also be able to maintain the tree stem in a vertical posture, and the branches at appropriate angles, while being able to absorb any physical stresses imposed by the environment without breaking.

Wood also has to conduct water efficiently and safely in conditions which may vary from extreme drought to flooding or freezing. In some cases, different species have adopted different anatomical strategies to cope with similar environmental conditions. Scots pine and silver birch live side by side in the boreal forests of Scandinavia and northern Europe, yet their wood anatomies are quite different. However, their strategies for coping with winter drought and freezing conditions are equally successful.

If wood were simply dead material it would be unable to deal with many of the stresses encountered by the tree during its life. In fact, the wood of young trees and the outer or sapwood of older trees may contain as much as 50% of living parenchyma cells. These cells have been regarded as being mainly for storage and, in the case of rays, for radial transport of water and raw materials. As will be described below, however, they are also involved in defense and in controlling water movement. Wood is thus far more active in its own interests than appears at first sight.

The Cellular Structure of Wood

The anatomy of wood has been amply documented in the literature. It is made up of two cellular systems, the axial system, responsible for structural support and vertical water movement, and the ray system, which provides a pathway for radial movement of water, nutrients, and other materials. A few woody species, for example, members of the genus *Hebe*, lack rays, but this is comparatively unusual. The wood anatomy of coniferous trees (gymnosperms) is fundamentally different from that of broadleaved trees (angiosperms) in that the axial system comprises a single cell type, the tracheid, which is responsible for both support and water conduction (**Figures 1 and 2**). Angiosperms have evolved a system in which the water-conducting elements are aligned to form tubes (vessels). These are interspersed among other cell types, predominantly fibers and parenchyma cells (**Figures 3 and 4**). There are a few exceptions to this in primitive families such as the Winteraceae, Pseudowinteraceae, and Trochodendraceae, which have an anatomical structure superficially similar to that of gymnosperms.

Vessel Distribution and Function

The wood of angiosperms is commonly classified into two types based on the distribution of vessels. In the diffuse-porous type, vessels have a more or less uniform diameter across an annual ring and are dispersed more or less evenly throughout the wood (**Figure 3**). In the ring-porous type, large-diameter

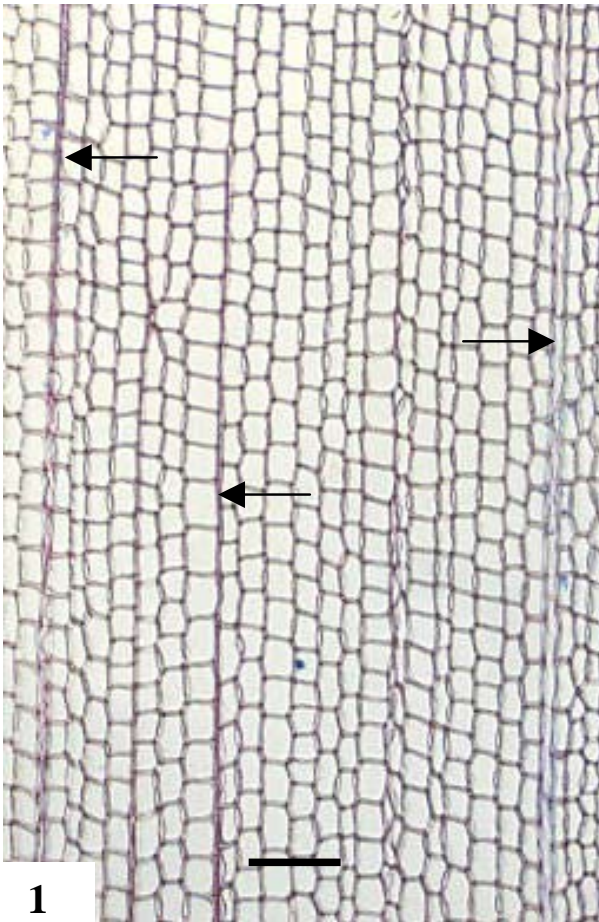


Figure 1 Transverse section through earlywood of *Pinus sylvestris*. The axial elements are all of one type (tracheids), giving the wood a homogeneous appearance. Rays are visible running at right angles to the long axis of the tracheids (arrows). Scale bar = 100 μm .

vessels, often visible to the naked eye, are formed in spring at the beginning of the growing season while smaller vessels are formed during the main period of growth (Figures 5 and 6).

Hydraulic Conductivity and Safety

The size and arrangement of vessel elements have evolved to optimize hydraulic conductivity. Ring-porous species conduct water in sufficient quantities to supply the needs of the crown through their outermost growth ring. They are able to do this because the diameter of their springwood vessels is large. Since the conductivity of a tube is proportional to the fourth power of its radius (Poiseuille's law), a ring-porous species such as *Quercus robur* in which earlywood vessels typically have a diameter of 400–500 μm is theoretically 625 times more efficient than a vessel in a diffuse-porous species like *Liquidambar styraciflua*, in which vessel diameter is 80–100 μm , and 10 000 times more efficient than a

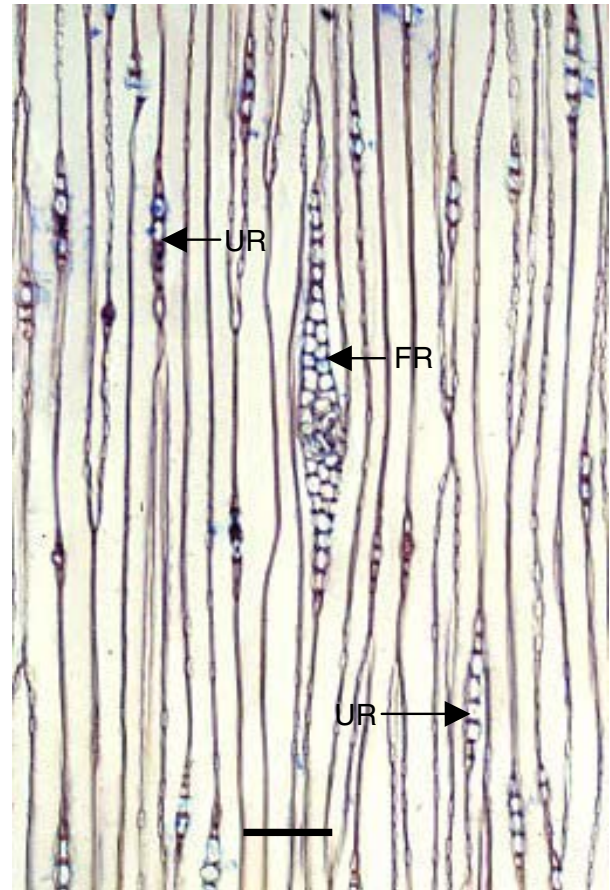


Figure 2 Tangential longitudinal section through earlywood of *Pinus sylvestris*. The tracheids are longer than the section, although a few ends may be seen. The cut ends of uniseriate rays (UR) and a large fusiform ray (FR) can also be seen. Scale bar = 100 μm .

tracheid in a conifer with a diameter of 40–50 μm . Diffuse-porous species and gymnosperms therefore require far more actively conducting elements than ring-porous species and conduct water through several of their outer growth rings. The situation is more complex than this, however. While oak vessels can be considered as relatively unobstructed pipes whose simple perforation plates hardly obtrude into the lumen of the vessel, they have finite length and closed ends. This means that water has to move to adjoining and overlapping vessels through the membranes of the numerous pits between them. Conductivity may also be restricted in some species by the presence of scalariform, reticulate or foraminant perforation plates between the cells which make up the vessels. Measurements have shown that in vessels of *Betula pubescens* axial conductivity is about a third of that in an unobstructed capillary.

In gaining an advantage in terms of efficiency, ring-porous trees have compromised their hydraulic

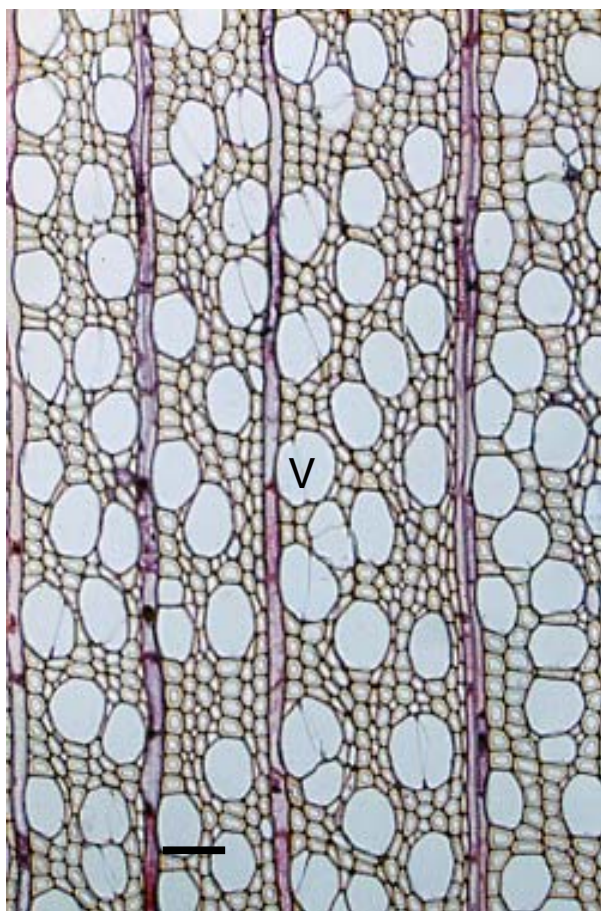


Figure 3 Transverse section through wood of *Liquidambar styraciflua*. Water-conducting vessels (V) are interspersed among smaller-diameter fibres and parenchyma. Scale bar = 100 μ m.



Figure 4 Tangential longitudinal section through wood of *Liquidambar styraciflua*. The cut ends of rays are seen interspersed among the fibers and vessels (arrows). The vessels (V) contain some tyloses (T). Scale bar = 100 μ m.

safety. Damage to a single vessel is much more serious than damage to a single vessel in a diffuse-porous species. This was clearly demonstrated in the case of Dutch elm disease, in which the tree responded to a toxin secreted by the fungal pathogen *Ceratomyces ulmi* by forming tyloses in its vessels, blocking them and starving the crown of water.

In diffuse-porous species, the diameter of vessels increases markedly from juvenile to mature wood and from the top of the tree towards the base in any growth ring. As vessel diameter increases, their number per unit area of cross-section decreases (Figure 7). An explanation for this lies in the fact that, as the tree grows, there is a need for a larger proportion of fibers for support. To accommodate this while maintaining water flow to the larger crown, the tree produces fewer vessels of larger diameter.

Calculations using Poiseuille's relationship and compensating for the reduced area occupied by vessel elements suggest that the wood in outer growth rings in *Betula* has a conductivity three to

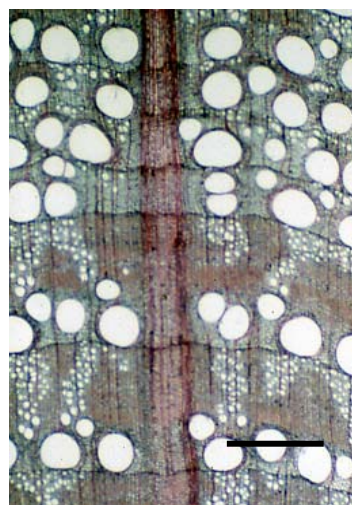


Figure 5 Low magnification of a transverse section through wood of *Quercus robur*. The ring-porous nature of the wood is clearly seen in the two growth rings at the bottom of the figure. At the top, the ring width in four successive years has been reduced by adverse growing conditions. Although the large springwood vessels have been produced in each year, the summer wood is much reduced. Scale bar = 1 mm.

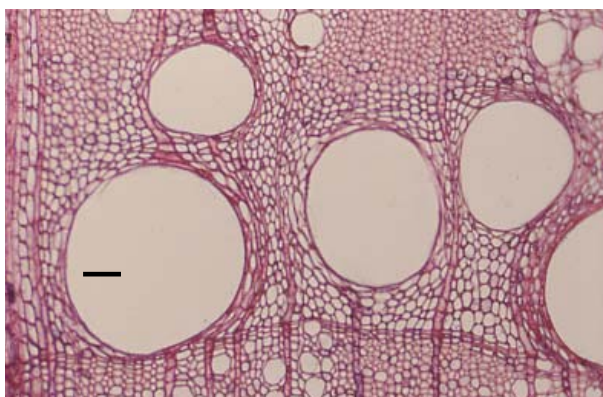


Figure 6 Greater magnification of springwood in *Quercus robur* showing the large diameter of earlywood vessels. Small-diameter latewood vessels are visible at the end of the previous year's growth (bottom of the micrograph) and at the beginning of the summerwood (top of the micrograph). Scale bar = 100 μ m.

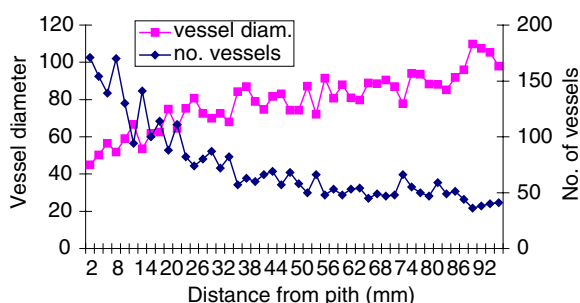


Figure 7 Number of vessels per mm² and vessel diameter in *Betula pendula* plotted against distance from the pith. There is a clear inverse relationship between vessel number and diameter.

five times greater than that in the innermost growth rings. The real difference is probably less than this owing to the restrictions on movement imposed by scalariform perforation plates and pit membranes, although the effect of this would be the same for all vessels, regardless of diameter.

Freezing

Trees in boreal regions must be adapted to cope with low winter temperatures which may freeze the water in their conducting elements. During freezing, air comes out of solution and forms small bubbles which in vessels or tracheids of trees will necessarily be small, and provided the water thaws before the sapstream goes into tension in spring, will be redissolved. If allowed to coalesce with other bubbles before redissolving, however, there is a possibility that embolisms could form. Scalariform perforation plates in the vessels of boreal angiosperms preclude this by preventing movement of small bubbles between vessel elements, while bordered pits do the same for conifer tracheids.

It has been suggested that, since conifers show almost no loss in xylem conductivity following freezing, the vesselless condition of the Winteraceae may in fact represent an evolution from a form possessing vessels. The loss of vessels and the return to a system of tracheids for water conduction enabled the retention of leaves and photosynthesis under freezing conditions.

Xylem Parenchyma

Students are often taught that wood is a dead structure resulting from terminal differentiation of cambial derivatives. As far as the sapwood is concerned, nothing could be further from the truth. In some species 50% or more may comprise living parenchyma. As parenchyma contributes little to the physical strength of wood, and is to some extent undesirable as fines in pulp, its functions in the wood have not been thoroughly investigated. It is, however, certain that it provides storage for materials such as starch and proteins, and secondary compounds such as tannins. It is also certain that it forms the pathway for transport of raw materials from the phloem to the cambium, its differentiating derivatives and developing heartwood. In the latter case they may also be involved in synthesis of the secondary compounds deposited in heartwood.

In addition to the axial parenchyma cells, the ray system is made up entirely of parenchyma cells in all but a few members of the Pinaceae, which also have ray tracheids. Individual parenchyma cells do not exist in isolation but all are interconnected by plasmodesmata, their protoplasts thus forming part of a great symplasm running throughout the living tissues of the tree. Recent work has shown that a system of microtubules and microfilaments, which is continuous with the system present in the axial parenchyma cells of the xylem and parenchyma cells and companion cells of the phloem, runs through the ray system via the plasmodesmata. In view of the known transport functions of these cytoskeletal components it is likely that they provide the system for moving materials around the developing and mature secondary tissues in the stem.

Parenchyma cells actively assist water movement, particularly when transpiration is not possible. Deciduous trees need to build up internal turgor to swell their buds and developing leaves in the spring. They do this by breaking down starch in their parenchyma cells and transferring the sugars to the lumens of adjacent vessels. This creates an osmotic potential, increasing internal pressure and providing turgor for growth. Humans have exploited this phenomenon in the collection of maple syrup and

birch sap, both of which are collected in late winter before budbreak. It is a common misconception that the sugary solution is produced by the phloem, when in fact it is the wood which is tapped to obtain the liquid. Trees in cloud forest, where relative humidity may approach 100%, appear to use the same technique to move water when significant transpiration is not occurring, switching back to transpiration for this purpose and restoring starch levels when the relative humidity falls.

In addition to these functions, the parenchyma system plays a key part in protecting the tree from pathogen attack. Its role can range from blocking damaged vessels by producing tyloses to repairing small cavities caused by the activity of insect pathogens such as cambium miners or by removing bark by accidental damage or herbivore activity. It is also involved in creating barrier zones to resist the spread of decay fungi through the wood.

Tyloses

Tyloses form in some ring and diffuse porous species when embolisms arise in vessels either during drought or in response to wounding (Figure 8a–d). In normally conducting sapwood, the tendency for net water movement from vessels through pit membranes into adjoining living parenchyma cells by osmosis is countered by the tension in the sapstream. When the sapstream is broken, this balance is destroyed and there is a net osmotic flow of water into the parenchyma cells. The resulting pressure increase causes the pit membranes to swell into the vessel lumen (Figure 8a). To prevent rupture of the membrane, the protoplast actively consolidates the membrane and

may even move into the tylosis thus formed. An individual tylosis takes on the appearance of a balloon blown into the vessel lumen (Figure 8c). More usually, however, numerous tyloses arise simultaneously from all or most of the vessel/parenchyma pit membranes in the vicinity (Figure 8b), resulting in a network of cell wall material which may become lignified, blocking the vessel (Figure 8d). The blocking of vessels in this way, while locally useful in preventing water loss and pathogen entry, may have fatal consequences for the tree, as in the case of Dutch elm disease.

Tylosis-like structures have been described as forming in *Fraxinus*, although these structures are not true tyloses. They are in fact formed by extrusion of material into the vessel lumen through the pit membrane from adjacent parenchyma cells. The membrane itself does not grow and bulge into the lumen as in the case of tyloses.

Callus Formation

It is only by having living parenchyma cells that the sapwood can respond to damage caused by phenomena such as branches breaking and removal of bark by herbivores. On release of the constraining pressures by which they are normally surrounded, parenchyma cells dedifferentiate to form callus which eventually differentiates, forming new periderm or meristematic tissues. The role of parenchyma in repairing the damage caused by mining insects is illustrated by the case of *Phytobia betulae* which lays its eggs below the bark on young shoots of *Betula pendula*. The larva tunnels downwards through the layer of cambium and young, differentiating xylem cells. The tunnels are repaired and blocked by the production of callus from xylem ray parenchyma and eventually the cambium itself is restored in the wounded region.

Defense Against Fungal Pathogens

In the case of fungal penetration into the xylem by wood-rotting fungi, the response to infection is the production of a discolored zone of sapwood known as a barrier zone in an attempt to restrict further penetration of the pathogen. Microscopy has shown that vessels in the sapwood in the discolored areas are blocked either by tyloses or by vessel plugs made up of fibrillar material and so-called accessory compounds. In *B. pendula*, the protective layer disintegrates following wounding and it is possible that it is incorporated into the fibrillar deposits extruded into the vessel lumen. These changes, however, are not a specific response to fungal invasion; they can also be induced by simple

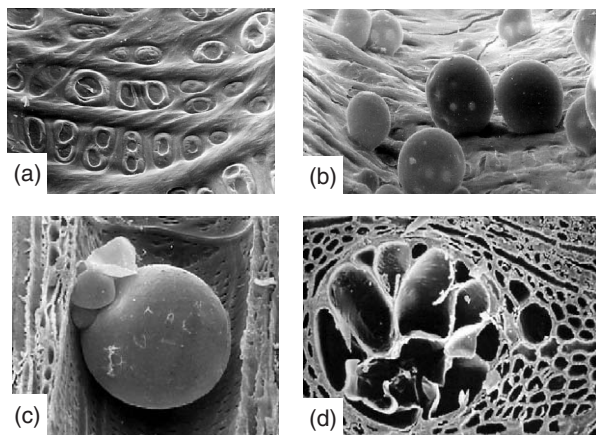


Figure 8 Stages in the formation of tyloses in *Quercus robur*. (a) Pit membranes beginning to bulge into the vessel lumen ($\times 350$). (b) Young tyloses ($\times 250$). (c) Older tyloses almost filling the cell lumen ($\times 80$). (d) Multiple tyloses completely blocking the vessel ($\times 80$).

wounding and are a normal response in branch and stem tissue close to pruning wounds.

Some tree species defend themselves by exuding resins or gums, produced by and stored in parenchyma cells associated with resin canals or gum ducts. Wounding stimulates activity of parenchymatous cells which form the epithelium of these canals and ducts and large quantities of resin or gums are moved to the wounded surface. This prevents or inhibits the penetration of pathogens into the wood through the wound.

The Role of Fibers and Tracheids

The fibers of angiosperm wood and the tracheids of gymnosperm wood are the load-bearing cells in the tree, and are thus the main determinants of the properties of timber in use. In angiosperms the morphology of fibers shows a gradation from cells which are superficially similar to the tracheids of conifers (and which are consequently referred to as tracheids), to libriform fibers, which are shorter and have very little pitting. Intermediate cell types are usually referred to as fiber tracheids. Although these cells are normally dead, the conditions being experienced by the tree when they are formed affect the way the cell wall is laid down, adapting them to their role in helping the tree to survive.

Remarkably, but perhaps unsurprisingly, the structure of the secondary cell wall (apart from some variation in pit size and form) is similar in all of these cell types. The cellulose of secondary walls is laid down as lamellae of parallel cellulose microfibrils. In fibers and tracheids these are clearly arranged into three layers known as the S_1 , S_2 , and S_3 layers, with the suffixed numbers referring to the sequence in which the layers are laid down, the S_1 being the first-formed and therefore outermost layer, the S_3 being the last-formed and innermost layer. The S_1 and S_3 layers have microfibrils arranged at a large angle to the cell axis, while the S_2 microfibrils are arranged at a smaller angle. This structure explains the ability of the cell to withstand, without collapsing, vertical and lateral compressive forces, and in the case of tracheids which are conducting water, the internal tension, to which it is subjected. The angle of microfibrils in the S_2 layer is responsible for many of the physical properties of fibers and tracheids. In the center of a tree where the wood was formed when the cambium was young (juvenile or corewood), the microfibril angle is large (45° or more is not uncommon in conifers). In later-formed wood (mature or outerwood), the microfibril angle is small, typically less than 10° .

A large microfibril angle confers flexibility on the young stem, enabling it to withstand high winds without breaking, while the small microfibril angle in mature wood confers the stiffness needed by an older tree to support large weights. This has survival advantages for the living tree but creates problems in utilization, where juvenile wood is insufficiently stiff to be used for high-value purposes such as construction. This was of little consequence when old trees were harvested and the majority of the wood in the tree was mature. As demand for timber products and pulp has increased, so has pressure for short-rotation cropping of fast-growing trees. Harvesting trees at 35 years of age, for example, means that 50% or more of the tree may comprise juvenile wood and be of low commercial value. This has led to an upsurge of interest in microfibril angle and whether it can be reduced in juvenile wood. The consequences of reducing the juvenile wood microfibril angle for the living tree, where it may make it susceptible to breaking in the wind, will have to be borne in mind by breeders and molecular biologists in deciding how far it is possible to go along this route.

Most interest in microfibril angle has centered on coniferous trees. Measurements on silver birch, however, have suggested that in this species the large microfibril angles associated with corewood in pines are not present. In fact, the angle rarely exceeds 20° in any part of the trunk. Those results that have been reported for hardwood species such as eucalypts and *Liriodendron tulipifera* suggest that microfibril angle in hardwood fibers is lower than that in conifer tracheids. It may be that the presence of vessels interspersed among fibers in a hardwood confers flexibility on the young stem that has to be countered by a smaller microfibril angle in the fibers.

In addition to cellulose, lignin has a major role in increasing the compressive strength of fibers and tracheids, typically comprising some 20% of the walls of fibers in angiosperms and 35% of the walls of tracheids in gymnosperms. It is laid down between the cellulose microfibrils to which it is bound by hemicelluloses. Without the evolution of lignification, trees could not have evolved as tall, massive organisms. Lignin is, however, a major problem for the paper industry where its removal in order to separate fibers and enable production of bright, white paper is expensive. Disposal of the extracted lignin also poses major problems. Genetic modification has been explored as a way of solving these problems, although the essential role of lignin in the successful life of trees means that improvement will have to be limited to producing trees whose lignin is easier to remove, rather than trees without lignin.

Reaction Wood

Trees can modify the structure of the walls of tracheids and fibers during their differentiation to deal with imposed stress. In gymnosperms, the tracheids formed under a compressive load on the lower side of branches and leaning stems, or the leeward side of the tree with respect to the prevailing wind, have a larger than normal microfibril angle and extra lignification. In this case the wood is known as compression wood. In angiosperms, fibers formed under tension on the upper side of branches and leaning stems and the windward side of the tree develop a special wall layer, the gelatinous layer, which comprises almost pure cellulose with a very small microfibril angle. Wood containing these fibers is known as tension wood. Collectively these two types are known as reaction wood and they are essential to the tree to maintain an upright main stem, correct branch angles, and prevent branches drooping under their own weight. However, reaction wood is a serious problem for the timber and pulp industries and has been the subject of intensive research. As with microfibril angle, however, any attempts to modify reaction wood production must also consider the consequences of doing so for the tree.

See also: **Hydrology:** Hydrological Cycle. **Tree Physiology:** A Whole Tree Perspective; Physiology and Silviculture. **Wood Formation and Properties:** Formation and Structure of Wood; Wood Quality.

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Tropical Tree Seed Physiology

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Introduction

Forest trees are a renewable natural resource. Understanding forest dynamics, trees, seeds, and seedlings as indisputable factors and basic units of regeneration has become important in developing effective techniques to promote conservation, management, and rational use of remaining forests. These are significant rudiments to implement successful reforestation programs.

The Angiosperm Seed

Seed Development

The fruit is the structure containing the seed. It develops from the gynoecium of the flower, which is frequently associated with other floral organs. The ovary wall forms the pericarp (fruit wall), and the fertilized ovule forms the seed. Fruit ripening is followed by senescence and, sometimes, dehiscence and abscission.

The process of seed development has three functional phases:

1. Cell divisions to produce the seedcoat, the endosperm, and the embryo (embryogenesis); this stage is characterized by an enhanced increase in fresh weight. Embryo development includes establishing a precise spatial organization of cells derived from the zygote (pattern of formation) and the generation of cell diversity inside the developing embryo (cytodifferentiation). These processes are coordinated to develop a recognizable morphological structure, regulated by the embryogenic pattern of the species (**Figure 1**).
2. Storage of reserves leading to an increase in dry weight.
3. Maturation drying leading to a stage of metabolic quiescence, interpolated between the end of seed development and the beginning of germination.