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Heart Rot and Wood Decay

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Introduction

In natural ecosystems, there is a dynamic equilibrium between the accumulation of woody biomass and its breakdown. In this way, a permanent cover of trees or shrubs is maintained, while the carbon and minerals that they have fixed are recycled. At the same time, the survival of a range of woodland plants is fueled by the energy released in the breakdown of wood. Decay fungi play a major role in the processes of breakdown since, alone among microorganisms, they have evolved the means to break down large volumes of wood completely.

The balance between trees and decay fungi represents the state of play in a coevolutionary battle that has lasted for hundreds of millions of years, and in which wood has been the main prize. The success of trees as a dominant form of land vegetation has depended on their being able to maintain a perennating woody structure, which is their means of attaining both height and longevity. This defensive strategy protects the woody stem against loss of integrity of both its water-conducting and its mechanical properties. A range of agents, especially decay fungi, whose mode of attack is the degradation of the woody cell wall, can cause such damage.

Colonization of the Standing Tree

Heart rots were for a long time regarded as the primary cause of decay in standing trees. Whilst it is now clear that this is a considerable oversimplification, it remains true that in high forest and mature

amenity trees heart rots are still a major cause of economic loss and deterioration. Based on the concept that either the distribution of water and its mutual relation with aeration are primary determinants of colonization patterns, five distinctive colonization strategies are recognized:

- heart rot
- active pathogenesis
- specialized opportunism
- unspecialized opportunism
- desiccation tolerance.

Most heart rot fungi have a stress-tolerant colonization strategy, i.e., they colonize the tree via exposed heartwood or ripewood (**Figure 1**). Although the heartwood of many tree species does exhibit a high concentration of antifungal extractives (e.g., polyphenols, tannins), heart rot fungi have adapted to the adverse conditions (low oxygen concentrations, high carbon dioxide concentrations, low moisture content). Thus, those features that render functionally intact sapwood nonsusceptible to decay are avoided. Moreover, after colonization of the tree via infection courts such as logging scars, branch stubs, fire scars, broken tops, pruning wounds, and severed roots, decay fungi can degrade the heartwood without inducing the host response system of the tree.

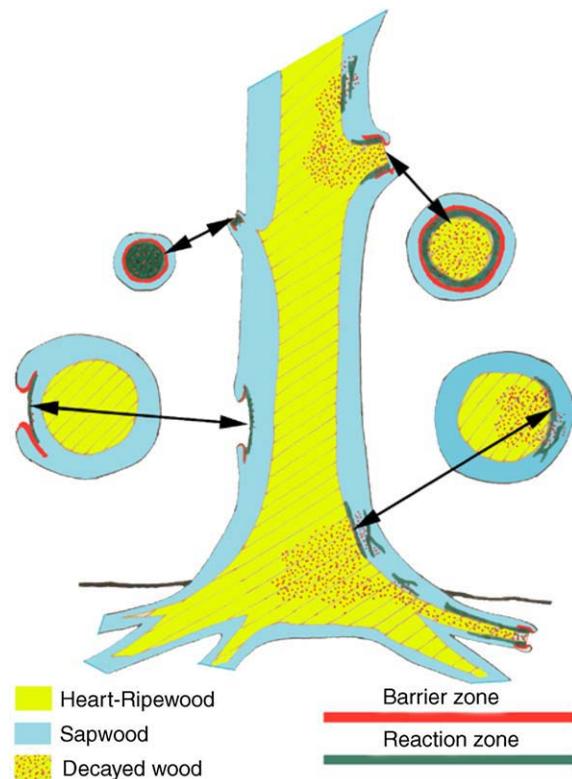


Figure 1 Infection points for decay fungi and associated host response mechanisms within the tree.

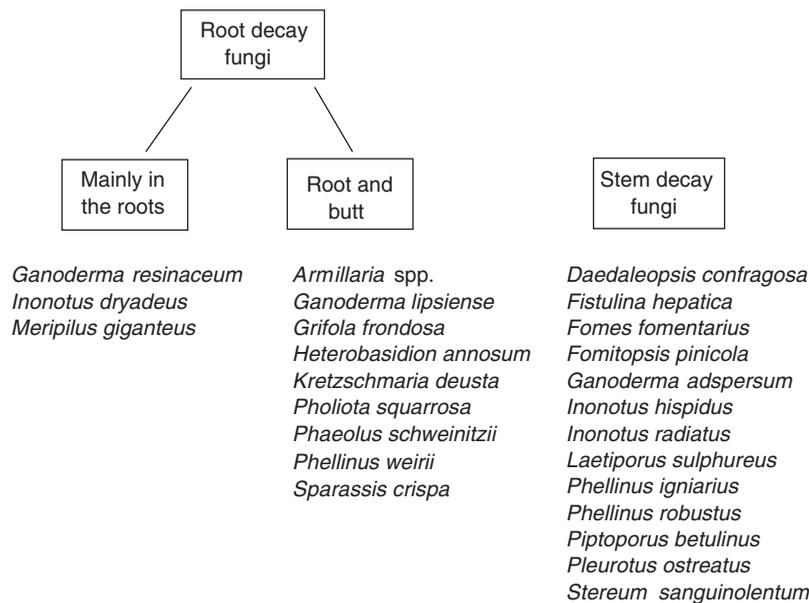


Figure 2 Classification of decay fungi according to the position of rot within the tree. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzzerlegung*. Rombach, Freiburg, Germany.

Wood decay fungi are separated into top rots and root or butt rots depending on which part of the tree is affected. Important agents of decay in trees are listed in **Figure 2**. Top rot decay fungi are found in the wood of the upper parts of trees. They seldom progress very far into the roots and therefore do not spread from one tree to another via roots. Root and butt rot fungi colonize the lower stem and roots of trees. Some parasitize the cambium of roots while others remain within the central xylem and can be classified as saprophytes.

The Construction of the Woody Cell Wall

A full understanding of the interactions between decay fungi and living trees requires studies at various levels; anatomical, physiological, and biochemical. In order to understand the alterations caused in woody cell walls by decay fungi, the micromorphological aspects of the sound wall will therefore be briefly described.

Conifer wood is relatively homogeneous in structure and consists primarily of tracheids, uniseriate xylem rays, and, in some genera, also axial parenchyma and epithelial cells surrounding resin canals. Tracheids are dual-purpose cells combining properties of both mechanical support and water conduction. By comparison, dicotyledonous wood is more heterogeneous, and its mechanical and water conducting functions are served by vessels, while fibers or fiber tracheids mainly supply strength and support. Parenchyma is a more prominent feature

in dicotyledonous wood than in coniferous wood, with most genera having multiseriate xylem rays and varying amounts of axial parenchyma.

The structure of woody cell walls can be seen in **Figure 3**. The cell wall proper consists of a thin primary wall, to which a much thicker secondary wall consisting of three layers (S_1 , S_2 , and S_3) is added after the initial formation of the cell. As in plant cells generally, the walls of adjacent cells are bonded together by a layer termed the middle lamella (**Figure 3**). The main structural component of the walls of juvenile wood cells is cellulose, whose long threadlike molecules are aggregated in microfibrils which provide the tensile strength of wood and are held within a matrix of other polysaccharides, known loosely as hemicellulose. The cellulose microfibrils in the various secondary layers show different orientations in relation to the cell wall axis (**Figure 3**).

During the maturation of wood cells, all the layers of the wall together with the middle lamella become to a greater or lesser extent impregnated with lignin, a hard polymer that provides stiffness and resists compressive forces. Of these, the two phenylpropanoid units guaiacyl and syringyl are the most important monomers of the lignin of trees. Conifer wood lignin consists almost exclusively of guaiacyl monomers, whereas hardwood lignin consists of approximately equal proportions of guaiacyl and syringyl. The proportions of these monomers vary between individual cell types. For example, water conducting cells such as the vessels and tracheids, and the middle layer in the cell walls, have a very

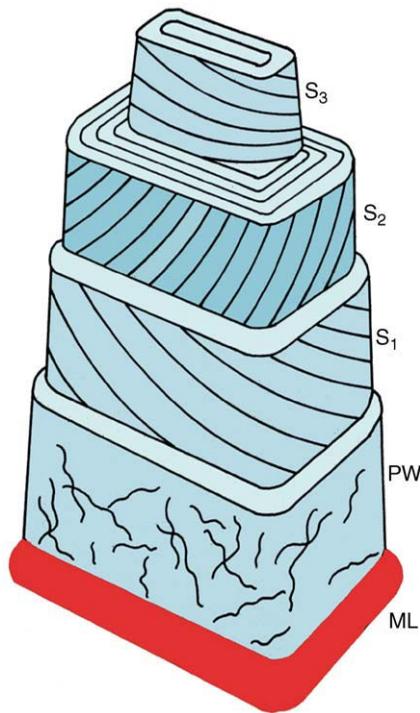


Figure 3 Conventional cell-wall model which distinguishes five cell-wall layers. These are the middle lamella (ML), the primary wall (PW), and the three-layer secondary wall (S): outer (S₁), middle (S₂), and inner secondary wall layer (S₃). The sloping lines indicate the angle of cellulose microfibrils. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Holzzeretzende pilze in Bäumen – Strategien der Holzzeretzung*. Rombach, Freiburg, Germany.

high concentration of guaiacyl and thus are particularly resistant to most soft-rot fungi.

Types of Wood Decay

Brown Rot

Brown rots, in which cellulose and hemicelluloses are broken down with little or no overt breakdown of lignin, are caused exclusively by basidiomycetes. This class contains many families, though the majority of the brown rot fungi belong to the family of the Polyporaceae. Moreover, they are predominantly associated with conifers, whereas most white rot fungi are associated with broadleaved trees. The correlation of brown rots with conifers coincides with the predominantly northern distribution of these fungi compared with the preferential tropical distribution of white rots. In brown rot, cellulose and hemicelluloses are broken down in the wood substrate, while lignin remains preserved in a slightly modified form. In contrast to white rot fungi, most brown rot fungi lack extracellular phenoloxidases. Because of the preferential degradation of carbohydrates, the decayed wood acquires a brittle consistency,

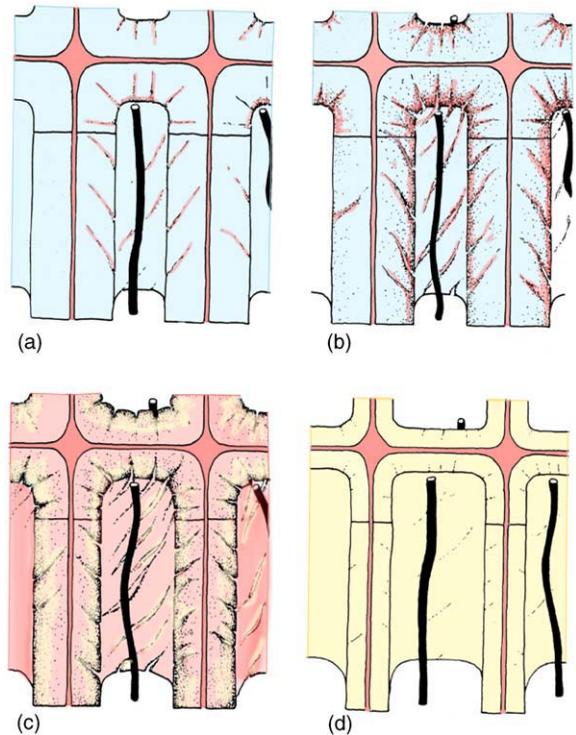


Figure 4 Different stages of brown rot. (a) In early stages enzymes (stippled) penetrate radially into the cell wall from hyphae of *Fomitopsis pinicola* growing in the lumen. (b) At a more advanced stage, enzymes have penetrated into the secondary wall, resulting in the extensive degradation of hemicellulose and cellulose. (c) As cell-wall volume decreases many cracks and clefts appear. (d) At an advanced stage a matrix of modified lignin persists. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Holzzeretzende pilze in Bäumen – Strategien der Holzzeretzung*. Rombach, Freiburg, Germany.

breaks up into cubes, and finally crumbles into powder. The modified lignin gives the decayed wood its characteristic color and consistency.

The breakdown of cellulose by brown rot fungi has been postulated to involve not only enzymes but also a nonenzymic system. In this system, hydrogen peroxidase and iron cause oxidative reactions in the cellulose molecule, thereby enhancing the activity of enzymes (endocellulases) which split the molecule at random points along its length. As a result, the cellulose microfibrils are cut into short lengths, so that a dramatic loss of tensile strength occurs within a very short period of exposure to the brown rot process. The enzymes can then make energy and carbon available to the fungus by further breaking down the remaining short chains and their constituent glucose subunits.

Brown rot fungi cause some alterations of lignin, but lack the enzymes to break it down substantially. Their hyphae cannot erode the lignified cell wall from the lumen outwards, especially since the innermost layer of the wall, the S₃, is especially resistant to physical penetration (Figure 4). Thus the cellulose-degrading

secretions of brown rot fungi have to diffuse into the cellulose-rich S_2 layer within the cell wall. Sufficient diffusion can occur from even a single hypha to cause breakdown of a substantial proportion of the cell wall material (Figure 4). The partial alteration of lignin may facilitate this diffusion, since the intact cell wall is thought to be impervious to large molecules such as enzymes. However, the molecules of the nonenzymic system, which break open the cellulose chain, are thought to diffuse through the cell wall even when lignin is unaltered.

The ontogeny of wood decay by brown rot fungi is uniform, apart from a few exceptions such as *Fistulina hepatica*. The reason for this is presumably the adaptation of these fungal species to the relatively simply structured softwood of conifers, and their restricted ability to degrade lignin. In contrast, white rot fungi, which preferentially occur on broadleaved trees, exhibit an extraordinary diversity in the ontogeny of wood decay.

White Rot

White rots are caused both by basidiomycetes and by certain ascomycetes. The common feature of all these fungi is that they can degrade lignin, as well as cellulose and hemicelluloses. However, the relative rates of degradation of lignin and cellulose vary greatly according to both species of fungus and the conditions within the wood. As with brown rots, there is additional variation related to the preferential decay of different zones within the annual ring. The adaptation of white rot fungi to the much more heterogeneously structured wood of broadleaves, plus their ability to degrade all the cell wall constituents extensively, leads to a multiplicity of different patterns of wood decay. Within this range of variation, two broad divisions are widely accepted: selective delignification and simultaneous rot. White rot fungi degrade lignin by an oxidative process which involves phenoloxidases such as laccase, tyrosinase, and peroxidase. They degrade cellulose in a less drastic way than brown rot fungi, since their cellulolytic enzymes attack the molecule only from the ends, splitting off glucose or cellobiose units. This reduces tensile strength only gradually, unlike the breakdown of cellulose in brown rots, which occurs at random points.

Selective delignification In selective delignification, lignin is degraded earlier in the decay process than cellulose or hemicellulose. The hyphae, which are responsible for secreting the lignin-degrading enzymes, grow in the cell lumina in some cases, so that the lignin is dissolved out of the adjacent cell wall. In other cases, the hyphae penetrate the compound middle lamella between the cells and delignify it so that the cells tend

to separate. As indicated above, cellulose is left relatively unaltered during selective delignification, at least in the early stages of decay. The resulting residual material is stringy in texture, having lost much of its stiffness and hardness while retaining considerable tensile strength. This contrasts very much with brown rots in which cellulose is removed while lignin remains, leaving a very brittle residue.

Many of the fungi that cause selective delignification tend to do so in discrete pockets which show up paler than the surrounding wood due to the high concentrations of cellulose that remain within them. An example of this 'white pocket rot' is caused by *Phellinus pini* or *Grifola frondosa*. When present in otherwise dark-colored heartwood, such pockets are particularly striking, showing up as bright, white scattered zones. It is not surprising that this remarkable pattern was one of the first types of decay investigated.

The different patterns of cell wall degradation during selective delignification can be observed in

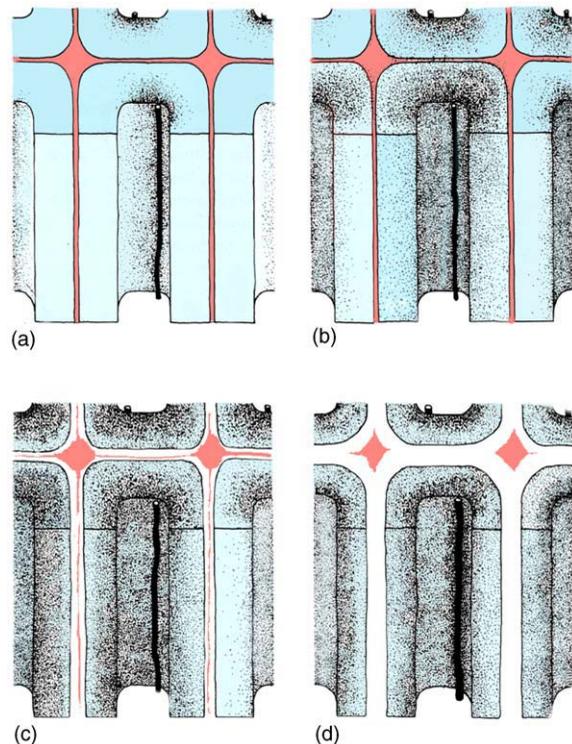


Figure 5 Different stages of selective delignification. (a–b) In early stages enzymes diffuse into the secondary wall from hyphae of *Heterobasidion annosum* growing in the cell lumen. Delignification extends from the secondary wall into the middle lamella. (c–d) During advanced stages, preferential degradation within the highly lignified middle lamellae results in the separation of single cells from one another. Cellulose remains intact during initial stages of decay. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

Figure 5. Initially degradation of the middle lamella, occurring in conjunction with extensive lignin degradation in the secondary wall, is apparent. At an advanced stage individual cells become separated from their matrix. Moreover, extensive delignification may occur in the S_2 layer, leading to the accentuation of radial structures within the secondary wall (S_2).

Although selective delignification is usually associated with cellulose degradation in wood, extreme forms of this type of decay are well known. From the temperate rainforests of southern Chile a type of wood decay which is called *palo podrido* is known. This is a name for decayed tree stems which are used as cattle fodder in southern Chile. Chemical analyses have shown that the wood of some decayed tree stems consists of 97% cellulose and merely 0.9% lignin. Native peasants in southern Chile use the term *palo blanco* for this incredibly white wood, whereas *palo podrido* is a general term for delignified wood.

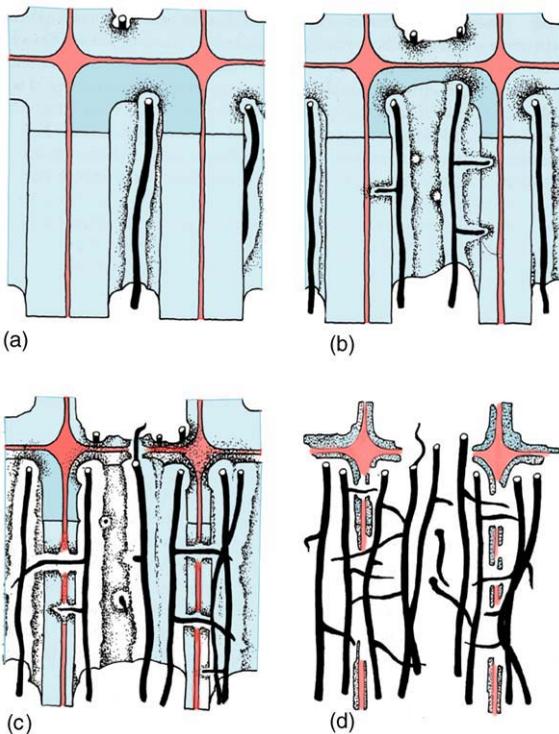


Figure 6 Different stages of simultaneous rot. (a) In early stages, degradation of the secondary wall occurs in the immediate vicinity of the hyphae. (b) The cell wall is progressively broken down from the lumen outwards. Individual hyphae of *Fomes fomentarius* penetrate into the cell wall at right angles to the cell axis. (c) The cell wall becomes increasingly thinner, and numerous boreholes appear between neighboring cells. (d) At an advanced stage, degradation of the compound middle lamella commences. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzzerstörung*. Rombach, Freiburg, Germany.

Simultaneous rot In simultaneous rot, lignin and structural polysaccharides including cellulose are degraded at similar rates by enzymes secreted by hyphae growing in the cell lumen (**Figure 6**). This form of degradation takes place close to the hyphae involved, and results in the formation of erosion troughs where they lie on the cell wall. Fungi causing a simultaneous rot comprise a large group of species which occur commonly in hardwoods, but only rarely in softwoods. The enzymes that they secrete are able to decompose all substances of the lignified cell wall. As the degradation of cellulose, hemicelluloses, and lignin occurs at nearly the same rate, the term simultaneous rot is appropriate, although the general term white rot is often applied. The coalescence of the erosion troughs induced by numerous hyphae results in a general cell wall thinning from the lumen outward (**Figure 6**). Unlike selective delignification, simultaneous rot can lead to a fairly brittle fracture because of the loss of tensile strength from cellulose degradation.

Soft Rot

Soft rots are considered to be chemically more similar to brown rots than to white rots, since they strongly decompose cellulose while leaving lignin only partially altered. Another common feature of both brown rot and soft rot fungi is the demethylation of methoxyl groups. However, the degradation of wall materials at the hyphal contact surface in soft rots is more reminiscent of white rot than of brown rot.

Although soft rot fungi are also able to degrade the lumen surface of the wood cell wall adjacent to the hyphae by erosion (type 2 attack) the formation of cavities within the S_2 layer of the secondary wall (type 1 attack) is the characteristic mechanism of cell wall degradation. Soft rot cavities are initiated by fine penetration hyphae formed from hyphae in the lumina of wood cell walls. The penetration hypha grows through the innermost S_3 layer of the cell wall to the cellulose-rich S_2 layer where it either branches and grows axially within the cell wall following the orientation of the cellulose microfibrils (**Figure 7**). Fine hyphae that exhibit branching continue hyphal extension for a short period, but then cease apical growth. At this stage a cavity is formed within the secondary wall around the fine hypha, which increases in diameter as the cavity develops. This is then followed by a further phase of apical growth at the hyphal tip, producing a needlelike proboscis hypha. This process repeats itself many times over, leading to the formation of a spiral chain of cavities within the wood cell wall, all orientated to the angle of the cellulose microfibrils and each showing different stages of cavity expansion (**Figure 7**). The repetitive start and stop pattern of apical hyphal

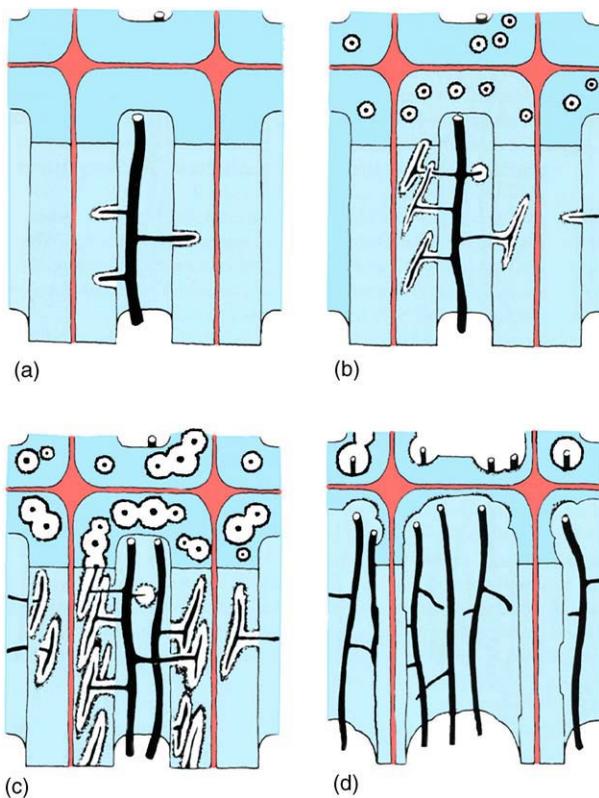


Figure 7 Different stages of soft rot type 1. (a) Penetration of hyphae into the secondary wall. (b) Branching and growth of the hyphae parallel to the alignment of the cellulose microfibrils in the S_2 layer. (c) Enzymatic degradation of the secondary wall around the hyphae results in the formation of cavities with conically shaped ends. (d) At an advanced stage of degradation by *Kretzschmaria deusta* the secondary wall is completely broken down, whereas the compound middle lamella persists. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzzerstörung*. Rombach, Freiburg, Germany.

growth of results in gradual breakdown of the wood cell wall as the cavities expand and the secondary wall is destroyed.

Traditionally, soft rots has been attributed to deuteromycete and ascomycete fungi (e.g., *Chaetomium* spp.) and have been generally thought not to be caused by basidiomycetes. A major supposed difference between soft rot fungi and wood-degrading basidiomycetes in general is that until recently only the latter were considered to occur deep within large volumes of wood and in the living sapwood of trees. Fungi of the types that are commonly associated with soft rot are active only in the outer layers of dead wood or timber, although they can progress inwards as the surface layers become eroded. In living trees, the most significant role so far attributed to soft rot fungi has been the decay of the bases of dead branches, which results in a form of natural pruning.

Various ascomycetes are known to cause limited amounts of decay in living trees, particularly

members of the Xylariaceae such as *Hypoxylon* spp. However, one member of this group, *Kretzschmaria deusta* (syn. *Hypoxylon deustum*) is exceptional in being able to cause deep-seated and extensive decay in large volumes of wood. It causes a distinctive pattern of decay in all its host species, in which many fine dark zone-lines can be seen. The ability of *K. deusta* to function as a soft rot fungus in living trees is of considerable interest, since this type of decay has not been previously thought to occur within living trees. However, one important aspect of the soft rot decay mechanism is that once fungal hyphae have penetrated into the cell wall and branched along the orientation of the cellulose microfibrils, they are able to avoid toxic compounds that may be present in the wood cell lumen. This can apply to wood preservative chemicals impregnated into the wood, but equally to natural products and extractives deposited in the lumen.

Soft rot caused by basidiomycetes Recent work has shown that the cavity-forming soft rot decay process is not exclusive to members of the lower acomycetes and deuteromycetes, but can be demonstrated in some wood-decay basidiomycetes. Thus, diamond-shaped or rhomboid cavities have been found in the cell walls of wood decayed by basidiomycetes causing white or brown rots. As in true soft rots, such cavities may follow the helical course of cellulose microfibrils. However, soft rot patterns have not until recently been found in the wood of living trees degraded by basidiomycete decay fungi. Observations showed that, the basidiomycete *Inonotus hispidus*, which occurs on living trees of several genera, causing a white rot of the heartwood and sapwood, could produce internal cavities both in artificially incubated wood blocks and naturally infected wood of London plane (*Platanus × hispanica*) and of ash (*Fraxinus excelsior*). Other conditions that seem to favor soft-rot mode of degradation in living trees by *I. hispidus* are found within reaction zones, i.e., regions where the living cells of sapwood have reacted to fungal invasion.

Development of Decay within the Tree

As the growth of decay fungi can effectively only be observed at the anatomical level, microscopical investigations of their modes of action are essential for a better understanding of their behavior within reaction zones.

Many studies attempting to explain the limitations of colonization at the host–pathogen interface have been restricted to the description of discoloration and decay patterns in wood. Alex Shigo’s CODIT-model

(‘compartmentalization of decay in trees’) proposed that, following fungal colonization of the xylem of trees, decay columns are confined within defined compartments in the wood. Such compartments have recognizable boundaries within xylem between a region of decay and surrounding sound wood. Different types of boundary have been identified representing regions of anatomical modification and deposition of materials. Within these zones, tyloses or gummy deposits are found blocking the lumina of vessels and fibers adjacent to parenchyma. In many cases, toxic phenolic substances are present, so that hyphal growth is both physically and chemically deterred within the cell lumina, which would other-

wise provide easy pathways for fungal colonization and surfaces for cell wall erosion (Figure 8). In response to wounding, reaction zones are apparent as areas of discoloration between healthy and infected tissue. Material deposited by the host as a defense mechanism and barrier to invasion is therefore viewed as a form of containment against ingress of air and subsequent colonization by decay fungi. Dynamically, the invasion of living sapwood at a reaction zone margin has been envisaged as a continuous process, the host tissue passing through the sequence functional sapwood, drier transition zone, reaction zone, incipient decay, and decayed wood. More recently, evidence has been obtained showing that in some

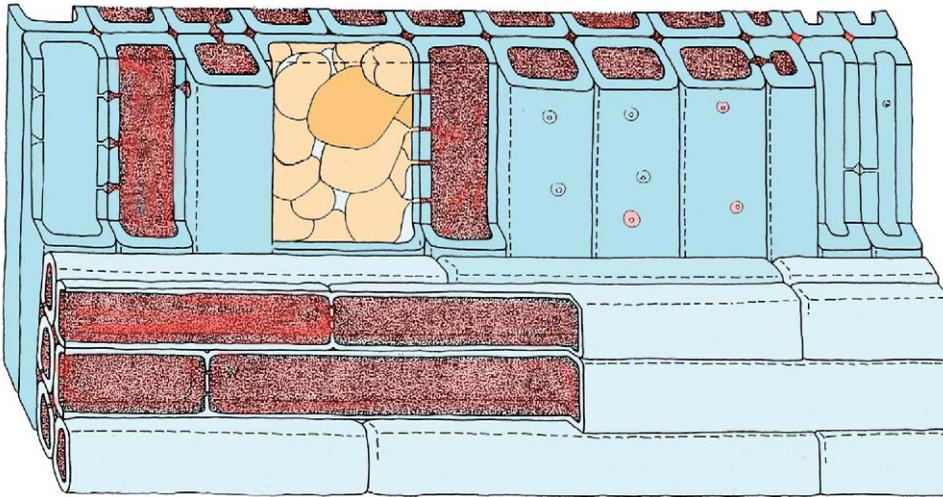


Figure 8 Schematic diagram illustrating the modified wood structure within a reaction zone of beech. Tylose formation is apparent within vessels. The inner cell wall of axial parenchyma cells is encrusted with a polyphenolic layer, whereas cell lumina fiber tracheids are occluded with abundant polyphenolic deposits. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

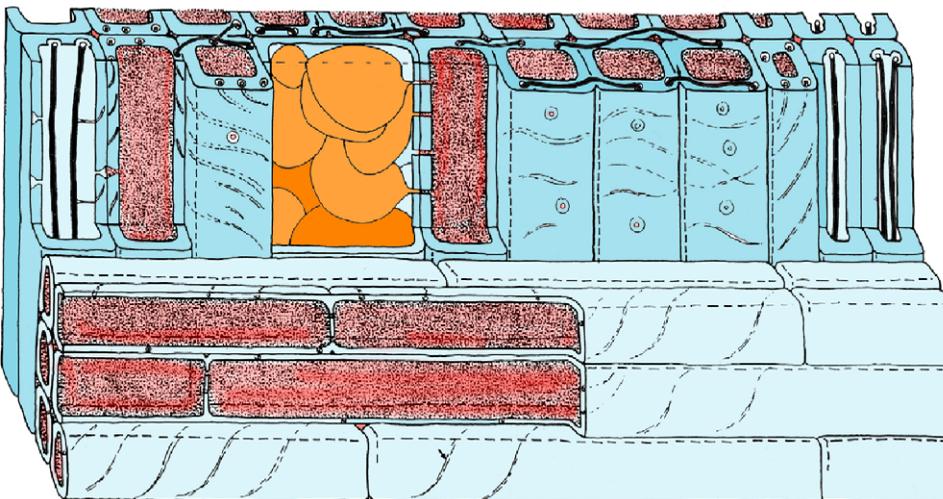


Figure 9 *Inonotus hispidus* defeats reaction zones by penetration hyphae and a soft rot mode within secondary walls of xylem ray parenchyma. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

angiosperms this sequence of continuous pathogen advance does not seem to occur. Thus, it appears that rather than forming a dynamic barrier, reaction zones essentially act as static boundaries to decay. Furthermore, this is supported by the presence of reaction zone relicts within decayed wood, indicating that the invasion of functional xylem tissues by decay fungi in these trees is discontinuous.

The fact that reaction zones can be breached by fungi and the nature of the mechanisms by which this occurs have particular relevance in understanding the invasive potential of decay fungi in standing trees. Knowledge of these mechanisms greatly improves interpretations of the dynamic interactions at the host–pathogen interface. It seems that some decay

fungi can partly escape the adverse conditions within reaction zones by switching their mode of action towards hyphal colonization within the cell walls. Reaction zone penetration by *Inonotus hispidus* in London plane (*Platanus × hispanica*) is accomplished by forming soft-rot-like tunnels through the cell wall (Figure 9). A soft rot mode of growth within reaction zones apparently enables hyphae to circumvent impedances within the cell lumina. Invasion of reaction zones in beech (*Fagus sylvatica*) by *Ganoderma adpersum* is characterized by the preferential degradation of polyphenols (Figure 10). In contrast, *Kretzschmaria deusta* defeats reaction zones in beech by soft rot and preferential degradation of the secondary walls without decomposition of polyphenols

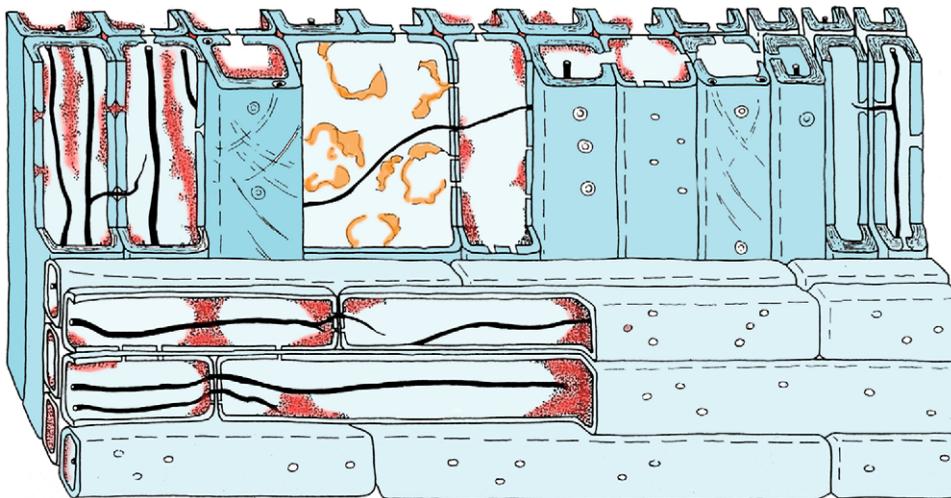


Figure 10 *Ganoderma adpersum* initially degrades polyphenols allowing subsequent hyphal growth through the cell lumina. At advanced stages of decay the fungus causes a selective delignification of the cell walls. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Holzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

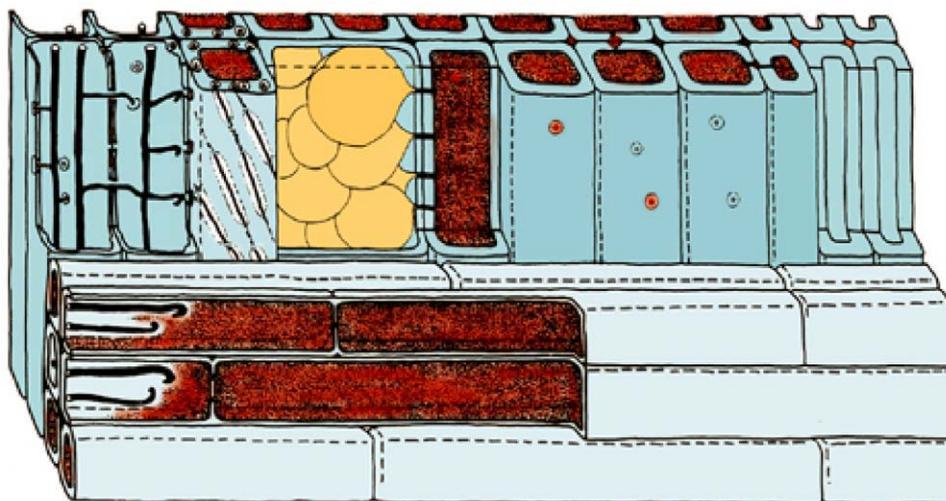


Figure 11 *Kretzschmaria deusta* defeats reaction zones by a soft rot mode without significant degradation of polyphenols. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Holzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

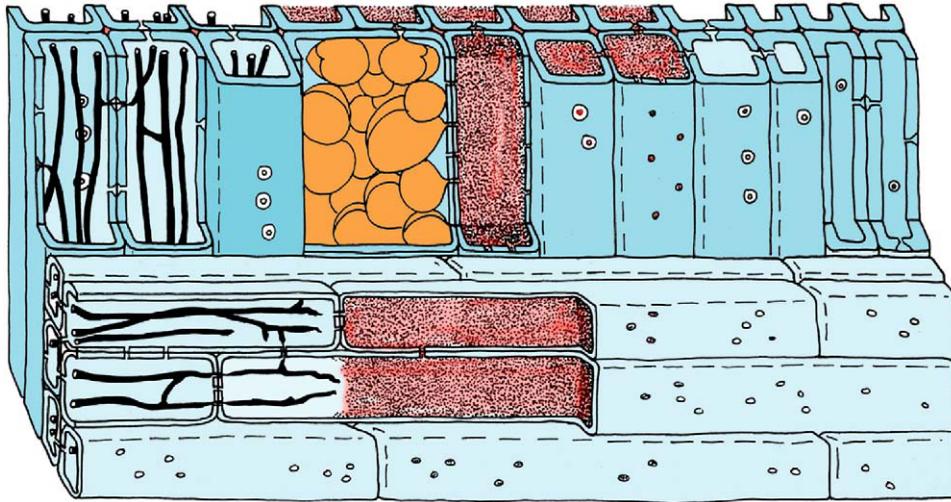


Figure 12 Hyphae of the brown rot fungus *Fomitopsis pinicola* can readily colonize and degrade cell walls of the unaltered sapwood. Due to their limited enzymatic ability they cannot readily penetrate reaction zones in beech. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Bäumen – Strategien der Holzersetzung*. Rombach, Freiburg, Germany.

(Figure 11). Failure of *Fomitopsis pinicola* to invade and defeat reaction zones in beech is apparently related to the limited enzymatic ability and inflexible behavior of brown rot fungi (Figure 12).

On the basis of these observations, it is postulated that *I. hispidus* and other basidiomycetes have the ability to cause a soft rot either in addition or alternatively to their more typical mode of action, i.e., a white rot may be a common phenomenon, which may play a significant role in lesion expansion for a range of other decay fungi. By contrast, more aggressive decay fungi may have a broader enzymatic potential capable of degrading polyphenols deposited in the wood cell lumina.

The relative aggressiveness of decay fungi seems to be a function of their ability to degrade both lignin and polyphenolic compounds formed in response to lesion expansion in the wood. The fact that less-invasive fungi appear to avoid polyphenolic deposits by tunneling into the cellulose-rich regions of the wood cell wall and do not display an ability to penetrate through the lignin-rich middle lamella adds weight to this view.

See also: **Pathology:** Diseases of Forest Trees; Root and Butt Rot Diseases. **Tree Breeding, Practices:** Breeding for Disease and Insect Resistance.

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Disease Affecting Exotic Plantation Species

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Introduction

Tree pathogens in natural forests are typically in balance with their environment. This delicate balance can easily be disturbed through the introduction of an exotic pest or pathogen (see **Pathology:** Diseases of Forest Trees). In natural forests, pathogens play an important role in maintaining genetic diversity of the tree species in these ecosystems. They are also important in removing weak trees from the