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## White-rots, chlorine and the environment – a tale of many twists

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### ABSTRACT

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*Phanerochaete*  
*Phellinus*  
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White-rot fungi possess a unique oxidative mechanism by which the recalcitrant lignin component of wood is mineralised. The activity of lignin-degrading enzymes, chiefly lignin and manganese peroxidases, depends on several small organic molecules. Some of these (e.g. chloroanisyl alcohols) are chloroaromatics and may act as environmental pollutants in the forest soil, whereas the synthesis of others (e.g. veratryl alcohol) requires chloromethane. Certain white-rot genera, notably *Phellinus* and *Inonotus*, release excess quantities of chloromethane into the atmosphere where it acts as a greenhouse gas. On the other hand, their powerful ligninolytic system enables white-rot fungi to degrade a wide range of man-made environmental pollutants, including recalcitrant chloroaromatics such as DDT, PCP, 2,4-D and 2,4,5-T. This review describes the multifarious interactions of white-rot fungi with their environment via the chlorine cycle.

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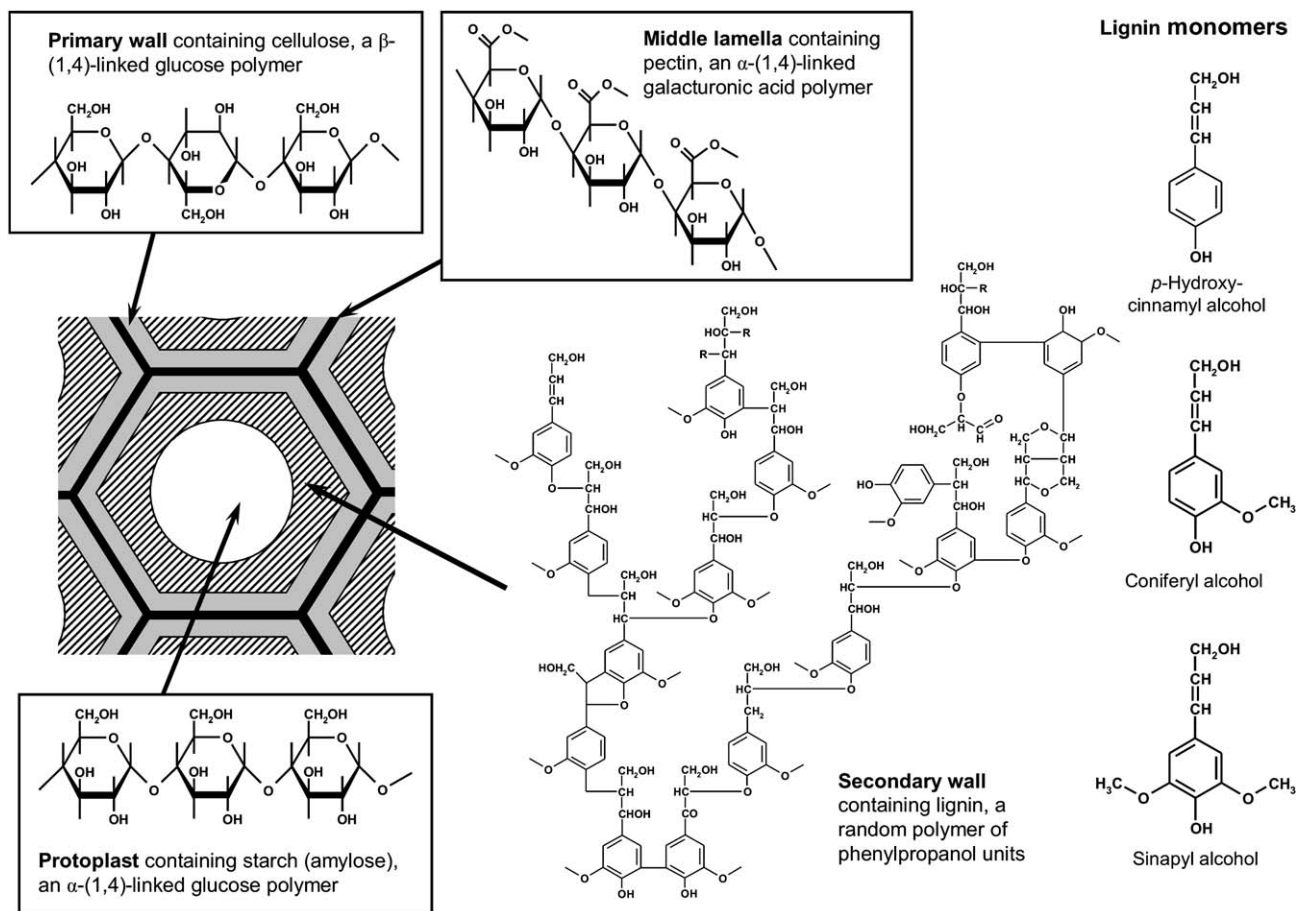
### 1. White-rots and brown-rots

Wood is formed when the protoplasts of plant cells, initially separated by the middle lamella and the primary wall, lay down a thick secondary wall and eventually die. The main polymers of both the middle lamella and the primary wall – pectin and cellulose, respectively – consist of chains of repeated sugar units which are assembled in a regular fashion by means of specific enzymes (Fig. 1). A further important cell wall polymer, hemicellulose, consists of a number of different sugar moieties, but these, like pectin and cellulose, are linked in a more or less regular way which renders them accessible to cleavage by hydrolytic enzymes. Further, the sugars, once released, are readily assimilated and utilised by most living organisms. In contrast, the subunits of lignin, the material making up the secondary wall, consist of phenolic substances which are difficult to degrade. Furthermore, during lignin

biosynthesis these recalcitrant building blocks are cross-linked in a random fashion by way of free radical reactions. Lignin therefore has a complex, non-repetitive three-dimensional structure which renders it resistant to attack by hydrolytic enzymes. In fact, the only organisms capable of mineralising lignin into water and carbon dioxide are a select group of basidiomycetes, the so-called white-rot fungi (Fig. 2). However, even white-rots cannot live on lignin alone but require other, more easily utilised carbon sources to sustain lignin degradation which is thus said to be co-metabolic. Other fungi attacking wood, notably brown-rotting and soft-rotting species, are more or less confined to degrading pectin, cellulose and hemicellulose, leaving behind the lignin which assumes a distinctly brown colour especially when oxidised (Figs 2 and 3). Since the structural coherence is lost with the disintegration of the middle lamella and primary walls, wood attacked by brown-rots cracks, crumbles and ultimately becomes incorporated into

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**Fig. 1** – Carbon-containing polymers and their localisation in plant tissue. Lignin consists of a complex polymer of the three phenylpropanoid units shown, which may be linked in numerous different combinations. The example drawn here has been modified from [Adler \(1977\)](#). Hemicelluloses, heterogeneous chains made up of glucose, xylose, arabinose and mannose, are localised in the primary and secondary cell walls (not shown). Reprinted from [Webster and Weber \(in press\)](#), with permission by Cambridge University Press.

humus. Although the methods by which brown-rot fungi decay wood are in themselves remarkable (see [Green & Highley 1997](#)), the present review will focus on white-rots because of the unsuspected and potentially far-reaching impact of their

activities on the environment. These are directly related to the unique mechanism of white-rot attack on lignin by means of oxidative enzymes.

## 2. The mechanism of lignin degradation

Lignin is degraded by way of free radical intermediates similar to those involved in its synthesis. In order to avoid a futile depolymerisation-repolymerisation cycle, the concerted action of several enzymes is required to break down lignin. Much of the initial work on lignin degradation, including the discovery of the major lignin-degrading enzymes and development of theories on their mode of action, was carried out with *Phanerochaete chrysosporium*, the most thoroughly studied of all white-rot fungi ([Glenn et al. 1983](#); [Tien & Kirk 1984](#)). The initial attack on lignin is mediated by lignin peroxidases (LiP) or manganese peroxidases (MnP), and either or both of them are produced by most white-rots ([de Jong et al. 1994a](#); [Heinzkill & Messner 1997](#)). It is unlikely that there is any direct contact between these enzymes and their substrate since the pore size of lignin would be too small to permit the diffusion of



**Fig. 2** – Beech wood colonised by the white-rot fungus *Trametes hirsuta* (left) and by an unidentified brown-rot fungus (right).

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