The Institute of Biology's
Studies in Biology no. 32

Fungal Saprophytism

Second Edition

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General Preface to the Series

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Preface to the Second Edition

Saprophytic fungi are indispensable for the maintenance of the carbon and mineral cycles in nature and are particularly important in the utilization of cellulosic materials which form the bulk of decomposing plant remains. As a group they can grow in almost all conceivable habitats in which some form of organic carbon is available. They occur in aquatic environments both fresh water and marine. Some even prefer to grow in much more concentrated solutions such as 40–60% sucrose or in very dry environments. They grow from −6 to 60°C, on refrigerated foods and on microbially self-heating composts.

Although much is known about those of economic importance such as wood-degrading fungi, there is a dearth of information about many of the others. It is only in the last few decades that studies have been made on fungal ecology. There is adequate scope here for fieldwork and laboratory experimentation. This booklet deals with fungal saprophytes with a bias towards the ecological approach. It omits to cover studies on soil fungi but many of the broad concepts introduced apply equally to these. No attempt has been made to give any taxonomic treatment of the fungi. The scheme followed is that used by WEBSTER (1970).

Cambridge, 1979

H. J. H.

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1 Nutrition of Saprophytic Fungi

1.1 Saprophytism and parasitism

Fungi are heterotrophic for carbon compounds. They are unable to use carbon dioxide as their sole carbon source as green plants can. They require complex organic compounds synthesized by other organisms, especially autotrophic seed plants. Saprophytic fungi either colonize dead plant and animal remains or they absorb organic materials which have exuded or leaked from living or dead organisms. The distinction between saprophytism and parasitism by fungi cannot always be clearly demarcated. Many parasitic fungi can also live as saprophytes either on the host which they have killed or on other dead organisms. The ability to invade living tissues distinguishes them from true saprophytes. They are considered as facultative parasites as distinct from obligate parasites which can only grow and fully develop in association with an appropriate living host. Most saprophytes and facultative parasites can be grown readily in culture whereas it is only recently that a number of the obligate parasites have been cultured axenically.

Many fungi may switch from one type of nutrition to another according to circumstances. A good example is the Basidiomycete, *Armillaria mellea*, the honey fungus, a devastating root parasite of forest trees. After killing its host, it lives on as a saprophyte utilizing the carbon and nitrogen sources in the dead trunk and roots. In addition it can also enter into a balanced mycorrhizal association with some orchids, such as *Gastrodia elata*. Similarly in many green orchids the *Rhizoctonia* endophytes are capable of maintaining themselves indefinitely in the soil either as vigorous saprophytes on cellulosic materials or as facultative parasites causing 'damping off' diseases of seedlings.

This text is concerned with saprophytic fungi which can go through their whole life cycle utilizing dead organic materials, although reference will be made to facultative parasitism where parasitism is an advantage in prior colonization of a particular food base or substratum.

1.2 Carbon sources

Simple sugars are the most readily utilized carbon sources and may serve as the sole source for the majority of fungi. Glucose is utilized by virtually all fungi and, for most, fructose and mannose are equivalent. The only exceptions to this are found in one odd order of Mastigomycetes, the Leptomitales, which includes fungi, such as *Leptomitus lacteus*, that are incapable of utilizing hexoses and other sugars; they grow on acetates and fatty acids in water polluted by sewage.

Xylose is the most generally utilizable of the pentoses and may be superior to glucose for some fungi. Sorbose is anomalous in that it supports good growth of very few fungi and if present may inhibit the utilization of other sugars which alone are readily utilized. It is definitely toxic to others, a property which enables it to be used as a suppressant to retard lateral spread of hyphae in culture.

Sucrose, the characteristic disaccharide of seed plants, is a good source of carbon but is not so universally available as is maltose. Before these can be utilized the fungus must produce the necessary extracellular hydrolytic enzymes to split the disaccharides into their component monosaccharides for absorption. Some Chytridiales, Mucorales, such as *Rhizopus oligosporus*, and Sphaeriales, such as *Sordaria fimicola*, lack sucrase and are thus unable to utilize sucrose. But these are by far in the minority. Many of those which can utilize sucrose preferentially use the glucose moiety before fructose. Cellobiose, one of the hydrolytic products of cellulose is also widely used.

Of the polysaccharides, starch, the principal reserve of seed plants, is a good source for most fungi. It is often a better source for growth than is glucose. The utilization of a slowly hydrolyzable compound, such as starch, is often accompanied by the production and accumulation of smaller quantities of toxic by-products, such as acids, than is the utilization of the equivalent quantity of monosaccharides. The accumulation of such by-products in the immediate environment of the hyphae may eventually inhibit further growth. The very widespread ability of fungi to use such carbohydrates is reflected in the composition of standard culture media. The three commonest media employed are Czapek–Dox solution or agar, a basic mineral medium containing 3% sucrose, 2% malt extract agar containing maltose, dextrose (D-glucose) and dextrin (Table 1) and potato dextrose agar containing potato starch and 2% dextrose (DEVERALL, 1969).

Cellulose, the most abundant organic material on earth, cannot be utilized by all fungi but is slowly hydrolyzed by many. In order to degrade cellulose, fungi must again be able to produce the necessary hydrolytic enzymes. There are thought to be at least two different enzymes involved in its degradation since some fungi can hydrolyze modified cellulose, such as carboxymethylcellulose, but not native cellulose, such as cotton (Fig. 1–1). The exact mode of action of the first of these, called C_1, is not known but it produces linear chains. The second enzyme, Cx, which may be regarded as a 1-4,β-glucanase, catalyzes the hydrolytic cleavage of these to cellobiose. This enzyme also acts on modified cellulose. The cellobiose is then hydrolyzed to glucose by a β-glucosidase. Cellulases are usually only produced in the presence of cellulose and are not secreted in the presence of other readily available carbon sources. They are either bound to the surface of the hyphae and act on the surface with which the hyphae are in contact or they are secreted freely into the environment diffusing away from the hyphae. In the former case one sees zones of erosion around

Table 1 Constituents of Czapek–Dox agar and malt extract agar.

Czapek–Dox agar	
Sodium nitrate ($NaNO_3$)	3.0 g
Potassium phosphate (K_2HPO_4 or KH_2PO_4)	1.0 g
Magnesium sulphate ($MgSO_4 . 7H_2O$)	0.5 g
Potassium chloride (KCl)	0.5 g
Ferrous sulphate ($FeSO_4 . 7H_2O$)	0.01 g
Sucrose	30.0 g
Agar	15.0 g
Distilled water	1.0 l
If glass distilled water is used traces of zinc, copper and manganese must be added. Sterilize at 121°C for 15 min.	
Malt extract agar	
Malt extract	20.0 g
Agar	15.0 g
Distilled water	1.0 l
Unamended proprietary malt extract is suitable. Dissolve malt extract in warm water, add agar and steam until dissolved. Sterilize at 121°C for 15 min.	

hyphae. The latter can be demonstrated by the clearing of finely powdered cellulose dispersed in agar in a Petri dish (Table 2, p. 16). Many cellulolytic fungi will clear the agar in front of the growing colony margin.

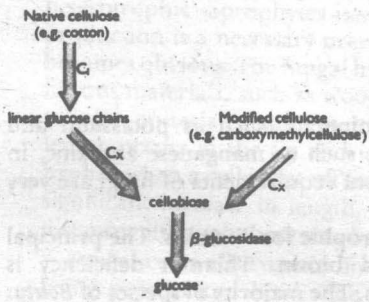


Fig. 1–1 A scheme for the degradation of cellulose.

The list of carbon compounds reported to be utilized for growth by fungi is almost infinite and includes, besides many other carbohydrates, amino acids, organic acids, sugar alcohols, lipids and alkaloids. Amino acids, in addition to providing a nitrogen source, may also serve as a sole carbon source but generally under such conditions ammonia accumulates and raises the pH to levels unfavourable for growth. Of the sugar alcohols, mannitol can be utilized by a much wider variety of fungi than can any of the others. For some it is equivalent to glucose as a carbon source. With trehalose and glycogen it is a widespread storage compound in fungi.

It is difficult to find a carbon-containing compound which some fungus cannot utilize. Certain fluorine containing plastics and a few detergents whose carbon cannot be used by micro-organisms may be the only examples.

1.3 Nitrogen sources

Fungi utilize inorganic or organic sources of nitrogen. Nitrates may be an excellent source for many fungi but inability to utilize them is common and ecologically important. Many Mucorales, such as *Mucor hiemalis* and *Rhizopus oligosporus*, cannot utilize nitrate and thus will not grow on culture media and natural substrata containing simple carbohydrates and nitrogen only as nitrate. This is also true of some Saprolegniales, many Blastocladiales and many wood-degrading Aphyllophorales and Agaricales, such as *Ganoderma lucidum* and *Pleurotus ostreatus*.

Few fungi are unable to utilize ammonia. Many reports of failure to utilize ammonia in culture may be due to inadequate buffering. The large fall in pH, following its uptake, is sufficient to stop growth. In mixtures of ammonia and nitrate, the former is preferentially absorbed. The very few fungi which are unable to utilize ammonia depend upon amino acids. These fungi include some of the aquatic Mastigomycetes, such as *Leptomitus lacteus*. Amino acids are thought to be used as such and built up directly to proteins rather than being degraded to ammonia first. Many fungi can use almost any amino acid as a sole nitrogen source. Asparagine is most often used in synthetic culture media. However, some fungi require one or two specific amino acids, others a whole range. Casein hydrolyzate is a good nitrogen source on which to culture such fastidious fungi.

Claims have been made that some soil fungi at least can fix atmospheric nitrogen. These have never been confirmed. In aerobic microorganisms nitrogen fixation is restricted to some blue-green algae and a few bacteria, such as *Azotobacter*.

1.4 Other requirements

Fungi also require a range of minerals, such as potassium and phosphorus, in quantity and others, such as manganese and zinc, in traces. These major and minor element requirements of fungi are very similar to those of other organisms.

In addition many fungi are heterotrophic for vitamins. The principal vitamins required are thiamin and biotin. Thiamin deficiency is particularly common in the Agaricales. The majority of species of *Boletus* and *Coprinus* are heterotrophic for thiamin. Some fungi are capable of synthesizing the thiazole moiety of the molecule and only need pyrimidine. The ability to synthesize pyrimidine but not thiazole is less common (SCOTT, 1969). Vitamins are required in exceedingly small quantities, in the order of 1–10 $\mu g\ l^{-1}$ or from 4–25 $ng\ mg^{-1}$ of mycelial dry mass as compared with about 5 $mg\ mg^{-1}$ mycelial dry mass of, for example, sucrose.

2 Cellulose Degradation and Wood Decay

2.1 Cellulose and the carbon balance

About one third of the organic matter produced by green plants is cellulose. It is an integral part of the primary and secondary cell wall. In fully mature woody tissues 40–60% of the dry mass is cellulose. In aspen wood, *Populus tremula*, for example, cellulose forms 44–48% of the dry mass. Cereal straws contain about 40% cellulose and seed hairs of cotton, some 95%. It is the major carbohydrate remaining in seed plants on their death and furthermore, it is not withdrawn from plant parts, such as leaves, when they are shed. Degradation of this cellulose is an indispensable process for the maintenance of the carbon balance in nature. Its degradation returns an estimated 85 billion tonnes (megagrammes) of carbon as carbon dioxide to the atmosphere each year. It has been stressed that if its degradation ceased while photosynthesis continued unabated, life on earth would stagnate for lack of atmospheric carbon dioxide in under 20 years.

2.2 Fungi and cellulose degradation

If we accept that the bulk crude source of organic carbon for heterotrophic saprophytes is wood and that to degrade wood cellulase production is a necessary prerequisite, the importance of fungi at once becomes obvious. The fungal hypha is well adapted to attack tough, bulky fibrous materials, such as wood. Fungal hyphae are septate or aseptate, tubular, uniseriate filaments, on average 1–15 μm in diameter. Growth in length occurs at the tip and is confined to this area so that in septate hyphae when a cell is cut off from the apex it is no longer capable of any significant increase in length. There is thus no increase in interseptal distances although there may be increases in diameter and wall thickness.

Fungal cell walls contain 80–90% polysaccharides with the remainder being protein and lipid. The two commonest building blocks of the former are D-glucose in glucans and 2-acetamide-2-deoxy-D-glucose in chitin. The majority of fungi with septate hyphae contain chitin and glucan in their walls. Chitin makes up 3–60% of the dry mass of the walls. The glucans are non-cellulosic and contain in the main 1–3, β- and 1–6, β-linked glucose. They are thus not degraded by cellulases. The Oomycete Mastigomycetes, such as the Saprolegniales and Peronosporales, have been traditionally regarded as possessing cellulosic hyphal walls with no chitin. In *Phytophthora*, for instance, glucans constitute about 90% of the dry mass of the walls and about one quarter of

this has been reported to be cellulose, 1–4, β-linked glucose (Fig. 2–1). The remainder is a highly branched 1–3, β-linked glucan with 1–6, β-linked branches. The cellulose in the hyphal walls of such Oomycetes is poorly refractive and it seems more likely that it is not pure cellulose but a complex branched polymer with mixed 1–3, β- and 1–4, β-linkages. The other large group of aseptate fungi, the Zygomycetes, also appear to possess their own distinctive wall components. The two major components appear to be chitin and chitosan, which is like chitin but non-acetylated. D-mannose in mannans has been reported primarily from yeast cell walls and the combination of mannan and glucan appears to be characteristic of true yeasts and the yeast-like phases of other fungi.

Hyphal walls are usually two-layered with an inner layer of microfibrillar material, usually chitin but cellulose-like in Oomycetes, and an outer layer of amorphous glucan. They are significantly thinner at the apex but both layers are present to form the extendable wall. Behind the apex additional strength and rigidity are given by an increase in diameter, number and packing of the chitin microfibrils and an increase in thickness of the amorphous glucan (Fig. 2–2). Such addition must also mean that there is appreciable incorporation of wall materials behind the growing apex. Autoradiographs made of hyphae which have been fed with brief pulses of tritiated wall precursors have demonstrated that incorporation is highest in the apical 1 μm and falls off rapidly after the

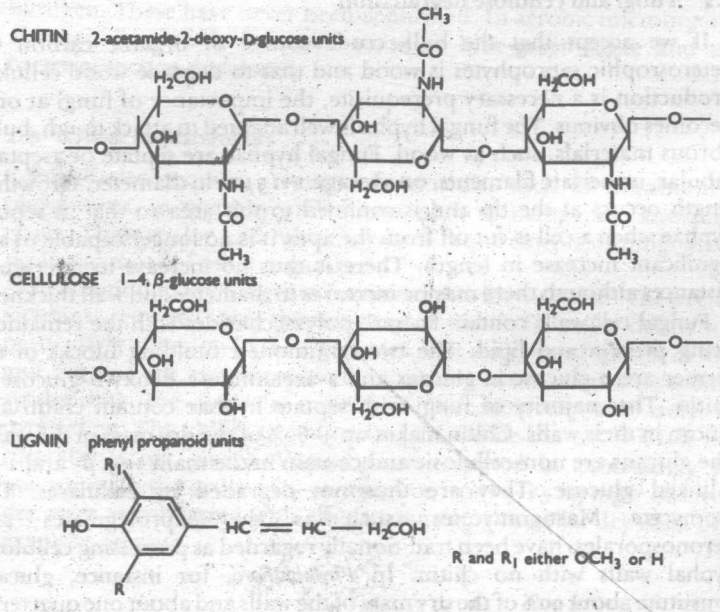


Fig. 2–1 Building units of chitin, cellulose and lignin.

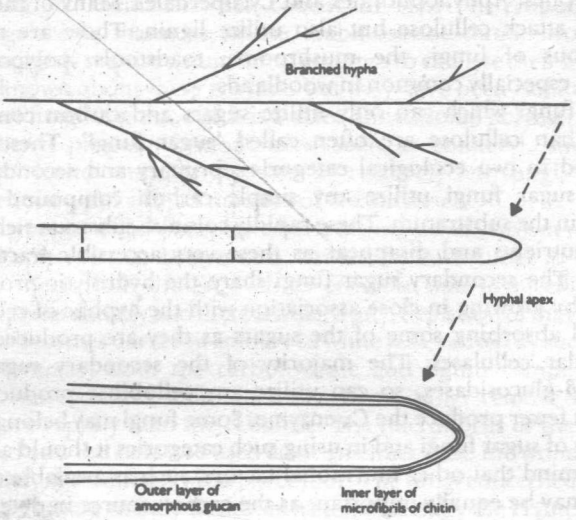


Fig. 2–2 Hyphal structure.

first 5 μm but that there is still appreciable incorporation from 5–75 μm behind the tip. This rigid nature of the wall behind the apex and the complex system of branching ensure that the older rearward part of the hypha is firmly anchored in the substratum and enable the hyphal tip to exert very considerable forward mechanical pressure as it extends under turgor. This, coupled with the production of extracellular enzymes which erode away the substratum, enables the hyphae to produce minute bore holes through cell walls. The much branched hyphal system can thus completely permeate even the hardest woody tissues. Thus cellulolytic fungi have an advantage over cellulolytic bacteria which can only accomplish breakdown by enzymic erosion at an already available free surface. They have no powers of rapid extension by mechanical penetration. They are of lesser importance than the fungi in the decomposition of wood under natural conditions, although they play a part in some heartwood rots and in rotting water-logged wood.

2.3 Sources of cellulases

The distribution of cellulolytic ability amongst the various classes of fungi is of considerable significance. Only a very few Mastigomycete and Zygomycete fungi, such as some members of the Chytridiales, produce cellulases. Cellulolytic ability is common, but not general in Ascomycetes and Fungi Imperfecti. The extent of the ability varies enormously from only slightly to markedly so. The most vigorous cellulolytic fungi are found in the Hymenomycete and Gasteromycete Basidiomycetes such as

the Agaricales, Aphyllophorales and Lycoperdales. Many of these fungi not only attack cellulose but also utilize lignin. These are the most conspicuous of fungi, the mushrooms, toadstools, polypores and puffballs, especially common in woodlands.

Those fungi which can only utilize sugars and carbon compounds simpler than cellulose are often called 'sugar fungi'. These can be considered in two ecological categories, primary and secondary. The primary sugar fungi utilize any simple carbon compound initially available in the substratum. These rapidly colonize substrata rich in such soluble nutrients and disappear as these very accessible fractions are depleted. The secondary sugar fungi share the hydrolytic products of cellulose by growing in close association with the hyphae of cellulolytic fungi and absorbing some of the sugars as they are produced by the extracellular cellulases. The majority of the secondary sugar fungi produce β-glucosidases, so can utilize any cellobiose produced, and somewhat fewer produce the C_x enzyme. Some fungi may belong to both categories of sugar fungi and in using such categories it should always be borne in mind that other nutritional factors, such as available nitrogen sources, may be equally important as the carbon source in determining the ecological niche of these fungi.

Cellulolytic bacteria are more active in anaerobic or near anaerobic environments especially where there is a very large free surface area to volume ratio in their substrata, such as is found in the food material in the rumen of ruminant herbivores. The habit of 'chewing the cud' by the ruminant fragments the cellulose and presents a much larger surface area on which the bacterial cellulases can act.

Amongst animals, some insects, molluscs, a few Crustacea and Protozoa are said to produce cellulases. The best known cellulase producing animal is the snail, *Helix pomatia*, but although it is a voracious herbivore it rarely feeds on bulk cellulose, such as wood. Amongst arthropods, the silver fish (*Ctenolepisma lineata*) and the larvae of the death watch beetle (*Xestobium rufovillosum*) have been shown to produce cellulases in their intestines. This is also true of the earthworm, *Lumbricus terrestris*, but it is not always certain that these cellulases are not produced by bacteria as they are in the intestines of ruminants. The extent to which these, and other animals, utilize cellulose may be, in terms of the overall decomposition rate, secondary in importance to the comminution of the material. Their faecal pellets are usually a much more favourable habitat for fungi and bacteria than are the original food materials (section 3.10).

Compared with the relatively few animal sources of cellulases, there is a much more impressive list of cellulolytic fungi and it is these which are the principal decomposers of wood.

2.4 Wood decay

In addition to cellulose, wood contains 10–30% hemicelluloses and

20–30% lignin. Hemicelluloses consist of short heteropolymers of glucose, galactose, mannose, xylose, arabinose and certain uronic acids. These obviously require a number of enzymes to catalyse their hydrolysis. Little is known about these enzymes but they have been isolated from a number of fungi. Lignin, which is a three dimensional polymer of one or more phenyl propanoid monomers, such as coniferyl, sinapyl and coumary alcohol units, is attacked by relatively few fungi, primarily Basidiomycetes and a small number of Ascomycetes.

Three types of wood decay have been distinguished, brown rots, white rots and soft rots. In brown rots, caused by such fungi as *Piptoporus betulinus*, the carbohydrates, such as cellulose and hemicellulose, are attacked preferentially and there is little, if any, depletion of the lignin thus the wood becomes darker in colour. In white rots, caused by such fungi as *Coriolus versicolor*, both the carbohydrate and lignin components are attacked more or less simultaneously. Some fungi remove the lignin much more rapidly than the cellulose. The microfibrils of the latter are uncovered and the cellulose used later. In either case, the wood becomes much paler, often almost white, in colour. The fungi concerned in brown and white rots are mainly Basidiomycetes, especially the Hymenomycete Agaricales but more so the Aphyllophorales which are almost entirely confined to wood. Their hyphae ramify in the cell lumina and penetrate walls via pits or by producing bore holes somewhat wider than the hyphae. In white rots, there is a general progressive thinning of the secondary cell walls of the xylem outwards from the cell cavity, the enzymes acting in the near vicinity of the hyphae. Decomposition also occurs uniformly in the region of the attack. Whereas in brown rots there is no thinning of the walls. The enzymes diffuse away from the hyphae and act on the cellulose of the entire cell wall at some distance from the hyphae. This leaves a framework of lignin which maintains the general cell shape but with the structural fibrillar components removed, the walls have very little tensile strength and easily crumble. Decomposition also occurs in irregular patches in the attacked wood. This leads to the cubically cracked appearance of brown rotted wood.

The brown and white rots penetrate deep into the wood whereas soft rots are more conspicuous near the surface. In these latter rots carbohydrates are again principally utilized and they are caused by a number of Ascomycetes, such as species of *Chaetomium* and *Ceratocystis*, and some Fungi Imperfecti. Such rots occur in wood with an unusually high water content for example the fill of water cooling towers, underground mining timbers and river and marine timbers. The hyphae penetrate and grow within the secondary cell walls where they create enzymatically chains of cylindrical cavities, with pointed ends, more or less parallel with the microfibrils of the wall (Fig. 2–3).

Many actively cellulolytic fungi are restricted in their ability to utilize the cellulose in lignified plant cell walls by virtue of the intimate nature of the association between cellulose and lignin. A particularly good example

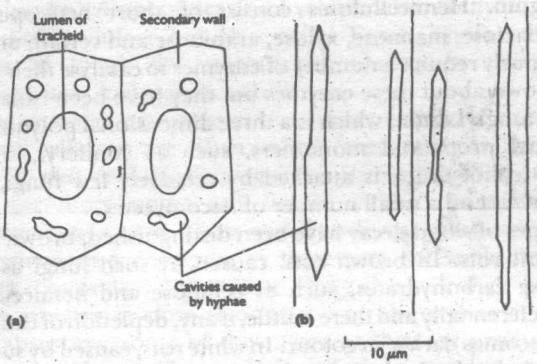


Fig. 2–3 Diagram of (a) transverse and (b) longitudinal sections of tracheids of *Pinus sylvestris* with soft rot cavities in the secondary walls. Note the characteristic pointed ends in (b).

is *Chaetomium globosum* which rapidly degrades cotton cellulose but only attacks wood of high water content and then merely produces cavities inside the cell walls as seen in soft rots. Lignin appears to act as a physical barrier that prevents the cellulases from reaching sufficient glycosidic bonds in the cellulose to permit large scale hydrolysis. Thus the accessibility of the cellulose to the degrading enzymes is a most important factor. This helps to explain the differences between brown and soft rots. The cellulases produced by the two types of rot are similar so that the differences are not associated with the different properties of the cellulases. It is suggested that the brown rots probably have other more effective enzymes which degrade substances, such as hemicelluloses which encrust the cellulose, and others which depolymerize lignin or at least disrupt its association with cellulose. This increases the accessibility of the cellulases so that they can diffuse freely away from the hyphae in contact with the cell walls. After such decay only the skeleton of predominantly lignin remains, which gives the decayed wood its brown colour. In soft rots other such enzymes are lacking and the activity of the cellulases is restricted to the exposed cellulose in the immediate vicinity of the growing hyphae. Similar increased accessibility can be achieved by fragmentation of the wood by, for example, ball milling. Increased hydrolysis of cellulose occurs in sawdust after ball milling and addition of cellulases, rather than addition prior to ball milling. The milling further breaks down the wood into much finer particles exposing a large surface of the cellulose free of its association with lignin. This may be the function of the chewing action of the termite, *Termes obesus*, which is a non-cellulolytic wood feeder. The fragmentation of the wood enables the cellulases produced by protozoans in its intestine to gain access to the cellulose. The termite is dependent upon these protozoans for its nourishment.

2.5 Resistance of wood to decay

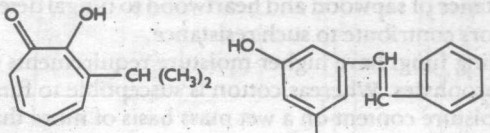
Lignification of cell walls is thus an important factor that contributes to the natural resistance of sapwood and heartwood to fungal deterioration. Many other factors contribute to such resistance.

Wood degrading fungi have higher moisture requirements than most other fungal saprophytes. Whereas cotton is susceptible to fungal attack when it has a moisture content on a wet mass basis of more than 8% and cereal grains more than 13%, wood decay can only be initiated at moisture levels of about 26–32%, depending upon the wood. Dry timbers are thus not susceptible to fungal attack. The optimum moisture content of wood for fungal growth lies around 40% but again this varies with the wood and the fungus. Above the optimum moisture content fungal growth declines as less oxygen becomes available and the cell walls become saturated.

The low nitrogen content of wood also increases its resistance to decay. Woody tissues usually contain 0.03–0.10% nitrogen as compared with 1.0–5.0% in herbaceous tissues. Furthermore the nitrogen in wood is not uniformly distributed. It is highest in the cambium and pith and lowest just outside the pith. The carbon/nitrogen ratio of most woody tissues is thus high, in the order of 350–500:1, and may exceed 1000:1 in some heartwoods. For most fungi a culture medium with such a high carbon/nitrogen ratio would be nitrogen deficient and growth limiting. The wood-degrading fungi are adapted to this by possessing efficient mechanisms of assimilating, utilizing and conserving the meagre supply of nitrogen present. They use large amounts of carbohydrates to obtain sufficient nitrogen from wood in order to form their vegetative mycelium and reproductive structures. The vegetative mycelium of most fungi contains 3–6% nitrogen. This may fall to just above 1.0% in starvation. In some wood-degrading fungi, such as *Coriolus versicolor*, the level may fall lower to 0.2% in starvation. They also conserve nitrogen by the process of autolysis and re-use of the nitrogen content of their mycelium. Obviously this also contributes to their ability to bring about rapid decay despite the comparative deficiency of nitrogen. Although limited, the nitrogen content of wood is very variable and includes proteins, peptides, amino acids and amides, nucleic acids and inorganic nitrogen. All wood-degrading fungi can use ammonia, only a few use nitrate and they grow best on amino sources. They can thus use the majority of nitrogen sources in the wood.

The principal sources of decay resistance in wood are toxic substances deposited during the formation of the heartwood. Most attention has been paid to gymnosperm wood where many phenolic and other compounds have been extracted and shown to inhibit decay. These include terpenoids, tropolones, flavonoids and stilbenes (Fig. 2–4). Their mechanism of fungicidal action varies. Some of the stilbenes probably act as uncoupling agents which inhibit oxidative phosphorylation and thus

decrease the main energy source of the fungi. In angiosperm wood tannins are more important and they would inhibit any fungal phenoloxidases.



A TROPOLONE (THUJAPLICIN) A STILBENE (PINOSYLVIN)

Fig. 2–4 Structure of two toxic chemicals extracted from gymnosperm wood.

2.6 Dry rot

Any wood is completely immune to fungal attack as long as it remains continuously dry. This also applies to structural wood work in buildings. In houses, rotting begins in damp wood in embedded joists, behind skirting boards and in cellars. The most serious cause of wood decay in houses is *Serpula lacrymans*, the dry rot fungus. It establishes itself on a piece of damp wood and during active growth water is formed from the metabolism of the cellulose and excess is exuded in droplets, hence its specific name. The fungus once established and growing vigorously is thus able to provide itself with all the water it needs for growth and may then spread rapidly through dry timbers. It also produces mycelial strands which are an important feature of the fungus. The separate hyphae aggregate into complex strands which are more resistant to desiccation than are the individual hyphae so that they can grow out over exposed drier and non-nutrient surfaces such as bricks and plaster. It is this effective means of extension that makes it so potentially destructive once established. They also, and more important perhaps, form a means by which water and nutrients can be transported from a damp food base or substratum to be utilized in initiating an attack on dry timbers elsewhere in the house and thus its spread from room to room. Attacked wood gradually discolours brown as the cellulose is utilized and cracks into characteristic three dimensional cubes. Decayed wood is friable, light, dry, hence the name dry rot, and powders easily.

None of the timbers commonly used in this country are resistant to attack by *S. lacrymans* when placed under conditions favourable to the fungus, i.e. pockets with high moisture content and lack of ventilation to maintain high relative humidities. Such timbers can be treated with preservatives which confer immunity. Others such as wood of *Thuja plicata* (Canadian western red cedar), *Sequoia sempervirens* (red wood), *Cupressus nootkatensis* (yellow cedar) and *Tectona grandis* (teak) show a high resistance to attack. This resistance is conferred by the presence of such toxic chemicals as the thujaplicins (tropolones) formed in the heartwood.