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The Natural History of the Degradation of Wood [and Discussion]

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The natural history of the degradation of wood

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To the succession of bacteria and fungi colonizing it, wood consists of a series of conveniently oriented holes surrounded by food. The degradation of wood leading to the utilization of that food supply takes place in a number of clearly defined stages, each of which results from the activity of a particular group of organisms. The success of the entire process is governed by the moisture content of the wood. This has to be high enough to promote a flow path for the products of enzyme action yet low enough to prevent water logging, which might produce an anaerobic habitat hostile to the normal wood-decay organisms.

Wood in soil contact takes up an equilibrium moisture content with its surroundings, so that a post or pole will be wet below ground level and comparatively dry above it. Capillary action takes water along the conducting elements of the wood, but once above ground level evaporation will ensure flow through the wood from the high water potential in the soil to a low water potential in the atmosphere. Soil nutrients are carried by the water and subsequent attack by wood-rotting organisms will occur mainly at about ground level where supplies of atmospheric oxygen, soil water and nutrients are plentiful.

The initial colonizers are bacteria, some of which destroy the pit membranes, thereby increasing aeration of the wood by gaseous diffusion. They facilitate access to the supplies of nutrient in the wood by the subsequent scavengers, the primary moulds and sapstain fungi. Later still the true wood-rotting fungi, the soft, white and brown rots, make their appearance; each of these has its own particular pattern of cell-wall breakdown. The latter two groups ultimately dominate the soft rots and open up the structure of the wood cell walls. The partial decay of the walls will finally permit the cellulolytic secondary moulds to gain access to and therefore compete for the carbohydrate contents of the wall.

The situation out of ground contact (for example, window joinery), is similar, moisture being equally important and the occurrence of a similar sequence of colonizing organisms, suggesting that the structure and composition of the wood itself has a part to play in selecting the 'pecking order'.

Introduction

The natural history of the degradation of wood is a part of that greater natural history of living things, whereby the materials manufactured by the green plants and eaten by animals to form their component parts are, after death, broken down into their constituent elements for recycling to form new plants and animals. Were it not for the processes of biodegradation, it has been estimated that it would only take a matter of some twenty years for the Earth's surface to be so thickly littered with plant and animal remains that life as we know it would no longer be possible.

Degradation of wood, therefore, is an overall benefit to Mankind and it is only when Man interferes with this process and expects wood to be a durable material in exposed situations, such as contact with the ground, that it becomes a problem. It then requires both science and technology to prevent the degradation of wood by inducing an effective durability by wood preservation methods.

Wood can be degraded in a number of ways; by mechanical wear and tear; by chemical action; by fire; by weathering; and by the action of organisms, particularly the microorganisms. We are chiefly concerned, at this Discussion Meeting, with the last of these, although some of the reactions involved in the weathering process of wood are also relevant.

WOOD: ANATOMICAL STRUCTURE AND ITS SIGNIFICANCE

The main biodegradation of wood is brought about by animals, such as the wood-boring insects (including the termites, the most destructive agency for degradation of wood in the tropics and sub-tropics) and marine borers, and by bacteria and fungi. The insects and marine borers destroy wood by mechanical means by biting or grinding tunnels through it. Those groups that ingest the bore dust use the wood fragments as a food source that is subsequently degraded by a microbial gut flora inside them by reactions that bear a close resemblance to those brought about by free-living bacteria and fungi. These latter organisms colonize the wood and some may scavenge for cell contents such as protoplast remains or the stored food reserves of the tree, while others utilize the complex polymers of the wood cell wall as their food source.

To the succession of bacteria and fungi colonizing it, wood consists of a series of conveniently oriented holes surrounded by food. The shape, size and orientation of the holes relate directly to the anatomy of the species of wood being colonized, and differences in the chemical constitution of the cell walls or cell contents may affect the ability of a particular fungus to utilize them as a nutrient source.

Softwoods (gymnosperms) are formed largely by tracheids, with the cell lumen completely enclosed by a cell wall, so that movement of water or microorganisms must involve passage through a cell wall or pit membrane. Hardwoods (angiosperms), however, consist of vessels, fibres and parenchyma as well as some tracheids, and here the vessels are usually formed from open-ended vessel elements so that both water and microorganisms can move along the grain in the vessels without necessarily passing through either a cell wall or pit membrane. In addition, the hemicellulose component of the cell wall differs between softwood and hardwood, and in both groups there is a considerable difference between sapwood and heartwood of the same species. Sapwood is likely to contain accumulated nutrients such as starch, residual protoplasts or lipids stored by the tree in the ray parenchyma, which is absent in heartwood. The heartwood is likely to have additional materials deposited in the cell walls during the process of heartwood formation. Such materials are known as extractives and often provide the dark coloration typical of such woods as mahogany (*Swietenia macrophylla*) or ebony (*Diospyros* spp.). In some heartwoods these extractives have some degree of toxicity to microorganisms and may impart a natural durability, as is shown in western red cedar (*Thuja plicata*), teak (*Tectona grandis*) or greenheart (*Ocotea rodiaei*).

The colonization sequence of wood by microorganisms and the development of decay will be affected by these structural and chemical differences, which constitute some of the ecological factors that will determine the process of decay. Other factors include: the rate of growth of the wood when it was being formed in the tree; the orientation of the grain of the wood with respect to the source of invading organisms and water; the moisture content of the wood, both static and in movement; the presence, movement or accumulation of nutrients, pH and temperature. Such factors give rise to a series of ecological niches that may be filled by a range of microorganisms depending upon the particular circumstances.

Water and nutrients

The degradation of wood leading to the utilization of the food supply takes place in a number of clearly defined stages, each of which results from the activity of a particular group of organisms. The success of the entire process is governed by the moisture content of the wood. This has to be high enough to promote a flow path for the products of enzyme action yet low enough to prevent waterlogging, which might produce an anaerobic habitat hostile to the normal wood-decay organisms.

The anatomical structure of wood and its anisotropic nature (due to its cellular orientation) give rise to natural pathways for the movement of both microorganisms and liquids. Corbett (1963, 1965) demonstrated the importance of cellular orientation by showing that fungal hyphae pass quickly through wood along the grain, i.e. from transverse face to transverse face, and more slowly across the grain along the rays, i.e. from tangential face to tangential face. The slowest penetration occurred across both grain and rays, i.e. from radial face to radial face. Here, access must involve passage through either cell walls or pits or both. Bravery (1972) pointed out that this was also true for movement of liquids through wood.

A useful example of wood in ground contact is provided by fence posts (Levy 1968, 1982). These contain a vertical zonation of microhabitats, and yet are basically similar in structure throughout their length. For example, four moisture zones can be found.

(*a*) Conditions of intermittent wetting and drying at the top of the post, where rainwater, dew, frost or snow can accumulate and be adsorbed a short way along the grain before drying out.

(*b*) Permanent low water content above the ground where the air in movement will dry the surfaces and set up a moisture gradient that will give rise to an evaporation of the water in the wood and keep its final moisture content below 20%.

(*c*) Permanent high moisture content below ground level.

(*d*) Excess water producing anaerobiosis where the post penetrates below the water table.

The variety and activity of the microorganisms in each zone differ, and this progressively increases the differences between each zone in what is otherwise a relatively uniform structure of void spaces and cell walls. Baines & Levy (1979) demonstrated that a stick of wood with the grain parallel to its long axis will act as a wick if there is a moisture gradient between the two ends. They quantified this wick action by measuring the rate of water movement through sticks of Scots pine (*Pinus sylvestris*) under different rates of evaporation. A wooden post in soil contact, therefore, takes up an equilibrium moisture content with its surroundings, so that the post will be wet below ground level and comparatively dry above it. Capillary action takes water along the conducting elements of the wood, but once above ground level evaporation will ensure flow through the wood from the high water potential in the soil to a low water potential in the atmosphere. Soil nutrients are carried by the water and subsequent attack by wood-rotting organisms will ocur mainly at about ground level where supplies of atmospheric oxygen, soil water and nutrients are plentiful.

Baines (1983) showed that for a post in the ground, the equilibrium moisture contents of the four zones along its length will remain constant, but nevertheless water will move from zone (*d*) to zone (*c*) and will evaporate at the boundary between zones (*c*) and (*b*). In this region, materials dissolved in or carried by the water will be deposited where evaporation takes place. This is the ground-line region where the most active decay occurs and any such materials may be nutrients for the decay organisms present. Above the ground line, the movement of air across the surface dries the wood to moisture contents at which decay cannot take place. It is thus only at, or near, the ground line that the conditions are both wet enough and yet sufficiently aerobic to allow fungal growth. It is in this region of the post that biodeterioration will occur. The loss of strength that results is normally caused by decay by basidiomycetes, and is the climax of a series of events that have taken place since the post was first put into the ground. Yet basidiomycetes cannot be isolated for at least the first three months of exposure (Corbett & Levy 1963; Butcher 1971; Käärik 1967, 1968; Banerjee & Levy 1971; Clubbe 1978).

Cowling (1965), discussing the nutritional aspects of wood-inhabiting fungi including the basidiomycetes, pointed out the importance of the low nitrogen content of wood. He also considered the availability of cellulose in cell walls and how far the other wall constituents prevented breakdown of the cellulose. Cowling & Merrill (1966) also discussed nitrogen relations of wood and their role in wood deterioration. Greaves (1966) demonstrated that readily available food reserves in the parenchyma of the rays of the sapwood are also important for the initial colonization of the wood. In laboratory experiments with monocultures of fungi and bacteria, he showed that the ray parenchyma was usually the first tissue to be substantially colonized before the initiation of decay in the cell walls. If the nutrients are water soluble they can move through wood and be deposited near the surfaces of cut timber in normal drying and seasoning processes (King *et al.* 1974). Evaporation from the surface causes a movement of water and materials in solution towards the surfaces, and the solutes remain as food sources that encourage scavenging microorganisms to colonize wood.

Although wood is initially a nitrogen-poor environment for basidiomycetes, the nitrogen content can increase by microbial and physical processes. Sharp & Millbank (1974), Levy *et al.* (1974), Baines & Millbank (1976) and Baines *et al.* (1977) demonstrated that the phenomenon of nitrogen fixation can occur in wood providing it is wet enough. Baines & Millbank (1976) also demonstrated the progressive penetration of nitrogen-fixing organisms into wood from an exposed face, probably via the ray parenchyma. Uju (1979) carried out an investigation of the nitrogen relations of wood in ground contact, by adding a solution of a soluble inorganic nitrate to sterile soil in which sterile sticks of Scots pine had been half buried. He showed that an increase in nitrogen content took place not only in that half of the stick below soil level but also in the half projecting above the soil level. He subsequently demonstrated this increase in nitrogen in the wood above ground level in a variety of conditions, and produced evidence to show that some of the increase was caused by the movement of soluble nitrogen, because it could not be correlated with the presence of any organism (Uju *et al.* 1980).

DECAY OF WOOD IN GROUND CONTACT

The decay of wood in ground contact is an interesting example of microbial ecology. A wide range of microorganisms from many diverse taxonomic groups are readily available to colonize and destroy wood in contact with the ground. Some are specific to a particular wood under certain precise conditions of exposure. Others are more opportunist and may play a different role in the decay process under varying conditions. It is not possible to define or restrict each decay type within taxonomic frontiers, because the same organism (e.g. *Phialophora fastigiata*) may, given suitable environmental conditions, fill one or several ecological niches or 'physiological groups' (Clubbe 1978).

Studies on the microorganisms colonizing wood and on the sequence of events leading to the onset of decay have shown the importance of assigning the species involved, irrespective of their taxonomic identity, into a small number of groups relevant to their effect on the wood (Banerjee 1969; Banerjee & Levu 1971; Butcher 1968*a*, *b*, 1971; Carey 1980; Clubbe 1978, 1980*a*, *b*; Corbett 1963; Corbett & Levy 1963; Cowling 1965; Greaves 1966; Käärik 1967, 1968; Levy 1968, 1971, 1973, 1975, 1982; Levy & Dickinson 1980, 1982; Levy *et al.* 1985; Merrill & French 1966). Clubbe (1980*a*, *b*) recognized six such groupings, based on his own observations and other studies published in the literature. (*a*) bacteria; (*b*) primary moulds; (*c*) sapstain fungi; (*d*) soft-rot fungi; (*e*) wood-rotting basidiomycetes (white-rot fungi, brown-rot fungi); (*f*) secondary moulds. These groups are characterized as follows.

(*a*) *Bacteria*

This group includes a range of true bacteria, mainly Gram-positive rods, some of which are capable of fixing atmospheric nitrogen. It also includes some actinomycetes such as *Streptomyces* species, which often show a somewhat random distribution. These microorganisms are usually the first colonizers and may have one or several effects on the wood. (i) A progressive breakdown of the membrane of pits in the sapwood is evident. This opens up the wood structure, allows gaseous diffusion to occur, provides an open pathway for water, and gives access to colonizing microorganisms incapable of causing lysis of a wall or pit (Levy 1973, 1975). (ii) Fixation of atmospheric nitrogen has been demonstrated to increase progressively from an exposed surface into wood (Levy *et al.* 1974; Baines & Millbank 1976; Baines *et al.* 1977). This could provide an additional source of nitrogen, increasing the low level normally found in wood. (iii) There is antagonism or synergism with fungal colonists (Levy 1975). (iv) The presence of bacterial cells and their metabolic products will have changed the internal environment, although no other effect mav be observed.

(*b*) *Primary moulds*

These organisms comprise the first fungal colonists, and can be regarded as akin to Garrett's sugar fungi (Garrett 1951, 1955). They do not appear to possess enzymes capable of degrading cellulose or lignin and do not seem able to attack the wood cell walls. Their food source is likely to be sugars or simple carbohydrates either present in the ray parenchyma of the sapwood or derived from the soil. They can penetrate into wood only through natural openings, such as end-grain apertures or openings through the walls produced by other organisms, i.e. through pits after bacteria have destroyed the pit membrane. Phycomycetes, ascomycetes, and fungi imperfecti are all represented in this group.

(*c*) *Sapstain fungi*

This group, mainly ascomycetes and fungi imperfecti, is characterized by the pigmentation of the hyphal walls that gives rise to a discoloration of the sapwood of infected wood. Like the 'primary moulds', their nutrients are chiefly the food reserves of the tree stored in the ray parenchyma of the sapwood, or residual sugars and simple carbohydrates present elsewhere in the wood. Hyphae of these organisms are able to penetrate through cell walls in a characteristic manner by means of a fine constriction of the hypha in the wall and resumption of its normal size and shape on emergence into the lumen; a single hypha may pass through a number of cells in this way. Several 'stainers' have been shown to be capable of causing soft rot in wood.

(*d*) *Soft-rot fungi*

This group is composed of ascomycetes and fungi imperfecti. They are the first of the wood-rotting fungi to colonize wood in ground contact. They are grouped together on the basis of forming cavities in the S_2 layer of the cell wall (Käärik 1974), which is destroyed by the formation of chains of such cavities. Their micromorphology was first illustrated in the middle of the last century, but their economic significance was not realized until nearly a hundred years later. Findlay & Savory first reported their activities in 1950, and Savory (1954*a*, *b*, 1955) published a series of papers that established the term 'soft rot'. He demonstrated that these fungi were responsible for the decay of the timber fill in water cooling towers. This degradation was previously thought to be caused by chemical breakdown and not to be the result of biological action. The soft-rot fungi become established where there is little competition from other fungi and are known to give rise to serious economic losses of timber. Where the basidiomycetes are able to establish dominance, the soft-rot fungi, although present, never become the main causal organism of wood decay.

Savory showed that soft-rot fungi grew in the S_2 layer of the secondary cell wall of wood cells, forming chains of cavities with pointed ends that were oriented parallel to the cellulose microfibrils in the cell walls. However, Corbett (1963, 1965) was the first to observe the way in which the fungal hyphae penetrated the S_2 layer of the wood cell wall. A short side branch of a hypha lying in the cell lumen penetrated the S_2 layer perpendicular to the cell wall, and, on reaching the S_2 layer of that wall (or after having passed into the S_2 layer of the adjacent cell wall), the penetration hypha appeared to turn through an angle of 90° to lie parallel to the cellulose microfibrils, and branched at 180° to form what Corbett called a 'T-branch'. A cavity was eroded around the hyphal branches forming the cross of the T, and the hyphae increased in girth. Fine hyphal strands, termed 'proboscis' hyphae (Corbett 1963, 1965; Crossley & Levy 1977), formed the initial extension growth of the hypha in the cavity.

Leightley (1977), Leightley & Eaton (1977) and Hale & Eaton (1985*a*, *b* and *c*) studied the development of the proboscis hypha by time-lapse photography. A fine hypha penetrates from the distal ends of the cavities in a direction parallel to the cellulose microfibrils. After a period of growth, further extension of the proboscis hypha ceases; the hypha increases in girth and a new cavity forms around it. After some time, extension growth continues by the development of a new proboscis hypha and the process is repeated time and again. A hypha in a cavity appears to be capable of forming a new T-branch, so setting up a new helical chain of cavities. The cavity itself is straight edged even when viewed under a transmission electron microscope (Findlay 1970). This suggests that the action of the system in forming the cavity is very exact, and that at no time does the enyme system diffuse freely into the wood cell wall beyond the sharp edge of the cavity. Montgomery (1982) and Green (1980) suggest a possible reason for this behaviour.

The pointed ends of the cavities have given rise to much speculation and many authors have attempted to explain their formation in relation to the fine structure of the cell wall. Preston (1979) suggested a mechanism based on the differential rates of flow of the system through the non-crystalline regions of the cellulose microfibrils. Hale & Eaton (1986) have also recently published on the subject.

Whatever the mechanism by which these cavities are formed, the effect on the wood structure can be devastating. Zainal's transmission electron photomicrographs (Zainal 1976*a*, *b*) show that the entire secondary wall apart from a residue of the S_3 layer can be removed during soft-rot attack on a birch (*Betula*) fibre. Dickinson (1982) has pointed out the importance of these organisms for decay in circumstances when basidiomycetes do not develop.

(*e*) *Wood-rotting basidiomycetes: white-rot and brown-rot fungi*

Until 1950, when Findlay & Savory first reported soft-rot fungi, basidiomycetes were regarded as the only fungi capable of causing severe economic loss of timber. *White rots* destroy both the holocellulose and lignin in the wood cell walls, bleaching the wood, whereas the *brown rots* only utilize the holocellulose, leaving the lignin of the wood as a brown, brittle, and friable residue.

Bravery (1971, 1972, 1975, 1976) published an outstanding series of scanning electron photomicrographs that illustrated another fundamental difference between the attack by white-rot and brown-rot fungi. His observations were confirmed by Nasroun (1971) with other basidiomycetes. Bravery showed that the hypha of a white-rot fungus penetrated into the cell lumen and lay on the inner surface of the wood cell wall. Lysis of the wall occurred along the hyphal contact, forming a groove or trough with a central ridge on which the hypha rested. As the hypha branched, so new troughs were formed and eventually the new troughs coalesced, eroding the wall of the wood cell. The hypha was able to penetrate through the S_3 layer of the cell wall and well into the S_2 layer; if the trough was parallel to the microfibrils its edges were smooth, but if it cut across their orientation the edges were ragged and the ends of the cellulose microfibrils could be seen clearly. The formation by white-rot fungi of troughs in the cell wall suggests some restriction to the free diffusion of enzyme away from the hypha. Montgomery (1982), Green (1980) and Green *et al.* (1980) give possible explanations for these characteristics.

The brown-rot fungi show a different micromorphology (Bravery 1971; Nasroun 1971). The hypha again penetrates the lumen and lies on the inner surface of the cell wall. The appearance of both the hypha and the S_3 wall layer change very little, but the other layers are completely altered by breakdown of the holocellulose. The resulting friable residue, with its high lignin content, looks more like expanded polystyrene or foam rubber than the normal smooth texture of unattacked walls.

In this case, the active agent appears to be unrestricted and some component of the enzyme system seems to diffuse completely through the wall layers, although it does not penetrate through the primary wall–middle lamella complex into adjacent cells (Crossley 1979). The concept of the activation of a small radical, i.e. veratryl alcohol, capable of penetrating through the cell wall polymers and breaking them down at a distance from the enzyme source (Harvey *et al.* 1986) provides a simple explanation to these observations.

(*f*) *Secondary moulds*

The final group of organisms are 'secondary moulds'. This group includes all those fungi that do not appear to attack wood itself but possess an active cellulase system, as exemplified by a clearance of ball-milled cellulose in agar culture. Their position in the succession seems to be associated with the appearance and eventual dominance of the decay fungi, particularly the basidiomycetes. The role of the 'secondary moulds', predominantly *Trichoderma viride* and *Gliocladium roseum*, is probably one of utilizing the cellulose, derived from the breakdown of the wood, which is in excess of the requirements of the decay fungi. This cellulose food source may be a true nutritional excess, or the result of competition between the two groups of organisms for the partially decayed substrate.

MICROBIAL SUCCESSION

Clubbe (1980*a*, *b*) and Clubbe & Levy (1982) described a field experiment of Scots pine and birch sapwood stakes, some of which had been treated with a wood preservative. Clubbe emphasized that the identification of individual species did not help to determine patterns of succession amongst the colonizing organisms or provide a clue to their importance in the onset and development of decay. However, if the effect of each individual organism on the wood structure was taken into account, it was possible to group them into the categories. It was then possible to see patterns of development in both colonization and decay.

The results of Clubbe's isolation technique showed the colonization of birch sapwood stakes at the ground line in the course of a year by the six groups of organism. The bacteria appeared first and were the first colonizers at each depth, but they were isolated with decreasing frequency towards the end of the year. They were followed by the 'primary moulds' that also decreased towards the end of the year. The 'stainers' followed the 'primary moulds' and also showed some decline by the end of a year. The 'soft rots' and basidiomycetes did not appear until three months had elapsed. Both groups had penetrated to 40 mm depth at six months, after which the 'soft rots' declined in frequency of isolation, while the basidiomycetes were clearly the dominant mycoflora with a very high percentage frequency. The 'secondary moulds' followed the basidiomycetes and built up in importance with them. Thus there appeared to be a clearly defined succession of the mycoflora, with the basidiomycetes forming the climax.

A similar sequence of events was shown to occur in Scots pine stakes, although it took a longer time, with no colonization to 40 mm depth from the exposed tangential surface for the first nine months. There was some decline in the frequency of isolation of bacteria and 'primary moulds' by the end of a year, while the basidiomycetes were clearly increasing and appeared likely to become the climax organisms. The soft-rot fungi were never a major component of the mycoflora, while the 'secondary moulds' were building up at the end of the year.

A direct-observation technique (Clubbe 1980*a*, *b*) confirmed these observations and showed some soft-rot decay in birch and a very small amount in Scots pine. After eighteen months' exposure, considerable basidiomycete decay had occurred in both species at a depth of 3 mm from the exposed tangential surface, with birch showing greater decay. In wood treated with a 1% treating solution of a copper chrome arsenate (CCA) wood preservative, the wood-rotting basidiomycetes were totally eliminated (Clubbe & Levy 1982), the soft-rot becoming the climax microflora. In treated birch there was a clear evidence of soft-rot attack, while in Scots pine there was no sign of wall decay although these organisms were isolated with high percentage frequency. Murphy (1982) infers that the basidiomycetes do not colonize the treated wood because they have been excluded from the soil immediately adjacent to it. Here, the soil fungal flora changes as the preservative-tolerant species increase in number and build up an innoculum potential of fungi tolerant to the preservative and thus capable of colonizing the treated wood, where they may reach an untreated portion that they can decay (Murphy & Dickinson 1981).

DECAY OF WOOD NOT IN GROUND CONTACT

The decay of wood in an exposed situation out of ground contact, such as external-window joinery, has been shown to be remarkably similar to the ground-contact situation. Carey (1980, 1983), Mendes (1982) and Le Poidevin (1986) have examined the microbiology involved in the colonization and initiation of decay in simulated window-joinery exposure trials with L-joints on racks out of ground contact. The unexpected initial result was the discovery of Carey of the similarity in the ecological succession of microorganisms, where the same sequence of events took place, although at a shortened time scale. The interesting inference to be drawn from this was the appreciation that it must be the wood itself that 'selects' the microorganisms colonizing it at any period of exposure. In the case of ground contact, the colonization could arise from mycelium and spores in the ground, whereas the L-joints out of ground contact must have been colonized only from air-borne spores deposited by chance on the timber. The anatomical features of the wood and their relation to water form a constant characteristic of both habitats and provide consistency of substrate for the change of conditions that enable specific groups of organisms to develop and at a later stage to be replaced by others.

The natural history of the degradation of wood, therefore, comprises a consistent series of interactions between the anatomical and chemical nature of the wood and the water and microorganisms that enter it and give rise to the breakdown of the complex polymers of the wood cell wall. Access to the reaction sites within the wall will, in general, depend on the sequence of events that constitute the 'pecking order' in the microbial ecology of the habitat.

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Discussion

D. E. Eveleigh. The protozoon *Trichomitopsis termopsidis* has been shown (Odelson & Breznak 1985) to be cellulolytic and to utilize only particulate cellulose in an endocytotic manner.

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