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# Diffuse cavity formation in soft rot of pine

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**Summary** A new type of soft rot of southern pine longitudinal tracheids is described. In this type, soft-rot cavities form by diffuse degradation of the S2 cell wall layer by hyphae growing within the cell wall. Cavity formation is diffuse and irregular as opposed to the restricted, periodic cavity formation typical of type 1 soft rot. Proboscis hyphae are small (diameter 0.6 to 0.9 μm) and rapidly autolyse. These proboscis hyphae are not easily recognizable with light microscopy, especially at later stages of decay, but require transmission electron microscopy to confirm their presence. This may be an alternative interpretation of the type 2 soft rot of softwoods described previously as being caused by lumenal hyphae through an intact S3. Chemical analysis of pine test blocks revealed a greater loss of glucose and an increase of galactose with diffuse type 1 species compared to typical type 1 soft rot species. The term "diffuse type 1" is suggested to describe this soft rot.

## Introduction

Soft rot was first defined anatomically as the spiralling growth of hyphae within the S2 cell wall resulting in chains of cavities with conical ends caused by some Ascomycetes and Fungi Imperfecti (Savory 1954). Courtois (1963) first described the erosion of the cell wall from the lumen surface as different than typical soft rot and later (1965) Corbett used the terms type 1 and type 2 to describe the two types of decay by microfungi. According to Corbett (1965) type 1 was cavity formation as described by Savory (1954) and was observed in the hardwood, birch and in the softwood, Scots pine. Type 2 consisted of a dissolution of the wall (S3 and S2) beneath hyphae in the cell lumen resulting in erosion troughs and V-shaped notches. Type 2 was found in birch but not in Scots pine. Later, Nilsson (1973) in his study of wood-degrading ability of many microfungi, observed erosion of the S2 in pine and spruce by hyphae in the lumen with the intervening S3 layer remaining intact. He expanded the definition of type 2 soft rot to include any degradation by microfungi of the cell wall by hyphae lying in the lumen.

As part of a study to test the soft-rot capabilities of microfungi isolated from fumigated utility poles, light microscopy of pine (*Pinus taeda* L.) and birch (*Betula alleghaniensis* Britton)

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test blocks with potential soft rot (> 2% weight loss) revealed several patterns of cell wall damage (Worrall, Wang 1992). In birch, soft rot types 1 and 2 were observed. Type 1 consisted of chains of conical or tapering, cylindrical cavities in the S2 cell wall layer (typical soft-rot diamond-shaped cavities). Type 2 consisted of erosion notches and troughs in cell walls beneath lumenal hyphae. In pine, type 1 diamond-shaped cavities were observed in longitudinal section. Also in pine, another type of damage was observed which was difficult to classify as either type 1 or type 2. The degradation appeared as large, oblong, irregular cavities most often with rounded edges, but occasionally with tapering or pointed edges within the S2 layer of the cell wall with the S3 remaining intact. Fungal species which caused this type of soft rot were *Alternaria alternata* (Fr.) Keissler, *Scytalidium lignicola* Pesante, *Arthrographis cuboidea* (Sacc. &

Ellis) Sigler, *Chaetomium funicola* Cooke, *Chaetomium aureum* Chivers, *Chaetomium globosum* Kunze, *Phialophora melinii* (Nannf.) Conant, *Bispora betulina* (Corda) Hughes, and *Bipolaris sorokiniana* (Sacc.) *Shoemaker.*

Following the definitions of Corbett (1965), these irregular cavities could not be classified as type 1 because cavities typical of type 1 soft rot were not observed and hyphae were not observed within them. Because hyphae were observed in the cell lumen and not in the degraded S2, it was initially considered that this degradation was the second type 2 soft rot of softwoods that had been described by Nilsson (1973). However, there was a question whether the irregular, oblong cavities observed here fit Nilsson's concept of erosion of the S2 from lumenal hyphae. *Alternaria alternata* has been reported to cause type 2 soft rot of pine (Morrell, Zabel 1985) and to cause both types 1 and 2 in Douglas-fir and pine (Meyer et al. 1988, Zabel et al. 1991). *Scytalidium lignicola* caused type 2 soft rot of pine according to Nilsson (1973) and caused both types in southern pine and Douglas-fir (Meyer et al. 1988; Wang, Zabel 1990). *Chaetomium funicola* was found to cause both types 1 and 2 soft rot of pine (Nilsson 1973). *Phialocephala dimorphosphora* has been considered a type 1 and 2 soft-rotter (Morrell, Zabel 1985) and in some studies caused only type 1 soft rot of pine (Meyer et al. 1988; Worrall, Wang 1992).

The aim of this study was to characterize and elucidate the development of the anomalous type of soft rot.

## Materials and methods

A slide culture technique was utilized to observe *in vivo* the sequential development of the anomalous type of soft rot. Slide cultures were prepared by first autoclaving in separate glass Petri plates at 121 °C for 15 minutes: plastic mesh (needlepoint canvas) rectangles (5.5 by 4 cm; 1.3 mm thick), microscope slides, microtomed radial sections (12 to 18 μm thickness) of southern yellow pine (*Pinus taeda*) soaked in reduced salts nutrient solution (RS, see below) and cover slips. Slide cultures were assembled by placing those items in that order on top of RS agar in a plastic Petri dish. RS consisted of 1.5 g $NH_4NO_3$, 2.5 g $KH_2PO_4$, 2 g $K_2HPO_4$, 1 g $MgSO_4$*7 $H_2O$ and 2.5 g glucose per liter and was shown previously to optimize the amount of degradation (Worrall et al. 1991). Inoculum from two-week-old cultures was placed adjacent to the cover slip in contact with the wood section. Inoculum included *Arthrographis cuboidea* P540, *Scytalidium lignicola* P53, *Chaetomium funicola* ED189, *Alternaria alternata* ED113, and *Chaetomium globosum* P591. The Petri dishes were sealed with parafilm and incubated at 28 °C for two to four weeks. Slides were removed weekly and examined with the light microscope to observe the decay in progress and could be returned to the decay chamber for further incubation. A Nikon Optiphot microscope with Nomarski Differential Interference Contrast (DIC) optics was used for light microscopic observations of unstained sections.

Soft-rot tests were conducted with blocks 20 × 10 × 5 mm in Petri dishes on RS agar for twelve weeks (Worrall et al. 1991). Twelve blocks per fungus were tested. Inoculum included the isolates: *Arthrographis cuboidea* P540, *Scytalidium lignicola* P53, *Chaetomium funicola* ED189, *Alternaria alternata* ED113, *Chaetomium globosum* P591, *Phialocephala dimorphosphora* P109, *Phialophora botulispora* P209, *Phialophora* sp. 3, *Chaetomium aureum* P722 and *Bipolaris soro-*

*kiniana* DAOM 170 607. Blocks were removed from the dishes and prepared for light microscopic and transmission electron microscopic observations. For light microscopic observations, portions of blocks were fixed in FAA (formaldehyde, acetic acid, alcohol) solution. Radial and tangential sections (14 to 18 μm thick), cut with a sliding microtome, were examined unstained with brightfield and DIC optics. Portions of blocks were fixed and embedded for transmission electron microscopy. The blocks were trimmed to approximately 1 mm by 1 mm by 3 mm, fixed in a modified Karnovsky's solution: 2.5% glutaraldehyde, 2% paraformaldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) plus 0.001 g/L $CaCl_2$, post-fixed in 1% osmium tetroxide in 0.1 M sodium cacodylate buffer (pH 7.2) and rinsed in distilled water. The tissue was dehydrated in an alcohol series, exchanged with propylene oxide, embedded in Epok and allowed to cure for two days at 65 °C. Sections 60 to 90 nm thickness (silver to pale gold) were cut on a Sorvall MT2-B Ultramicrotome, placed on Cu grids and stained with uranyl acetate (2%) and Reynolds' lead citrate (Reynolds 1963). Sections were examined on a JEOL 2 000EX transmission electron microscope.



Analyses of residual wood sugars were performed on selected soft rot test blocks and sound blocks (Worrall, Anderson 1993).

## Results

In pine blocks following soft-rot tests, patches of large cavities with rounded or angular edges were studied with the light microscope (Fig. 1 A). These patches, although barely discernible in unstained sections examined in brightfield, were readily visible with DIC optics. In pine blocks decayed by *Arthrographis cuboidea*, hyphae were not visible within the cell wall but were visible in the cell lumens (Fig. 1 A, B). This led to uncertainty over the origin of these cavities, and whether they could be categorized as type 1 or as Nilsson's type 2 (Nilsson 1973 ). These patches of decay are similar to patches of type 1 degradation caused by *Phialocephala dimorphospora* in pine test blocks in that the S2 cell wall in the center of the patch is totally decayed (Fig. 2). The

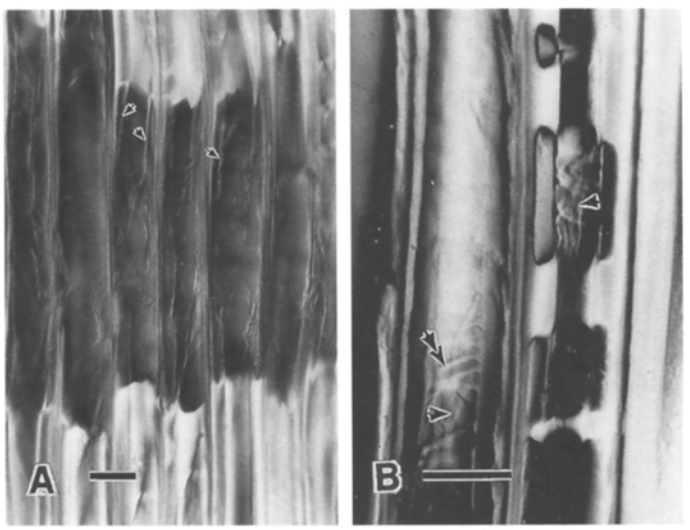


Fig. 1 A, B. Soft rot in radial sections of pine test blocks by *Arthrographis cuboidea* P540 incubated for twelve weeks. Cavities are large with mostly rounded ends. Note the apparent lack of hyphae in the cell wall. A A patch of degradation showing complete removal of the S2 with the S3 (arrows) remaining intact. Bar = 20 μm. B Another area showing oblong cavities with rounded ends. Hyphae (arrows) are visible in the lumen and not in the cavities. The white bars extending across the cell lumen are spiral thickenings (double arrow). Bar = 20 μm

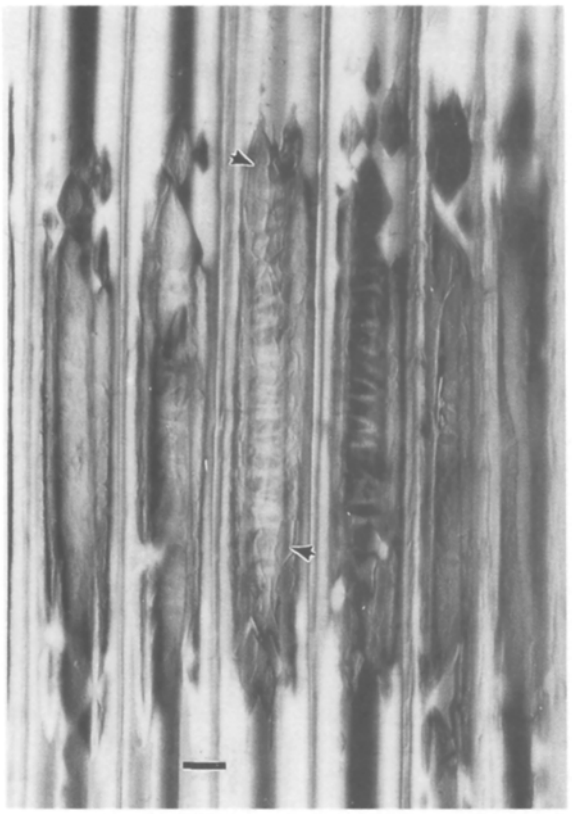

Fig. 2. A patch of type 1 soft rot caused by *Phialocephala dimorphosphora* P109 in a pine block decayed for twelve weeks. Hyphae are evident within the cavities (arrows). Diamond-shaped cavities are visible at the decay fronts. Bar = 10 μm

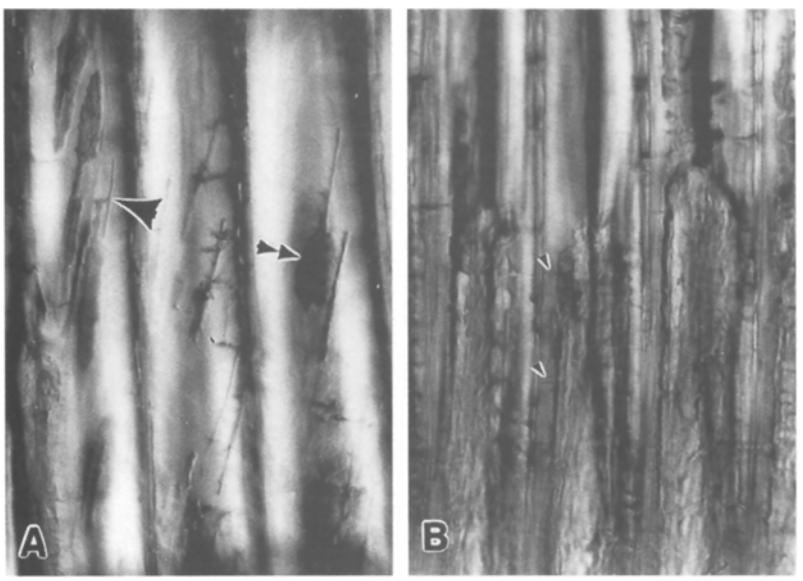


Fig. 3 A, B. Initiation and expansion of diffuse soft rot cavities in slide cultures of microtomed sections of pine. A Early stage of cavity formation by *Chaetomium funicola* ED189. T-branching (arrow), proboscis extension and early stage of cavity expansion (double arrows).
B A patch of almost complete loss of the S2 layer. Penetration bore holes are evident (arrows).
A, B Scale bars = 10 μm

differences are that, in decay caused by *P. dimorphosphora*, diamond-shaped cavities were evident at the decay fronts, and hyphae were obvious within the cavities and apparently expanded to fill the space as the wall was degraded (Fig. 2). *Phialocephala dimorphosphora* clearly caused type 1 soft rot. The soft rot type for *Arthrographis cuboidea* and the other species studied here was questionable.

Light microscopic observations *in vivo* of slide culture sections of pine decayed by *Chaetomium funicola* indicated t-branching and cavity initiation (Fig. 3 A) followed by irregular and diffuse cavity widening (Fig. 3 B). At later stages of decay, patches of erosion were evident that were similar to those observed in many of the pine soft-rot test blocks. When observed in longitudinal section, a cavity above or below a cell lumen (with respect to the plane of section) might appear to be erosion on the surface of the cell lumen.



Observations of other slide cultures indicated that at early stages a jagged or notched zone sometimes appeared in the inner S2 layer (Fig. 4 A) which resembled the normal type 2 notched erosion on the lumen surface common in hardwoods (Fig. 4 B). However, other sites indicated that these notched regions of the S2 were initiated by lateral penetration hyphae and t-branching. At a later decay stage, after t-branching, the hypha extended longitudinally through the inner S2 layer, forming a long narrow cavity, as opposed to the periodic proboscis-elongation/cavity-widening process of typical type 1 cavity formation.

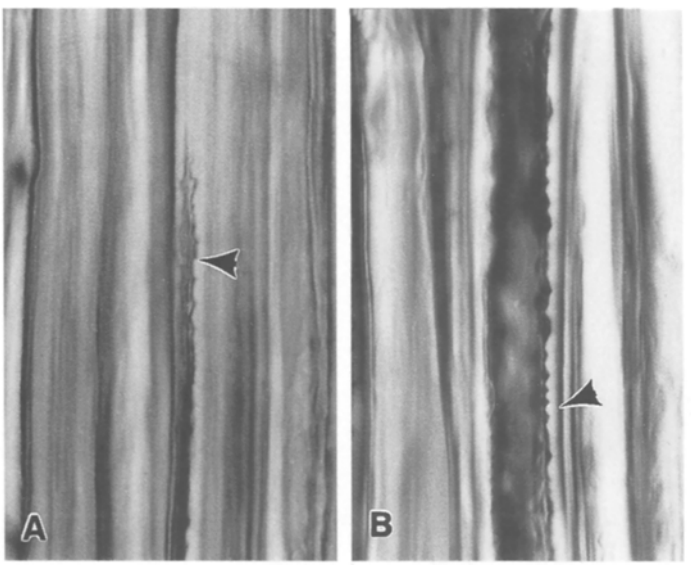


**Fig. 4 A.** Degradation of the inner S2 layer of pine by *Alternaria alternata* ED113 in a slide culture preparation. Irregular outline of the cavity (arrow) is similar in appearance to type 2 erosion on the lumen surface observed in birch. B Type 2 soft rot by *Chaetomium globosum* in a birch block showing V-shaped erosion beneath a lumenal hypha (arrow). Scale bars = 10 μm

In transmission electron micrographs of the same pine block that is presented in Fig. 1, proboscis hyphae were observed within the S2 layer of the wood cell wall with diameters ranging from 0.6 to 0.9 μm (Fig. 5 A). These are much smaller than proboscis or cavity hyphae of typical soft rot type 1, where hyphae enlarge as the wall is eroded and hyphal diameters of 1.5 to 2 μm are common (Fig. 5 B). Diameters of proboscis hyphae in type 1 can be as great as 5 μm (Fig. 2). Portions of the hyphal sheath extend from the hyphal surface into the degraded cell

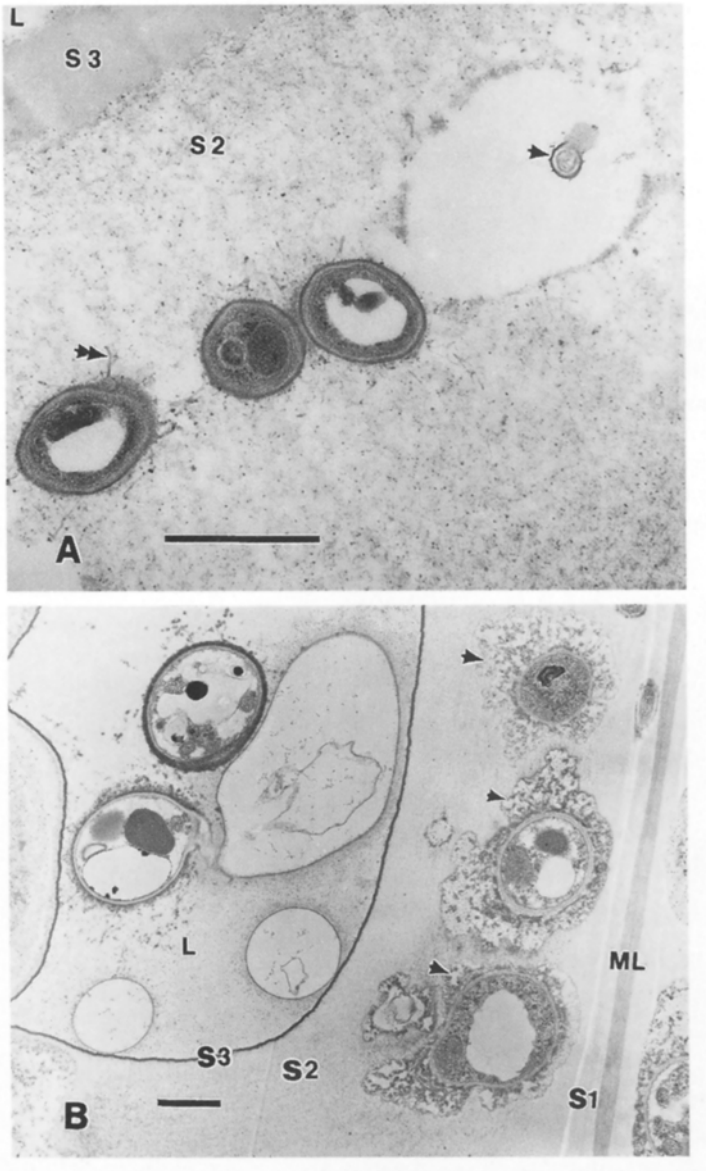


Fig. 5 A. Transmission electron micrograph of a transverse section of the same pine block in Fig. 1 decayed by *Arthrographis cuboidea* P540. Proboscis hyphae (diameter 0.7–0.9o μm) within the S2 cell wall. One hypha has deteriorated (arrow) leaving a void. Portions of the hyphal sheath extend into the degraded cell wall (double arrow). Bar = 1 μm. **B** Type 1 soft rot by *Phialocephala dimorphosphora* P109 in transverse section of birch decayed for 12 weeks. Note the discrete cavities (arrows). Bar = 1 μm. **A, B** L = lumen; ML = middle lamella; S1, S2, S3 = secondary cell wall layers

wall (Fig. 5 A). Void areas with diameters of 0.6 to 1.4 μm were often observed within the degraded S2 cell wall (Fig. 6). Deteriorated hyphae (diameter 0.16 to 0.25 μm) were also evident (Fig. 6). Because the void areas often contained hyphal remnants, they are assumed to have

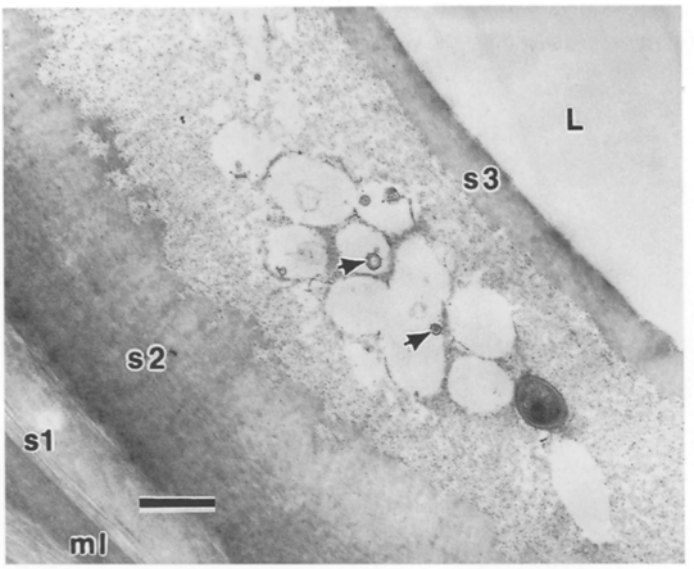


Fig. 6. Transmission electron micrograph of diffuse cavities in a pine block (same block as pictured in Fig. 1) decayed by *Arthrographis cuboidea* P540 showing voids within the degraded S2 cell wall which were once occupied by hyphae. Remnants of hyphae are present in some voids (arrows). Bar = 1 μm. L = lumen; ML = middle lamella; S1, S2, S3 = secondary cell wall layers

once been occupied by a hypha which has undergone autolysis. Light microscopic observation of the area pictured in Fig. 6 would reveal a large cavity in the S2 and no evidence of hyphae within the cell wall.

The hyphae growing in the cell lumen are larger (1.0 to 4.0 μm diameter) than those growing in the cell wall and are readily observed with the light microscope. Those growing in the cell wall are very difficult to observe with the light microscope; at later stages they autolyze and thus are no longer visible. By following the progression of diffuse cavity formation with slide cultures it was possible to observe hyphae during cavity initiation. Transmission electron micrographs of wood in transverse section clearly indicated that hyphae were present within the S2 cell wall.

Light microscopic observations of soft-rot test blocks indicated that *Arthrographis cuboidea*, *Scytalidium lignicola* and *Chaetomium globosum* caused diffuse cavities while the species *Phialophora sp.* 3, *Phialocephala dimorphospora* and *Phialophora botulispora* caused typical type 1 cavities. The results of chemical analysis of these soft-rot test blocks indicated slight differences between the species forming diffuse cavities and those forming typical type 1 cavities (Table 1). Those species causing diffuse type 1 soft rot caused appreciably greater losses of glucose (26, 25 and 15%) than the typical type 1 soft rot species (6, 4 and 7%). Also, unlike the typical type 1 species, the diffuse type 1 species caused an increase in galactose content.

## Discussion

What has been observed fits neither the current description of type 1 nor type 2 soft rot. Hyphae growing longitudinally within the S2 apparently release enzymes and/or other substances which are able to diffuse away from the hyphae and degrade the S2. This is evidenced by the extensive degradation of the S2 cell wall at transverse distances up to 2.5 μm from the hyphae (Fig. 6). Type 1 soft rot as described by Hale and Eaton (1985 a) consists of periodic, restricted cavity formation as a hypha grows parallel to the microfibrils through the S2 layer. Enzymatic

Table 1. Apparent weight loss (%) and loss of wood sugars (%)[a] in pine blocks exposed to soft-rot fungi for 12 weeks

| Isolate | Weight loss | Loss of wood sugars | | | | |
|---|---|---|---|---|---|---|
| | | Arabinose | Galactose | Glucose | Xylose | Mannose |
| Isolates producing diffuse type 1 soft rot cavities: | | | | | | |
| *Arthrographis cuboidea* P540 | 3.6 | 46 | −285 | 26 | 16 | 28 |
| *Scytalidium lignicola* P53 | 2.8 | 40 | −243 | 25 | 17 | 20 |
| *Chaetomium globosum* P591 | 3.6 | 36 | −51 | 15 | 16 | −6 |
| Isolates producing typical type 1 soft rot cavities: | | | | | | |
| *Phialophora sp. 3* | 3.4 | 49 | 31 | 6 | 6 | −10 |
| *Phialocepha dimorphosphora* P109 | 1.9 | 48 | 31 | 4 | 9 | −15 |
| *Phialophora botulispora* P209 | 4.2 | 34 | 7 | 7 | 16 | −2 |

[a] Percentages are based on the following composition of wood sugars in control blocks: 1.8% arabinose, 2.2% galactose, 50% glucose, 8% xylose, and 12.4% mannose



degradation is thought to occur only near the hyphal surface (Hale, Eaton 1985 b). For example, in transverse section of birch degraded by *Phialocephala dimorphospora* (a typical type 1 in this study), visible degradation extends approx. 1.2 µm from the hyphae (Fig. 5 B).

In this study, the degradation of southern pine caused by *A. cuboidea* was not limited to the hyphal surface. The hyphae growing through the S2 appeared to rapidly autolyze. Hyphae were also present within the cell lumen. It is unclear whether lumenal hyphae were degrading the cell wall, but the apparent resistance of the S3 layer of pine may present a formidable barrier to the passage of enzymes. Recent evidence suggests that in the case of brown rot and white rot, cell wall porosity would not allow the passage of enzymes, even during decay (Flournoy et al. 1991; Srebotnik, Messner 1991). Resistance of the S3 layer of softwoods is thought to be due to the amount or type of lignin present or to the presence of the hemicellulose, glucuroarabinoxylan (Liese 1970).

These results suggest another interpretation of the type 2 soft rot of softwoods as described by Nilsson (1973). Nilsson (1973) described erosion of the S2 layer by lumenal hyphae with the S3 layer remaining intact. The results of this study indicate that, although they are not readily apparent, hyphae are present within the S2 layer of the cell wall and appear to be associated with the degradation. This pattern more closely fits in the type 1 category. It may be that many of the prior type 2 designations based on light microscopy missed the longitudinal hyphae within the S2. Several authors have indicated that they observed type 2 degradation in softwoods (Nilsson 1973; Morrell, Smith 1988; Morrell, Zabel 1985; Morrell, Zabel 1987; Morrell, Zabel 1990; Zabel et al. 1991) but what they observed is unclear as no micrographs were presented. Greaves (1977) presented scanning electron micrographs of soft rot in *Eucalyptus* which he described as long diffuse cavities with rounded ends. They are similar to what was observed in this study. Regardless of what labels are used, this soft rot is clearly different from that described previously and is more closely related to type 1 than to type 2.

The differences in composition of residual wood sugars suggest that slightly different decay mechanisms are operating (Table 1). Fungi producing diffuse cavities caused greater

percent losses of both glucose, which comprises 50% of the components in control blocks, and mannose at similar weight losses. This may be an indication of attack on specific hemicelluloses and a more rapid destruction of cellulose. There was a substantial increase in the galactose content of blocks with diffuse cavities. Further analysis indicated that this was indeed galactose and not glucosamine, a component of fungal cell wall which co-elutes with galactose. It could be speculated that the fungus was producing galactose (also a fungal cell wall component) resulting in the appearance of a net increase in galactose in the decayed blocks.

The terms "type 1" and "type 2" were introduced by Corbett (1965) to describe the two observed morphologies of soft rot, cavity formation and erosion, respectively. Following Corbett's terminology and considering that what was observed here has a distinctive morphology, we suggest a new term to describe this soft rot. A redefinition and simplification of these soft rot categories may be helpful. We propose retaining type 1 and defining it as cases where hyphae develop longitudinally in the S2 from t-branching. The term "regular type 1" would refer to the conical, tapering, often diamond-shaped cavities; "diffuse type 1" would refer to irregular, diffuse cavities associated with evanescent hyphae in early stages of formation. Diffuse type 1 has been observed in softwoods. "Type 2" would be retained for cases where cell wall damage is clearly associated with lumenal hyphae and is primarily observed in hardwoods. It could alternatively be referred to as "erosion soft rot".



## Conclusions

Diffuse cavities in the S2 cell wall layer of pine longitudinal tracheids appear to be caused by hyphae growing within the cell wall. Observations *in vivo* of soft-rot development in thin radial sections revealed the formation of diffuse cavities. Cavities were initiated by t-branching and proboscis extension followed by diffuse expansion, cavity coalescence and complete destruction of the S2. During proboscis extension and cavity widening neither angular cavities nor the oscillatory growth pattern of type 1 soft rot were observed. The final stages of cavity formation in thin sections appeared similar to the patches of cavities observed in 12-week block decay tests. Transmission electron micrographs indicated the presence of hyphae within the extensively degraded S2 cell wall. Narrow hyphae appeared to be associated with decay. Some hyphae appeared viable, others appeared to be autolyzing and in extreme cases, a space and small hyphal remnant were all that remained. The extremely small size of the hyphae and their rapid autolysis explains why they are not evident in light microscopic preparations of blocks decayed for 12 weeks. These results and the chemical differences suggest that the mechanism is different from that of typical type 1 soft rot. We suggest that the term "diffuse type 1" be used to designate this type of soft rot.

Observations of wood in advanced stages of decay may not always provide the information leading to the true determination of the decay type. In some cases, decay progression from early to advanced stages must be studied in order to determine the mechanism involved.

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