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Studies on wood degradation and cellulolytic activity of microfungi

Studier över vednedbrytning och cellulolytisk aktivitet hos mikrosvampar

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Abstract

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The cellulolytic activity and wood-degrading ability of 160 different species of microfungi, mostly wood-inhabiting, have been investigated. The cellulolytic activity was determined by a cellulose clearing method. 109 of the species showed cellulolytic activity. The wood-degrading ability was determined microscopically on sections from decayed wood blocks. The attack on three hardwoods and two softwoods was examined. Most studies were performed with birch wood which was used as a "standard wood" for comparisons. Two morphologically distinct types of attack were observed, Type 1 (cavity formation) and Type 2 (erosion of cell walls). 120 of the tested species were found capable of degrading birch wood. These species could be classified into three groups with respect to their decay patterns, 1) species producing only Type 1 attack; 2) species producing only Type 2; 3) species producing both types of attack. The cavity-forming species formed cavities in both hardwoods and softwoods. All the species which produced Type 2 or Type 1+Type 2 attack in birch wood showed cellulolytic activity in the cellulose clearing test. Fifteen of the twenty-three species which only produced Type 1 attack, failed to produce clearing. The decay capacity (weight losses) of the wood-degrading species was also studied.

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Contents

1 Introduction

During investigations on deterioration of wood in different situations, a great number of microfungi have been isolated at this laboratory. Most of the isolates have been assayed for cellulolytic activity and wood-degrading capability. The aim of these studies was to examine which species are able to degrade wood, their type of attack and to investigate whether any correlations exist between wood degradation and cellulolytic activity on pure cellulose. The results for 160 different species are presented in a table.

The importance of the microfungi in wood deterioration was recognized by Findlay and Savory (1954) and by Savory (1954 and 1955). Since then numerous papers have been published which show that wood degradation by microfungi occur in vastly varying situations. As a result of the observation that the surface of wood was often very soft when decayed by microfungi, Savory (1954) proposed that the term "soft rot" be used "for decay caused by cellulose-destroying microfungi to distinguish it from the brown and white rots caused by the wood-destroying Basidiomycetes". Microscopic examination of the decayed wood revealed chains of cavities with conical ends in which the wood substance had been dissolved. The cavities were found in the secondary cell walls of the wood fibers. This type of wood degradation had previously been described by Bailey and Vestal (1937) and by Barghoorn and Linder (1944). The cavities have since been regarded as the typical form of deterioration caused by soft rot fungi.

An additional type of attack was described by Courtois (1963 a and 1963 b) who studied the micro-morphological decay patterns produced by different microfungi. He found that some of the fungi which formed soft rot cavities also caused an erosion of the wood cell walls which started from the cell lumen. Corbett (1965) found that *Chaetomium globosum* Kunze ex Fr. and *Coniothyrium fuckelii* Sacc. produced both types of attack simultaneously in birch wood, whereas *Stysanus stemonitis* (Pers.) Corda and a *Sphaeronema* sp. only formed cavities.

In birch wood decayed by *Camarosporium ambiens* only the erosion type of attack was found. The erosion type of attack was not observed in pine wood. In her paper, Corbett used the term "Type 1" to designate the decay type where cavities were formed and "Type 2" for the erosion type of decay.

Levy and Stevens (1966) studied the decay patterns produced by *Chaetomium globosum* Kunze ex Fr. and *Coniothyrium fuckelii* in five different softwoods and seven hardwoods. They found that these fungi formed soft rot cavities in all of the wood species. Erosion of the cell walls was observed in the hardwoods and in two of the softwoods.

Several other papers have been published on the different species of soft rot fungi and their action on wood. Barghoorn and Linder (1944) described soft rot attack by a number of species of marine fungi. Savory (1955) gave a list of ten species which had proved capable of causing soft rot. Duncan (1960) made an extensive study of several isolates of soft rot fungi, but few of them were named. Later identifications were made and a list of sixty-nine species of soft rot fungi was published by Duncan and Eslyn (1966). Duncan (1960) found that the basidiomycete, *Poria nigrescens* Bres., also could form cavities in wood fibers similar to those produced by microfungi. Courtois (1963 b) tested 49 strains

of microfungi. The weight losses caused by them on beech and pine wood blocks were measured. The decay patterns produced by several of the microfungi in beech wood were also described. Levy (1965) published a list of fungi known to cause soft rot. This list had been compiled by Corbett (1963). Levy (1969) also compiled a table with data obtained from other workers. The table gives information concerning the action of several species of microfungi in a number of hardwoods and softwoods.

Greaves and Savory (1965) assayed 241 isolates of microfungi obtained from preservative-treated timber for cellulolytic activity. The assays were done by cultivating the fungi on cellulose agar plates. A clear zone was formed in the opaque plates by those fungi which secreted cellulases. 56 of the isolates were found to be cellulolytic. Twelve of the isolates were tested both for cellulase activity and soft rot ability. They found that cavities were formed in birch wood by six of these isolates and that these were all cellulolytic. The other cellulolytic species formed no soft rot cavities.

Kerner-Gang (1966) and Gersonde and Kerner-Gang (1968) isolated several species of soft rot fungi that had not been previously recorded. They published data on the weight losses produced by the fungi in beech and pine wood. All of the isolates obtained which failed to grow on a cellulose agar medium were discarded and were not tested on wood. The most comprehensive list of species of soft rot fungi was published by Rösch and Liese (1968) who compiled a table with results from several laboratories. Information is given on the source of the isolates, their degree of attack on different wood species and, for some fungi, the decay pattern is also reported.

Haider and Domsch (1969) give data on the reduction in dry weight and tensile strength produced in thin maple wood foils by 27 species of microfungi isolated from soil.

The cellulolytic activity at different pH levels of twenty-two microfungi isolated from beech wood was studied by Sharp and Eggins (1970). They used a cellulose-clearing method which is performed in test tubes (Rautela & Cowling 1966). A comparison between the amount of clearing and the reduction in bending strength of beech wood veneers showed that some fungi produced a great amount of clearing while the wood degradation was slight. Conversely, some of the fungi which produced moderate clearing caused considerable wood degradation.

Findlay (1970) tested five species of microfungi against four hardwoods and two softwoods. Two of the species failed to produce cavities at all, while the remaining three produced cavities only in the hardwoods.

Eaton and Gareth Jones (1971) give information on weight losses and the presence of cavities in beech and Scots pine blocks for several microfungi isolated from cooling towers. The cavity formation in wood sections of European beech and Norway spruce was studied by Casagrande and Ouellette (1971). Their findings led them to place the tested fungi into three groups. The first group included fungi which produced cavities in both beech and spruce wood. Those fungi which produced cavities in beech wood were placed in the second group, while only cell wall perforations were observed in the spruce wood. The fungi in the third group could only form cell wall perforations in beech and spruce wood and no cavities. Lundström (1972) studied the cavity formation in the wood of a large number of plants caused by two soft rot fungi, viz. *Allescheria terrestris* Apinis and *Phialophora (Margarinomyces) luteo-viridis* (van Beyma) Schol-Schwarz.

Several papers have been published on cellulose degradation by wood destroying fungi. Some of the papers which show some relation with this study will be mentioned here. Two papers have already been referred to, viz. those by Greaves and Savory (1965) and by Sharp and Eggins (1970).

Johansson (1966) compared the cellulolytic activity of 70 strains of white and

brown rot fungi. He found that the two types of decay fungi differed in their ability to attack filter paper cellulose and to produce cellulase. None of the brown rots produced any significant C_1-activity whereas all white rots showed measurable activity. It had already been observed by Reese and Levinson (1952) that brown rot fungi produced only small reductions in the tensile strength of cotton whereas white rot fungi produced considerable strength losses. A similar phenomenon was reported by Yokota (1955) who studied the weight loss of filter paper in liquid cultures with ten species of white rot and nine species of brown rot fungi. The white rots produced weight losses from 4.5 up to 16.6 per cent, whereas all the brown rots, except one, produced weight losses below 1.6 per cent.

Rautela and Cowling (1966) and Levi and Cowling (1969) studied the clearing of cellulose that occurred in test tubes with white, brown and soft rot fungi. Most of the white rots and soft rots produced at least some clearing of the cellulose, whereas none of the brown rots produced any clearing. A similar phenomenon was studied in detail by Bravery (1968). Three unidentified strains of microfungi had been shown to produce soft rot within birch wood. They had been assayed for cellulolytic activity on a medium proposed by Eggins and Pugh (1962). No cellulase reaction occurred within 14 days' incubation. Bravery was able to demonstrate that the cellulolytic activity in this case was inhibited by small amounts of alternative carbon sources (viz. DL-asparagine and yeast extract). When these were removed a positive cellulolytic reaction was obtained for the three fungi.

Fuller (1970) studied the cellulolytic activity of six species of soft rot and blue stain fungi. All of them were found to produce extracellular cellulose-degrading enzymes. The amylolytic, cellulolytic and pectinolytic activity of thirty-three species of wood-inhabiting microfungi was studied by King and Eggins (1972). Cellulolytic activity was measured by viscometric determinations on carboxymethyl cellulose with extracts from liquid cultures, by the clearing of cellulose agar and by the reduction in tensile strength of fibrous cellulose.

2 Material and methods

2.1 **Origin of the species**

A total number of 160 different species of fungi are included in the table. Most of the species have been isolated at this institute. The others were obtained from "Centraalbureau voor Schimmelcultures" (CBS) in Baarn (25 species. Strain number preceeded by CBS), from Dr Kerner-Gang at the "Bundesanstalt für Materialprüfung", Berlin (2 species. Strain number preceeded by BAM), from Dr B. J. Wiley at the US Army Natick Laboratories (2 species. Strain number preceeded by QM) and from Dr C. L. Fergus at the Pennsylvania State University (1 species).

The List of Cultures of 1972 from "Centraalbureau vor Schimmelcultures" has been followed for the Latin names. A list of more common synonyms is given after the table. 130 of the tested fungi appearing in the table have been fully identified, while the others are identified with respect to the genus. Three sterile mycelia are also included.

Apart from the fungi accounted for in the table, a large number of more or less unidentified isolates have been tested for cellulolytic activity and ability to degrade wood. Results from tests with fungi from common genera such as *Aspergillus, Cladosporium, Cylindrocarpon, Fusarium* and *Penicillium* are presented in the comments to the table.

In the table information of source, wood species and year of isolation is given where known. When isolations have been made from preservative-treated wood, the name or composition of the preservative is given and, for some preservatives also the retention values. For the fungi obtained from CBS, data have been extracted from their List of Cultures 1972.

Fungi isolated from outside stored pulpwood chips contribute a large number of the species tested. Among other sources, fungi were isolated from logs with bluestain, foundation piles, and wood samples submerged in brackish seawater. Fungi were also isolated from preservative-treated timber such as railway sleepers, test stakes which had been standing in soil at testing fields and telegraph poles.

2.2 **Assay of cellulolytic activity**

Rautela-Cowling medium (R-C medium)

All of the fungi were assayed for cellulolytic activity according to a method described by Rautela and Cowling (1966) where sterile vertical columns of cellulose agar in test tubes are inoculated with fungi and the depth of clearing zone can be measured beneath the growing cultures. Sterile test tubes (18 mm diam) with the cellulose agar medium (R-C medium) were prepared in accordance with the description. The tubes were fitted with cotton plugs. The concentration of Walseth cellulose was 0.25 per cent and the height of the columns was approx. 40 mm. The test tubes were inoculated with small pieces of mycelium and agar taken from actively growing cultures on malt extract agar. Each fungus was inoculated in two tubes.

The test tubes with mesophilic fungi were incubated at the ambient room temperature (23—25°C), whereas the tubes with thermophilic fungi were incubated at 45°C. To avoid drying out of the agar, the cotton plugs were covered with an aluminium foil. The depth of clearing was measured after incubation for three and six weeks. If no clearing was obtained after six weeks, this was taken as an indication that cellulolytic

activity was absent. Since the degree and quality of clearing was very different and exact measurements were difficult, only the presence (+) or absence (−) of a clear zone is indicated in the table.

Bravery-VII medium (B-VII medium)

In addition forty-four of the fungi were tested with the same method but with a different cellulose agar medium (B-VII medium) which was a slight modification of a medium VII described by Bravery (1968). The medium used here had the following composition: Walseth cellulose 2.5 g, $(NH_4)_2SO_4$ 0.543 g, KH_2PO_4 1.0 g, KCl 0.5 g, $MgSO_4 \cdot 7H_20$ 0.2 g, $CaCl_2$ 0.1 g, thiamine hydrochloride 0.001 g, agar 15 g and 1000 ml deionized water. The main difference of this medium from that described by Rautela and Cowling (1966) is that it contains no carbon source except for the cellulose. The Rautela-Cowling medium contains 0.5 g yeast extract per litre.

The tubes with B-VII medium were inoculated with spores or aerial mycelium in order to avoid the addition of malt extract from the agar plates. The test tubes were incubated and measured as described above.

Several of the species, which failed to produce clearing, had dark-coloured hyphae which often penetrated deep into the agar. Since this might have obscured the clearing zones, the cellulose agar medium of some tubes in which no clearing had been observed, was examined for evidence of cellulose degradation. Thin slices of the agar were cut, just below the growing mycelium. The slices were then dried on microscope slides and examined in polarized light.

2.3 Determination of type of wood attack

The test fungi were inoculated in two types of agar media on slopes in test tubes. The first agar medium consisted of normal 2.5 per cent malt extract agar and the second medium had the following composition: Avicelcellulose 10 g, asparagin 1.0 g, NH_4NO_3 1.0 g, KH_2PO_4 1.0 g, $MgSO_4 \cdot 7H_2O$ 0.5 g, $FeSO_4 \cdot 7H_2O$ 0.01 g, $ZnSO_4 \cdot 7H_2O$ 0.01 g, yeast extract (Difco) 0.5 g, glucose 2.5 g, agar 15 g and 1000 ml of water. Each of the fungi was inoculated on both types of agar media. When some growth had occurred, wood blocks (approx. $5 \times 5 \times 10$ mm) were introduced into the tubes and placed on the growing mycelia. The blocks had previously been sterilised by autoclaving in petri dishes. During autoclaving they were immersed in a solution of the following composition: NH_4NO_3 3.0 g, KH_2PO_4 1.5 g, $MgSO_4 \cdot 7H_2O$ 0.5 g and 1000 ml of water. These mineral salts were used to enhance the activity of the fungi in the wood. To prevent drying out, cotton plugs of the test tubes were covered with aluminium foil and the test tubes were then placed in small perforated plastic bags. The tubes were incubated at ambient room temperature which varied between 23 and 25°C, or at 45°C when thermophilic fungi were tested.

The blocks were removed from the tubes after a period of time varying between one week and four months from inoculation. Unless both types of attack as described by Corbett (1965) were observed, the blocks were decayed up to four months. Cross and longitudial sections were made from the wood blocks and examined under a microscope for signs of attack. The cross sections were stained with safranin and the longitudinal sections were studied unstained in polarized light. The patterns of attack in a few blocks were also studied by the use of a scanning electron microscope.

The following wood species were employed in the tests: aspen (*Populus tremula* L.), beech (*Fagus silvatica* L.), birch (*Betula verrucosa* Ehrh.), larch (*Larix decidua* Mill), pine (*Pinus silvestris* L.) and spruce (*Picea abies* (L.) H Karst.). In all tests only the sapwood was used.

Corbett's (1965) terms have been used to describe the types of attack found. Thus, Type 1 indicates cavity formation and Type 2 indicates a form of cell wall erosion. The typical soft rot cavities are always

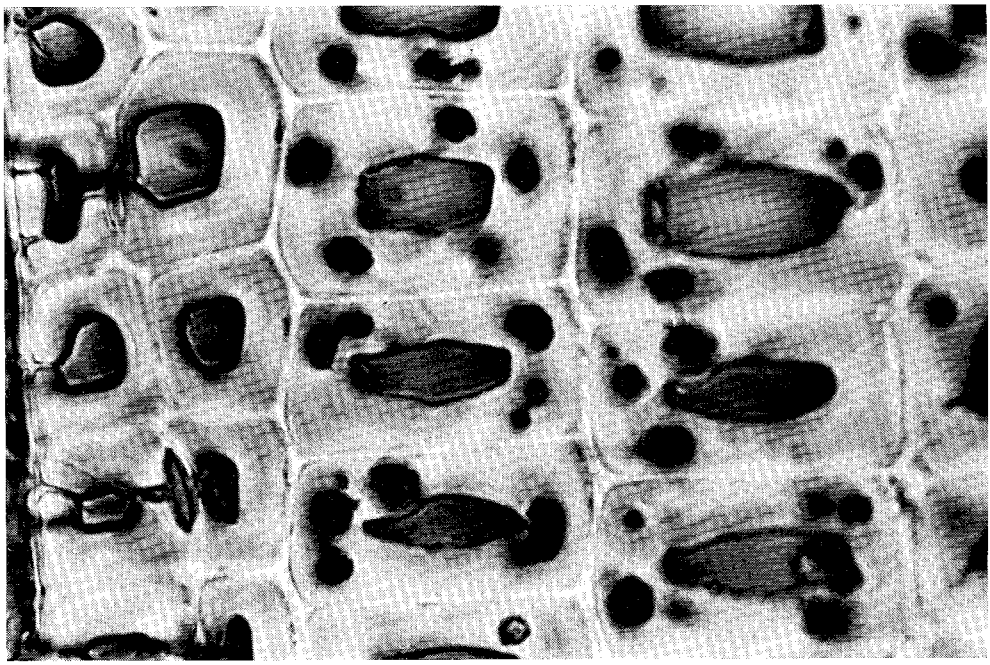

Figure 1. Transverse section of pine (*Pinus silvestris* L.) wood showing characteristic Type 1 attack. Approx. ×900

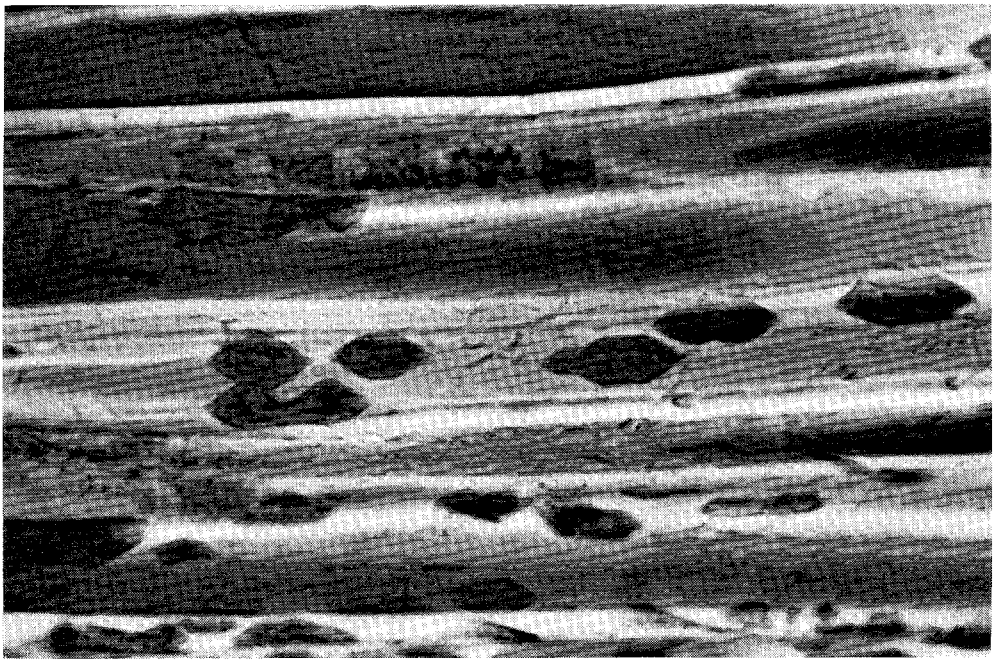

Figure 2. Longitudinal section of birch (*Betula verrucosa* Ehrh.) wood showing typical soft-rot cavities. Note the precence of hyphae within the cavities. Approx. ×650

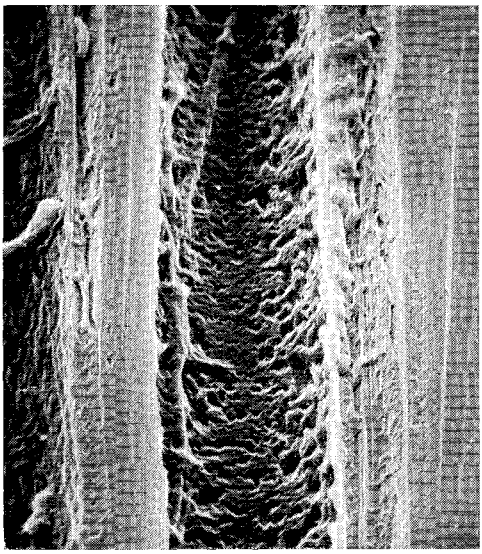

Figure 3. Scanning electron micrograph of a longitudinal section of birch (*Betula verrucosa* Ehrh.) wood showing characteristic Type 2 attack. Approx. ×2100

formed by hyphae growing within the S_2 layer of the wood cells. The cavities are produced in chains which follow the direction of the cellulose microfibrils. A characteristic feature is that a hypha is present in each cavity when it is formed. Figs. 1 and 2 show typical examples of Type 1 attack. All types of attack produced by hyphae in the cell lumena were regarded as Type 2 attacks. An example of Type 2 attack is shown in Fig. 3.

2.4 **Decay capacity tests**

The decay capacity of the fungi was determined as the weight losses of small sapwood blocks (10×10×20 mm). Ten blocks were used for each fungus. The blocks were dried overnight in an oven at 105°C and their dry weight was determined. The weighed blocks were placed in a layer of vermiculite (10 g) in 100 ml Erlenmeyer flasks, two blocks to each flask. 30 ml of nutrient solution was added to each flask which was then equipped with a cotton plug and autoclaved. The nutrient solution had the following composition: NH_4NO_3 6.0 g, K_2HPO_4 4.0 g, KH_2PO_4 5.0 g, $MgSO_4 \cdot 7H_2O$ 4.0 g, glucose 2.5 g and 1000 ml of water. After autoclaving, the dry content of the wood blocks was approx. 45 per cent. The flasks were inoculated with spore or mycelial suspensions of the fungi. The flasks were then incubated 3 months at the temperatures indicated in the table. After incubation the blocks were removed from the flasks and mycelia and adhering vermiculite particles were brushed off. The blocks were weighed after drying overnight at 105°C and the average weight loss for ten blocks was calculated.

The same wood species were employed as for the determination of type of wood attack. Decay capacity tests were only performed with fungi that were previously known to attack wood.

3 Results

All results concerning the cellulolytic activity, type of wood attack, and decay capacity of the tested microfungi are shown in Table 1 (page 15).

3.1 Cellulolytic activity

The majority of fungi produced at least some mycelial growth on the media used. The best growth was generally obtained with fungi that showed cellulolytic activity. However, some of the fungi produced considerable clearing with very sparse growth while others showed rather good growth but produced no clearing.

By the use of the cellulose-clearing method, cellulolytic activity was found in 109 (68.1 %) of the total number of 160 species. Of the forty-four species tested both on R-C and B-VII medium, thirty-eight produced clearing on both media, while four species, viz. *Humicola alopallonella, Phialocephala dimorphospora, Phialophora gregata* and *Scytalidium* sp. B failed to produce clearing on the R-C medium.

The quality of clearing was different among the cellulolytic species. Some fungi produced a completely clear zone due to dissolution of all the cellulose particles, whereas others produced a diffuse zone in which scattered cellulose particles were left. In the first case the zone front was distinct and the depth of clearing could easily be measured. In the second case it was often very difficult to observe the position of the zone front. The depth of clearing varied from below 1 mm up to about 20 mm. The rate of clearing was also very different. Most of the fungi produced clearing after 21 days while the others had produced clearing first at the second measurement after 42 days. Microscopical examinations of slices of cellulose agar from the tubes where no clearing had occurred, in no case indicated degradation of the cellulose.

3.2 Type of wood attack

Attack on birch wood in the form of cavities or cell wall erosion was found for 120 (75.0 %) of the examined fungi. The rest of fungi in several cases formed small bore holes through the wood cell walls but no other type of attack was found. It was found that the type of decay classified as erosion type attack was very often not a true erosion, i.e. an advancing dissolution of the cell wall layers starting from the cell lumen. The first visible attack on pine and spruce wood always was found in the part of S_2 adjacent to the S_3 layer. A considerable amount of the S_2 could be removed before any visible degradation of S_3 was observed. The S_3 layer in softwoods seemed to be very resistant since degradation was observed only after attack by a few of the species. Some decayed samples of pine wood with Type 2 attack were studied with a scanning electron microscope. No degradation of the S_3 layer was observed in these samples although large parts of the S_2 layer were degraded. This decay pattern was also observed in all of the hardwoods for several of the fungi, but examples of true erosion were also found. When there was a mixture of Type 1 and Type 2 attacks, it was often difficult to observe the Type 2 attack, especially in the softwoods, since the formation of cavities in great numbers obscured the erosion patterns.

When longitudinal sections of decayed birch wood were viewed in polarized light, essentially two kinds of erosion patterns were observed: 1) dissolution of the cell wall in discrete spots, often in the vicinity of hyphae, giving a pitted appearance to the

fiber; and 2) striated erosion of the cell wall possibly produced by enzymes acting over the whole wall surface. One fungus could produce both of these erosion types in the same piece of wood. Others produced only one of the types.

The cavity formation in birch wood was very rapid and numerous cavities could already be found in most cases after one week. The aspen wood was attacked as rapidly as the birch wood, whereas attack on beech wood was somewhat slower. Cavity formation in the softwoods pine and spruce was much slower than in birch wood. After three weeks, however, most of the cavity-forming fungi had formed cavities in the softwoods. An outstanding exception was *Ceratocystis piceae* which took 29 weeks to produce a few cavities. It was found that some species formed cavities exclusively in the late wood of the softwoods whereas others also formed cavities in the early wood. All of the species which formed cavities in birch wood and were tested on pine wood also proved capable of forming cavities in the pine wood. The S_3 layer of both hardwoods and softwoods was also very resistant during Type 1 attack. No degradation of the S_3 layer was observed in samples which had been decayed by fungi that only produced Type 1 attack. The S_3 layer persisted even when the S_2 layer was totally degraded.

The wood-decaying fungi were classified into three groups with respect to their type of attack in birch wood: 1) fungi producing attack of Type 1 (cavities) only; 2) fungi producing attack of Type 2 (erosion) only; and 3) fungi producing both types of attack. 23 (19.2 %) of the wood-decaying species were found to belong to the first group, 54 (45.0 %) belonged to the second group and 43 (35.8 %) to the third group.

It was observed that there was a difference in the mycelial growth and decay between the species when they were cultured on the two agar media used in the test tubes. The fungi in the first group, which had no activity in the cellulose clearing tests, grew well on malt extract agar while rather sparse growth was produced on cellulose agar. The cavity formation in birch wood was much more extensive in the test tubes with malt agar than in those with cellulose agar. The cellulolytic fungi in the first group produced, with some exceptions, almost equal growth on the two types of agar media. The fungi which grew well on the cellulose agar also produced equal, or more, cavity attack in the birch wood on the cellulose agar medium than on the malt agar.

With some exceptions, most of the fungi in the second and third groups produced equal or even more growth on the cellulose agar than on the malt extract agar. For most of the fungi, the Type 2 decay was more extensive on the cellulose agar. Some of the species even failed to produce Type 2 attack when grown on malt extract agar. The influence of the agar medium on the cavity formation in birch wood varied considerably among the different species. But most of them seemed to produce equal amounts of cavities on the two agar media.

3.3 Cellulolytic activity compared with attack of birch wood

In Table 2 (page 14) the results from the clearing tests are compared with the type of attack observed in birch wood. All but four of the 109 species which showed cellulolytic activity were able to attack birch wood. These four species were: *Ceratocystis cana, Ceratocystis tetropii, Oidiodendron echinulatum* and *Discula pinicola.* 54 (49.5 %) of the cellulolytic species produced attack of Type 2 in birch wood, 43 (39.4 %) produced attack of both Type 1 and Type 2 while 8 (7.3 %) produced only Type 1. The Type 2 pattern of decay clearly dominated since it was found in 97 of the cellulolytic species, while Type 1 was produced by 66 species.

Of the 51 species that did not produce clearing of the cellulose, 15 were able to attack birch wood. All of them produced attack of Type 1 only. Some of the samples showing Type 1 attack were studied with a scanning electron microscope. In no case was cell wall erosion observed.

Of the 120 species that attacked birch wood, 105 (87.5 %) produced clearing of the cellulose. It can be seen from the table that all fungi which produced attack of Type 2, either solely or in addition to Type 1, also showed cellulolytic activity. Of the 23 fungi which produced attack of Type 1 only, eight were cellulolytic while 15 failed to produce clearing. With the exception of *Mycelium radicis atrovirens* and *Phoma aposphaerioides,* all of these 15 species were tested on both R-C medium and B-VII medium. The following species formed cavities in birch wood but produced no clearing of the cellulose: *Bispora betulina, Catenularia heimii, Ceratocystis* sp. A, *Gonatobotrys* sp. A, *Graphium fragrans, Mollisia* sp. A, *Mycelium radicis atrovirens, Phialocephala* sp. A, *Phialocephala* sp. C, *Phialophora* sp. A, *Phoma aposphaerioides, Rhinocladiella* sp. A, Fungus A and Fungus B.

Table 2. Cellulolytic activity and type of attack observed in birch wood.

Cellulolytic activity	Type of attack	Number of species
Positive	2 (erosion)	54 (33.8)[a]
Positive	1 + 2 (erosion + cavities)	43 (26.9)
Positive	1 (cavities)	8 (5.0)
Positive	0 (no attack)	4 (2.5)
Negative	1 (cavities)	15 (9.4)
Negative	0 (no attack)	36 (22.5)
		160

[a] Values within brackets indicate the percentage of the total number of species tested.

3.4 **Decay capacity**

The decay capacity measured as weight losses in wood blocks was examined for fifty-one species. It is evident that there are great differences in activity between the species. The action on the different wood species also varied. Sufficient numbers of experiments were performed with aspen, birch and pine wood to permit calculation of the average weight losses. These were for aspen 18.0 per cent, birch 10.1 and pine 2.0 per cent. When six fungi were tested on five different wood species, the following order of decreasing susceptibility could be established: aspen, beech, birch, pine and spruce. The softwoods were, in all tests, more resistant than the hardwoods. With one exception, aspen was always more degraded than the birch wood. Some of the fungi showed only a slight difference in weight losses between aspen and birch wood, while others produced two or three times higher weight losses on aspen than on birch.

Gliocladium catenulatum and *Oidiodendron tenuissimum* were extreme in producing five respectively nine times higher weight losses in aspen.

Weight losses of twenty per cent or more on birch wood were obtained with the following fungi: *Chaetomium elatum, Chaetomium funicola, Chaetomium globosum, Chloridium chlamydosporum* and *Coniothyrium* sp. A. All of these produce both Type 1 and Type 2 attack. Insufficient data are provided to permit calculations of the influence of the type of wood attack on the weight losses. It is clear, however, that very great variations in decay capacity exist among species with the same decay pattern. For the fungi which produced Type 1 attack only and which were without activity in the cellulose clearing tests, the weight losses varied from 0.6 to 9.0 per cent on birch wood. For those fungi which only produced Type 1 but were cellulolytic in the clearing tests, the weight losses varied from 3.1 to 20.1 per cent. Weight losses produced by fungi producing only Type 2 attack varied from 2.1 to 15.4 per cent. Fungi which produced both types of attack caused weight losses of between 2.0 to 29.2 per cent.

Soft rot attack also occurred at surprisingly high temperatures. After 2 months at 45°C *Allescheria terrestris* and *Sporotrichum thermophile* caused weight losses of 11.4 and 15.4 per cent respectively. With *Chaetomium thermophile* at 50°C for four months a weight loss of 13.8 per cent was obtained.

Table 1. Cellulolytic activity, type of wood attack and decay capacity of tested microfungi.

Notes to table 1

Wood species

Aspen = *Populus tremula* L., Beech = *Fagus silvatica* L., Birch = *Betula verrucosa* Ehrh., Larch = *Larix decidua* Mill., Pine = *Pinus silvestris* L., Spruce = *Picea abies* (L.) H. Karst.

Cellulolytic activity

+ present, – absent

Type of attack

0 no attack, 1 Type 1 attack (cavities), 2 Type 2 attack (erosion)

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Acremoniella atra Sacc.	QM 1045				–		Birch	0			
Acremonium atro-griseum (Panasenko) W. Gams	SP35-7	Test stake Wolmanit UR 26.2 kg/m³	Pine	1970	+	+	Aspen Beech Birch Pine Spruce	1+2 1 1 1 1	Aspen Birch	23—25 23—25	13.9 11.0
Acremonium butyri (van Beyma) W. Gams	B77-A-24	Pulpwood chips	Spruce	1968	–		Birch	0			
Acremonium furcatum (M. & F. Moreau) ex W. Gams	SP65-113	Test stake Celcure A 11.3 kg/m³	Beech	1970	+		Birch	1+2			
Acremonium murorum (Corda) W. Gams	P184-12	Pulpwood chips	Birch	1969	+		Birch Pine	2 2			
Acremonium sp.	SP77-9	Rafter attacked by *Camponotus* sp.	Pine	1971	+		Birch	1			
Allescheria terrestris Apinis	H63-1	Pulpwood chips	Aspen	1965	+		Aspen Birch Pine Spruce	1+2 1+2 1+2 1+2	Aspen Beech Birch Pine Spruce	45 45 45 45 45	24.1[a] 12.0[a] 11.4[a] 1.5[a] 0.3[a]
Arthrobotrys superba Corda	K101-8	Pulpwood chips	Spruce	1967	+		Birch	2	Aspen Birch Pine	23—25 23—25 23—25	3.4 2.1 0.8

[a] Weight losses after 2 months.

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Aspergillus fumigatus Fres.	M31-2	Pulpwood chips	Birch	1964	+		Birch Pine	2 2	Aspen Birch	40 40	27.3 10.6
Aspergillus terreus Thom	K105-4	Pulpwood chips	Spruce	1967	+		Birch Pine	2 2			
Aureobasidium pullulans (de Bary) Arnaud	M178-1	Pulpwood chips	Birch	1965	–		Birch	0			
Beauveria bassiana (Balsamo) Vuill.	P180-37	Pulpwood chips	Birch	1968	–		Birch	0			
Bispora betulina (Corda) Hughes	P175-26	Pulpwood chips	Birch	1968	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Aspen Birch Pine	23—25 23—25 23—25	9.3 9.0 0
Bispora effusa Peck.	CBS 112.31	Mine timber			–	–	Birch	0			
Botryotrichum sp. A	SP65-119	Test stake Celcure A 11.3 kg/m^3	Beech	1970	+		Birch	1+2	Birch	23—25	8.9
Catenularia heimii Mangenot	CBS 141.53				–	–	Birch	1			
Ceratocystis brunneo-ciliata (Mathiesen-Käärik) Hunt	B-25	Log	Pine	1952	–		Birch	0			
Ceratocystis cana (Münch) C. Moreau	711-341-32	Log	Pine	1971	+		Birch	0			
Ceratocystis clavata (Mathiesen-Käärik) Hunt	B-9	Log	Pine	1952	–		Birch	0			
Ceratocystis coerulescens (Münch) Bakshi	B-12	Log	Spruce	1950	–		Birch	0			
Ceratocystis crassivaginata Griffin	711-183-11	Log	Aspen	1971	–		Birch	0			
Ceratocystis ips (Rumbold) C. Moreau	711-341-21	Log	Pine	1971	–		Birch	0			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Ceratocystis minor (Hedgcock) Hunt	A-1	Stump	Pine	1958	–		Birch	0			
Ceratocystis minuta (Siemaszko) Hunt	B-51	Log	Pine	1952	–		Birch	0			
Ceratocystis olivacea (Mathiesen) Hunt	B-57	Log	Spruce	1949	–		Birch	0			
Ceratocystis piceae (Münch) Bakshi	711-194	Log	Beech	1971	+		Birch Pine	1 1			
Ceratocystis pilifera (Fr.) C. Moreau	B-91	Log	Pine	1949	–	–	Birch	0			
Ceratocystis tetropii (Mathiesen) Hunt	B-110	Standing tree	Spruce	1949	+		Birch	0			
Ceratocystis sp. A	SP5-2	Soil burial test	Pine	1968	–	–	Birch	1			
Chaetomium elatum Kunze ex Fr.	CBS				+		Birch	1 + 2	Birch Pine	23—25 23—25	29.2 1.4
Chaetomium funicola Cooke	M179-A-1	Pulpwood chips	Birch	1967	+		Birch Pine	1 + 2 1 + 2	Aspen Beech Birch Pine Spruce	23—25 23—25 23—25 23—25 23—25	47.8 18.2 27.6 6.0 1.3
Chaetomium globosum Kunze ex Fr.	H56-A-2	Pulpwood chips	Aspen	1965	+		Birch Pine	1 + 2 1 + 2	Aspen Beech Birch Pine Spruce	23—25 23—25 23—25 23—25 23—25	35.8 23.9 25.2 2.7 0.6
Chaetomium thermophilum La Touche	K20-3	Pulpwood chips	Spruce	1966	+		Birch	1 + 2	Birch Spruce	50 50	13.8[b] 2.8[b]
Chalara sp.	K1-27	Pulpwood chips	Spruce	1969	–		Birch	0			
Chloridium chlamydosporum (van Beyma) Hughes	P152-6	Pulpwood chips	Birch	1967	+		Birch	1	Aspen Birch	23—25 23—25	22.5 20.1

[b] Weight losses after 4 months.

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Chrysosporium pannorum (Link) Hughes	K35-2	Pulpwood chips	Spruce	1966	+		Birch Pine	1+2 1+2	Birch Pine	23—25 23—25	10.8 2.2
Cladorrhinum sp. A	600-2	Test stake Wolmanit UA-Ref. 7.1 kg/m³	Pine	1969	+	+	Aspen Beech Birch Pine Spruce	1+2 1+2 1+2 1+2 1+2	Birch Pine	23—25 23—25	11.4 0.8
Cladosporium resinae (Lindau) de Vries	13385-1-22A	Test stake Creosote 35.4 kg/m³	Beech	1969	–	–	Birch	0			
Coniothyrium fuckelii Sacc. var. sporulosum W. Gams & Domsch	CBS 218.68	Soil			+	+	Aspen Beech Birch Pine Spruce	1+2 1+2 1+2 1 1			
Coniothyrium minitans Campbell	SP29-4	Test stake Wolmanit UA-Ref. 26.1 kg/m³	Pine	1970	+		Birch Pine	1+2 1+2	Birch Pine	23—25 23—25	15.3 1.9
Coniothyrium sp. A	B77-A-21	Pulpwood chips	Spruce	1967	+		Birch Pine	1+2 1+2	Aspen Beech Birch Larch Pine Spruce	23—25 23—25 23—25 23—25 23—25	25.3 8.9 21.3 4.5 3.0 0
Cordana pauciseptata Preuss	B63-A-25	Pulpwood chips	Spruce	1967	+	+	Aspen Beech Birch Pine Spruce	1+2 1 1+2 1+2 1	Birch	23—25	12.4
Coryne sarcoides (Jaquin ex Fr.) Tul.	H22-4	Pulpwood chips	Aspen	1964	+		Birch Pine	2 2			
Cylindrocarpon didymum (Hartig) Wollenw.	P111-4	Pulpwood chips	Pine	1964	+		Birch	2			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Cylindrocarpon gracile Bugn.	M187-A-1	Pulpwood chips	Birch	1967	+		Birch	2			
Cylindrocarpon lucidum Booth	K27-11	Pulpwood chips	Spruce	1966	+		Birch	2			
Cylindrocarpon magnusianum Wollenw.	SP36-5	Test stake untreated	Pine	1970	+		Birch	2			
Dictyosporium elegans Corda	SP5-16	Soil burial test	Pine	1968	+	+	Aspen Beech Birch Pine Spruce	1+2 1+2 1+2 1 1	Aspen Birch Pine	23—25 23—25 23—25	28.3 17.0 1.9
Discula pinicola (Naumov) Petrak	711-287	Log	Pine	1971	+		Birch	0			
Doratomyces microsporus (Sacc.) Morton & Smith	SP46-6	Telegraph pole Boliden S25	Pine	1970	+		Birch Pine	1+2 1	Birch	23—25	9.4
Dothichiza pityophila (Corda) Petrak	753-5-12	Pole untreated	Pine	1971	–		Birch	0			
Drechslera sorokiniana (Sacc.) Subram. & Jain	T104	Grain		1972	+	+	Birch	2			
Eladia saccula (Dale) G. Smith	701019-01-04-10	Electricity pole Boliden BIS-salt	Pine	1970	–		Birch	0			
Epicoccum purpurascens Ehrenb. ex Schlecht	CBS 239.59				+	+	Birch	2			
Fusarium solani (Mart.) Appel & Wollenw.	G1-22	Pulpwood chips	Birch	1967	+		Birch	2			
Gilmaniella humicola Barron	CBS 220.65	Soil			+	+	Birch	1+2			
Glenospora graphii Vuill.	BAM MG55	Soil burial test	Pine		+		Birch	1+2			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Gliocladium catenulatum Gilman & Abbott	G1-4	Pulpwood chips	Birch	1967	+		Birch Pine	2 2	Aspen Birch Pine	23—25 23—25 23—25	29.0 5.7 1.4
Gliocladium penicillioides Corda	19c	Sleeper	Beech	1969	+		Birch	2	Birch	23—25	8.7
Gliocladium viride Matr.	H150-11	Pulpwood chips	Aspen	1965	+		Birch	2	Birch Pine	23—25 23—25	7.1 1.8
Gonatobotrys sp. A	SP37-6	Test stake untreated	Pine	1970	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Birch Pine	23—25 23—25	5.8 0.3
Gongronella butleri (Lendner) Peyronel & Dal Vesco	P152-3	Pulpwood chips	Birch	1967	–		Birch	0			
Graphium fragrans Mathiesen	C32	Log	Pine	1952	–	–	Birch Pine	1 1			
Graphium sp. A	B68-A-16	Pulpwood chips	Spruce	1967	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Aspen Birch	23—25 23—25	5.9 3.9
Haplographium sp.	P188-15	Pulpwood chips	Birch	1969	–		Birch	0			
Helicoma maritimum Linder	CBS				+		Aspen Birch	1 + 2 1 + 2			
Humicola alopallonella Meyers & Moore	CBS 207.60	Wood in sea water	Tilia americana		–	+	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Birch	23—25	3.1
Humicola brevis (Gilman & Abbott) Gilman	CBS 171.27	Soil			+		Birch Pine	1 + 2 1 + 2			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Humicola grisea Traaen	SP37-22	Test stake untreated	Pine	1970	+	+	Aspen Beech Birch Pine Spruce	1+2 1+2 1+2 1+2 1	Birch Pine	23—25 23—25	18.8 1.2
Humicola grisea Traaen var. thermoidea Cooney & Emerson	CBS 225.63				+		Birch	1+2			
Humicola nigrescens Omvik	CBS 208.55	Soil			+		Birch	1+2			
Humicola sp. A	SP19-1	Foundation pile	Spruce	1969	+		Birch Pine	1+2 1+2	Birch Pine	23—25 23—25	9.0 1.3
Hyalodendron lignicola Diddens	CBS 829.68	Wood	Picea sp.		+		Birch	1+2			
Leptographium lundbergii Lagerberg & Melin	814-2-10	Pole untreated	Pine	1967	–		Birch	0			
Margarinomyces microsperma (Corda) Mangenot	F22-8	Pulpwood chips	Spruce	1965	+		Birch	1+2	Birch	23—25	3.9
Mollisia sp. A	T694C	Sleeper	Pine	1969	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Birch	23—25	0.6
Mortierella alpina Peyron.	CBS 343.66	Soil			–		Birch	0			
Mortierella isabellina Oudem.	B69-6	Pulpwood chips	Spruce	1965	–		Birch	0			
Mycelium radicis atrovirens Melin	C41-15	Pulpwood chips	Spruce	1970	–		Birch	1			
Myrothecium verrucaria Ditmar ex Fr.	CBS 328.52	Cotton bale			+	+	Birch	2			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Naemospora sp.	SP67-5	Telegraph pole Boliden K33	Pine	1970	+		Birch	2			
Oidiodendron echinulatum Barron	SP70-20	Telegraph pole Boliden K33	Pine	1970	+		Birch	0			
Oidiodendron griseum Robak	SP72-34	Telegraph pole Boliden K33	Pine	1970	+		Birch	2			
Oidiodendron tenuissimum (Peck) Hughes	E15-5	Pulpwood chips	Spruce	1966	+		Birch	1+2	Aspen Birch Pine	23—25 23—25 23—25	17.9 2.0 0
Paecilomyces elegans (Corda) Mason & Hughes	C20-21	Pulpwood chips	Spruce	1970	+		Birch	2			
Papularia arundis (Corda) Fr.	CBS				+		Birch	2			
Penicillium argillaceum Stolk & al.	P116-1	Pulpwood chips	Pine	1964	–		Birch	0			
Penicillium funiculosum Thom	P142-4	Pulpwood chips	Birch	1967	+		Birch	2	Aspen Birch	23—25 23—25	6.0 6.3
Petriella sordida (Zukal) Barron & Gilman	T100				+		Birch Pine	1+2 1			
Petriellidium boydii (Shear) Mallock	SP31-4	Soil burial test	Pine	1970	+	+	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Birch Pine	23—25 23—25	10.6 5.7
Phialocephala bactrospora Kendrick	CBS 299.62		Populus trichocarpa		+	+	Birch	1+2			
Phialocephala dimorphospora Kendrick	CBS 300.62.	Slime in pulp mill			–	+	Birch	1			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Phialocephala sp. A	P152-55	Pulpwood chips	Birch	1967	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Aspen Birch Pine	23—25 23—25 23—25	6.8 5.8 0
Phialocephala sp. B	814-1-1	Pole untreated	Pine	1967	+		Birch Pine	1+2 1+2	Birch	23—25	12.0
Phialocephala sp. C	71257-13	Log	Spruce	1971	–	–	Birch	1			
Phialophora bubakii (Laxa) Schol-Schwarz	H36-6	Pulpwood chips	Aspen	1966	+		Birch	2			
Phialophora cinerescens (Wollenw.) van Beyma	CBS				+		Birch	2			
Phialophora cyclaminis van Beyma	CBS 245.69	Wood			+		Aspen Birch	1 1			
Phialophora fastigiata (Lagerb. & Melin) Conant	731-1-3b	Pole untreated	Spruce	1968	+		Aspen Beech Birch Larch Pine Spruce	1+2 1+2 1+2 1 1 1	Aspen Birch Pine	23—25 23—25 23—25	11.7 8.7 1.5
Phialophora gregata (Allington & Chamberlain) W. Gams	CBS 184.70	From *Glycine soja*			–	+	Birch	2			
Phialophora hoffmannii (van Beyma) Schol-Schwarz	SP33-4	Test stake Wolmanit UA-Ref. 26.0 kg/m^3	Pine	1970	+	+	Aspen Beech Birch Pine Spruce	1+2 1+2 1+2 1 1	Aspen Birch Pine	23—25 23—25 23—25	15.8 11.6 1.8
Phialophora lignicola (Nannf.) Goid	CBS 267.33				+		Birch Pine Spruce	1+2 1+2 1	Aspen Birch Pine	23—25 23—25 23—25	20.9 8.2 1.8

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Phialophora lutco-viridis (van Beyma) Schol-Schwarz	CBS 206.38	Butter			+		Birch	1 + 2			
Phialophora mutabilis (van Beyma) Schol-Schwarz	SP65-170	Test stake Celcure A 11.3 kg/m³	Beech	1970	+		Birch Pine	1 + 2 1			
Phialophora richardsiae (Nannf.) Conant	KX21-10	Pulpwood chips	Spruce	1969	+		Birch Pine	1 + 2 1	Birch Pine	23—25 23—25	8.6 1.6
Phialophora verrucosa Medlar	P152-8	Pulpwood chips	Birch	1967	–	–	Birch	0			
Phialophora sp. A	SP35-1	Test stake Wolmanit UR 26.2 kg/m³	Pine	1970	–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Beech Pine	23—25 23—25	8.4[c] 7.9[c]
Phialophora sp. B	SP38-17	Telegraph pole Boliden BIS-salt	Pine	1970	+		Birch Pine	1 + 2 1	Aspen Birch Pine	23—25 23—25 23—25	4.5 3.2 0.8
Phialophora sp. C	SP68-31	Telegraph pole Boliden K33	Pine	1970	+		Birch	1 + 2			
Phialophora sp. D	SP60-15	Sleeper Boliden K33	Beech	1970	+		Birch	2			
Phialophora sp. E	SP62-20	Sleeper Boliden K33	Beech	1970	+		Birch	2			
Phialophora sp. F	SP44-13	Telegraph pole Boliden S25	Pine	1970	+		Birch	2			
Phialophora sp. G	P-T9	Wood in brackish water	Pine	1971	+		Birch	1 + 2			
Phoma aposphaerioides Briard & Har.	M72-1	Pulpwood chips	Birch	1965	–		Birch	1			

[c] Weight losses after 4 months.

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Phoma eupyrena Sacc.	SP28-13	Test block Boliden K33	Birch	1970	+		Birch	2	Birch	23—25	4.1
Phoma fimeti Brunaud	SP12-3	Pile		1969	+		Birch	1+2	Aspen	23—25	16.6
							Pine	1+2	Beech	23—25	3.8
									Birch	23—25	12.4
									Larch	23—25	5.1
									Pine	23—25	2.5
									Spruce	23—25	0
Phoma glomerata (Corda) Wollenw. & Hochapfel	Ö-T5	Wood in brackish water	Pine	1971	+		Birch	2			
Phoma macrostoma Mont.	KX4-1	Pulpwood chips	Pine	1969	+		Birch	2			
Pseudeurotium zonatum van Beyma	SP17-2	Foundation Pile	Spruce	1969	+	+	Birch	2	Birch	23—25	2.4
									Pine	23—25	1.0
Pseudeurotium sp.	Ö-B44	Wood in brackish water	Birch	1971	+	+	Birch	0			
Pseudogymnoascus roseus Raillo	SP68-35	Telegraph pole Boliden K33	Pine	1970	+		Birch	2			
Rhinocladiella anceps (Sacc. & Ellis) Hughes	SP35-15	Telegraph pole Boliden BIS-salt	Pine	1970	+	+	Birch	2	Aspen	23—25	1.0
									Birch	23—25	2.1
Rhinocladiella compacta (Carrión) Schol-Schwarz	CBS 555.69				+	+	Birch	2			
Rhinocladiella mansonii (Castell.) Schol-Schwarz	KT11-1	Pulpwood chips	Pine	1969	–		Birch	0			
Rhinocladiella sp. A	P160-14	Pulpwood chips	Birch	1967	–	–	Aspen	1	Aspen	23—25	13.9
							Beech	1	Birch	23—25	6.9
							Birch	1	Pine	23—25	3.5
							Pine	1			
							Spruce	1			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Rhizopus arrhizus Fischer	M168-1	Pulpwood chips	Birch	1966	–		Birch	0			
Scolecobasidium humicola Barron & Busch	P163-6	Pulpwood chips	Birch	1967	–		Birch	0			
Scytalidium album Beyer & Klingström	F2-3	Pulpwood chips	Spruce	1965	+		Aspen Birch	2 2	Aspen Birch Pine	23—25 23—25 23—25	8.4 5.7 1.4
Scytalidium aurantiacum Klingström & Beyer	D63	Pulpwood	Pine	1962	+		Birch	2			
Scytalidium lignicola Pesante	H97-1	Pulpwood chips	Aspen	1966	+	+	Aspen Beech Birch Pine	2 2 2 2	Aspen Birch Pine	30 30 30	17.8 10.0 2.1
Scytalidium sp. A	P175-50	Pulpwood chips	Birch	1968	–	–	Birch	0			
Scytalidium sp. B	721009-2	House flooring	Pine	1972	–	+	Birch	2			
Sepedonium chrysospermum (Bull ex Fr.) Link	QM 7791				–		Birch	0			
Sporotrichum thermophilum Apinis	M216-1	Pulpwood chips	Birch	1967	+		Birch Beech	2 2	Aspen Beech Birch Pine Spruce	45 45 45 45 45	26.3[d] 11.3[d] 15.4[d] 3.1[d] 1.2[d]
Stachybotrys atra Corda	611270	Test stake Cu-Cr-As	Pine		+		Birch	2			
Stilbella thermophila Fergus	Fergus				+		Birch	2			
Talaromyces bacillisporus (Swift) C. R. Benjamin	BB10-3	Pulpwood chips	Birch	1967	+		Birch	2			
Talaromyces helicus (Raper & Fennel) C. R. Benjamin	SP16-1	Foundation Pile	Spruce	1966	+		Birch	2			

[d] Weight losses after 2 months.

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Thermoascus aurantiacus Miehe	KT23-1	Pulpwood chips	Pine	1966	+		Birch	2			
Thermoascus thermophilus (Sopp) v. Arx	KT23-2	Pulpwood chips	Pine	1966	–		Birch	0			
Thermomyces languinosus Tsiklinsky	M11-2	Pulpwood chips	Birch	1964	–		Birch	0			
Thielavia thermophila Fergus & Sinden	CBS 174.70	Wheatstraw compost			+		Birch	2			
Thysanophora penicillioides (Roum.) Kendrick	A-B14	Wood in brackish water	Birch	1970	–	–	Birch	0			
Torula ligniperda (Willk.) Sacc.	CBS 383.36				+		Birch	2			
Trichocladium opacum (Corda) Hughes	36A-13591-3	Test stake untreated	Pine	1970	+		Birch Pine	1+2 1+2			
Trichoderma polysporum (Link ex Fr.) Rifai	71370			1971	+	+	Birch	2			
Trichoderma viride Pers. ex S. F. Gray	P40-10	Pulpwood chips	Pine	1965	+		Birch	2			
Trichosporiella cerebriformis (de Vries & Kleine-Natrop) W. Gams apud v. Arx	SP68-22	Telegraph pole Boliden K33	Pine	1970	+		Birch	2			
Trichurus spiralis Hasselbring	BAM MG31	Soil burial test	Pine		+		Birch	1+2			
Ulocladium consortiale (Thüm.) Simmons	H142-9	Pulpwood chips	Aspen	1966	+		Birch Pine	2 2			
Valsa ambiens (Pers.) Fr.	H42-3	Pulpwood chips	Aspen	1965	–		Birch	0			
Verticiladiella sp. A	H26-1	Pulpwood chips	Aspen	1965	–		Birch	0			
Verticillium falcatum (Petch) W. Gams	P173-54	Pulpwood chips	Birch	1968	+		Birch	2			

Species	Strain	Isolation			Cellulolytic activity		Type of attack		Weight losses		
		Source	Wood species	Year	R-C medium	B-VII medium	Wood species	Type	Wood species	Temp. °C	Weight loss %
Verticillium nigrescens Pethybr.	KX17-7	Pulpwood chips	Spruce	1969	+		Birch	2			
Verticillium psalliotae Treschow	KX12-2	Pulpwood chips	Spruce	1969	–		Birch	0			
Wardomyces inflatus (March) Hennebert	P180-62	Pulpwood chips	Birch	1968	+	+	Aspen Beech Birch Pine Spruce	1 + 2 1 1 + 2 1 1	Aspen Birch Pine	23—25 23—25 23—25	16.4 9.5 0.7
Xylogone sphaerospora v. Arx & Nilsson	P183-28	Pulpwood chips	Birch	1968	+	+	Birch Pine	2 2	Aspen Birch	30 30	29.3 8.0
Sterile mycelia											
Fungus A	A40-1	Telegraph pole Boliden BIS-salt	Pine		–	–	Aspen Beech Birch Pine Spruce	1 1 1 1 1	Birch Pine	23—25 23—25	4.3 2.5
Fungus B	SP3-10	Foundation Pile		1968	–	–	Aspen Birch Pine	1 1 1	Birch Pine	23—25 23—25	4.9 0.5
Fungus C	SP73-9	Telegraph pole Boliden K33	Pine	1970	+		Birch Pine	1 + 2 1			

List of synonyms

Absidia butleri Lendner
= Gongronella butleri (Lendner) Peyronel

Ascocoryne sarcoides (Jaquin ex S. F. Gray) Groves & Wilson
= Coryne sarcoides (Jaquin ex Fr.) Tul.

Allescheria boydii (Shear)
= Petriellidium boydii (Shear) Mallock

Alternaria consortialis (Thüm.) Groves & Hughes
= Ulocladium consortiale (Thüm.) Simmons

Bispora pusilla Sacc.
= Bispora betulina (Corda) Hughes

Bisporomyces chlamydosporis van Beyma
= Chloridium chlamydosporum (van Beyma) Hughes

Cephalosporium falcatum Petch
= Verticillium falcatum (Petch) W. Gams

Cephalosporium furcatum M. & F. Moreau
= Acremonium furcatum (M. & F. Moreau) W. Gams

Cephalosporium gregatum Allington & Chamberlain
= Phialophora gregata (Allington & Chamberlain) W. Gams

Dactylomyces thermophilus Sopp
= Thermoascus thermophilus (Sopp) v. Arx

Epicoccum nigrum Link
= Epicoccum purpurascens Ehrenb. ex. Schlecht

Gliocladium deliquescens Sopp
= Gliocladium viride Matr.

Glimastix murorum (Corda) Hughes
= Acremonium murorum (Corda) W. Gams

Gymnoascus roseus (Raillo) Apinis
= Pseudogymnoascus roseus Raillo

Helminthosporium sativum Pammel & al.
= Drechslera sorokiniana (Sacc.) Subram. & Jain

Humicola languinosa (Griff. & Maubl.) Bunce
= Thermomyces languinosus Tsiklinsky

Margarinomyces luteo-viridis van Beyma
= Phialophora luteo-viridis (van Beyma) Schol-Schwarz

Margarinomyces mutabilis van Beyma
= Phialophora mutabilis (van Beyma) Schol-Schwarz

Phaeoscopulariosis atrogrisea Panasenko
= Acremonium atro-griseum (Panasenko) W. Gams

Phialophora aurantiaca van Beyma
= Phialophora hoffmannii (van Beyma) Schol-Schwarz

Phialophora obscura (Nannf.) Conant
= Phialophora bubakii (Laxa) Schol-Schwarz

Pullularia pullulans (de Bary) Berkhout
= Aureobasidium pullulans (de Bary) Arnaud

Sclerophoma pityophila (Corda) Höhnel
= Dothichiza pityophila (Corda) Petrak

Stysanus microsporus Sacc.
= Doratomyces microsporus (Sacc.) Morton & Smith

Tilachlidium butyri van Beyma
= Acremonium butyri (van Beyma) W. Gams

Trichoderma lignorum (Tode) Harz
= Trichoderma viride Pers ex S. F. Gray

Trichoderma sporulosum (Link ex Pers.) Hughs
= Trichoderma polysporum (Link ex Pers.) Rifai

Trichosporiella hylalina Kamyschko ex W. Gams & Domsch
= Trichosporiella cerebriformis (de Vries & Kleine-Natrop) W. Gams apud v. Arx

Zalerion maritimum (Linder) Anastasiou
= Helicoma maritimum Linder

Comments to Table 1

Acremonium murorum (Corda) W. Gams
Syn.: Gliomastix murorum (Corda) Hughes
Only the erosion type of attack was found in birch and pine wood.

Casagrande and Ouellette (1971) reported that the fungus formed soft rot cavities in beech (*Fagus silvatica*) and spruce (*Picea abies*) wood.

Allescheria terrestris Apinis
A thermophilic soft rot fungus which has been found to be very common in pulpwood chips piles (Bergman & Nilsson 1967, 1968 and 1971). Soft rot cavities were produced in aspen, beech, birch, pine and spruce wood.

The cavity formation in birch wood have been studied in detail by Lundström (1972). He also studied the cavity formation in a great number of wood species but in contrast to my results, he did not obtain cavities in spruce wood.

Aspergillus spp.
Several non-identified *Aspergillus* strains were tested. Most of them produced clearing of the cellulose in the R-C medium. A slight attack of the erosion type was obtained in birch wood with the cellulolytic strains. None of the tested strains formed soft rot cavities in birch wood.

Aureobasidium pullulans (de Bary) Arnaud
Syn.: Pullularia pullulans (de Bary) Berkhout
No clearing was obtained on the R-C medium and no attack, except for small bore holes, was observed in birch wood.

The cellulolytic activity of *A. pullulans* has been examined by several workers. Most of them have reported that *A. pullulans* is non-cellulolytic (White et al. 1948, Marsh et al. 1949, Reese & Levinson 1952 and Dennis 1972). Levy (1969) reported that no attack except staining occurred in wood of *Betula* sp. and *Pinus silvestris*. Butcher (1968) obtained no weight losses of beech (*Fagus silvatica*) wood veneers after incubation for eight weeks. Rösch et al. (1969) found that carboxymethyl cellulase was produced in nutrient solutions with glucose or CMC. Greaves and Savory (1965) reported clearing of cellulose agar by *A. pullulans* but no soft rot cavities were found in birch wood. Seifert (1964) reported that approximately 7 percent of the cellulose and 3—4 percent of the hemicelluloses in pine wood were lost due to decay by *A. pullulans*.

Bispora effusa Peck
The strain obtained from CBS produced no clearing on the R-C medium nor on the B-VII medium. No attack, except for small bore holes, was observed in birch wood.

B. effusa has been listed as a soft rot fungus by Savory (1955) and by Duncan and Eslyn (1966).

Botryotrichum sp. A
This fungus is identical with a *Botryotrichum* species isolated from soil and described by Gams and Domsch (1969). Haider and Domsch (1969) found that this fungus reduced the dry weight of thin maple wood foils by 41 percent after 3 months.

Ceratocystis coerulescens (Münch) Bakshi
No clearing was obtained on the R-C medium. No attack, except for small bore holes, was observed in birch wood.

Levi and Cowling (1969) have also tested *C. coerulescens* on cellulose agar in test tubes. No clearing was observed. Levy (1969) reported that no attack except staining occurred in wood of *Betula* sp. and *Pinus silvestris*. King and Eggins (1972) found that the fungus produced carboxymethyl cellulase.

Ceratocystis minor (Hedgcock) Hunt
This fungus produced no clearing on the R-C medium and no attack, except small bore holes, was observed in birch wood.

Rösch et al. (1969) found that carboxymethyl cellulase was produced in nutrient solutions with glucose or CMC.

Ceratocystis piceae (Münch) Bakshi
Numerous cavities were found in the birch wood already after four weeks, while no cavities were found in pine wood after 15 weeks. After 29 weeks, however, a few cavities were found.

This extreme difference between the attack on birch and the attack on pine wood might explain the reports by Levy (1969) and Findlay (1970) that *C. piceae* only formed cavities in hardwoods and not in softwoods.

Ceratocystis pilifera (Fr.) C. Moreau
No clearing of cellulose was obtained on the R-C or the B-VII medium. The only attack observed in birch wood consisted of small bore holes.

Levy (1969) reported that no attack except staining occurred in wood of *Betula* sp. and *Pinus silvestris*. Findlay (1970) found no soft rot attack in six wood species tested. King and Eggins (1972) reported that *C. pilifera* produced clearing in cellulose agar.

Chaetomium thermophilum La Touche
Thermophilic soft rot fungus.

Cladosporium resinae (Lindav) de Vries
No clearing of cellulose was obtained. Birch wood was not attacked. Parbery (1969) found that one out of five isolates tested was able to break down cellulose.

Cladosporium spp.
Several non-identified *Cladosporium* strains have been tested. Some of the strains produced clearing of cellulose on the R-C medium and a slight attack of the erosion type in birch wood. None of the tested strains formed soft rot cavities in birch wood.

A species in this genus, *Cladosporium herbarum*, was listed as a soft rot fungus by Duncan and Eslyn (1966) but no information was given as to whether cavities were formed or not. In a paper by Gersonde and Kerner-Gang (1968) a picture is shown of a cross-section of pine wood attacked by *C. herbarum*. Typical soft rot cavities can be seen in the secondary cell walls. Levy (1969) reported cavity formation in wood of *Betula* sp. by a *Cladosporium* sp.

Coniothyrium spp.
Several isolates of *Coniothyrium* strains were obtained, especially from the test stakes. All strains tested cleared cellulose agar. Both the erosion type of attack and cavities were obtained in birch wood.

Cylindrocarpon spp.
Several isolates of non-identified *Cylindrocarpon* strains have been tested. All strains produced clearing on the R-C medium and slight attack of the erosion type in birch wood. None of the strains formed cavities in birch wood.

Gersonde and Kerner-Gang (1968) show a picture of a cross section of beech wood attacked by *Cylindrocarpon didymum*. Typical soft rot cavities can be seen in the secondary cell walls.

Drechslera sorokiniana (Sacc.) Subram & Jain
Syn.: Helminthosporium sativum Pammel et al.
Clearing occurred both on the R-C medium and on the B-VII medium.

Panasenko (1938) obtained 48 percent decomposition of cellulose after 30 days. Garrett (1963) cultured the fungus on filter paper which lost 14.8 percent of its weight after seven weeks. In contrast Muse et al. (1972) found no cellulolytic activity.

Fusarium spp.
All the tested *Fusarium* strains produced clearing on the R-C medium and most of them caused a slight erosion of the cell walls of birch wood. Only one of the strains was able to form cavities in birch wood. This strain was isolated from an untreated pole.

Humicola grisea Traaen var. *thermoidea* Cooney & Emerson
Thermophilic soft rot fungus.

Leptographium lundbergii Lagerberg & Melin
No clearing was obtained on the R-C medium and no attack occurred in birch wood.

Levy (1969) reported that no attack except staining occurred in wood of *Betula* sp. and *Pinus silvestris*. King and Eggins (1972) found that *L. lundbergii* cleared cellulose agar.

Paecilomyces elegans (Corda) Mason & Hughes
A slight attack of the erosion type was obtained in birch wood. Soft rot cavities were not found.

Levy (1969) reported that *P. elegans* formed cavities in birch (*Betula* sp.), beech (*Fagus silvatica*) and pine (*Pinus silvestris*) wood.

Penicillium spp.
Several non-identified *Penicillium* strains have been tested. Some of them caused a slight attack of the erosion type in birch wood and produced clearing on the R-C medium. None of the strains formed soft rot cavities in birch wood.

According to Levy (1969) *Penicillium cyclopium* formed cavities in birch (*Betula* sp.) and beech (*Fagus silvatica*) wood.

Phialocephala sp. A
This fungus was very common in a two year old birch chip pile. The species identification is not complete. One strain was sent to CBS in Baarn where it was considered to be a *Phialocephala* sp. But the type of spore formation differs from other described *Phialocephala* species. Only the first spores are produced within phialides with collarettes. In later stages the sporogenous tissue elevates considerably above the collarette and several spores develop concurrently from the sporogenous apex.

Phialophora fastigiata (Lagerberg & Melin) Conant
Soft rot cavities were found in all of the six wood species tested. Numerous cavities were found in the softwood after seven weeks. In addition the erosion type of attack was obtained in the hardwoods.

According to Levy (1969) and Findlay (1970) *P. fastigiata* is not able to form cavities in softwoods.

Phialophora hoffmannii (van Beyma) Schol-Schwarz
Syn.: Phialophora aurantiaca van Beyma.
This soft rot was very common in preservative-treated test stakes.

Phialophora lignicola (Nannf.) Goid.
Cavities were formed in birch, pine and spruce wood. The erosion type of attack was obtained both in birch and pine wood.

Casagrande and Ouellette (1971) found cavity formation in beech but not in spruce wood.

Phialophora richardsiae (Nannf.) Conant
Cavities were formed both in birch and pine wood.

Casagrande and Ouellette (1971) found cavity formation in beech but not in spruce wood.

Phialophora sp. A
This soft rot has been found to be one of the most common fungi in preservative treated test stakes. It has been isolated from test stakes treated with the following types of preservatives: Zn-Cr-As, Zn-Cu-Cr-As, Cu-Cr-As, Cu-Cr, F-Cr-As, F-Cr and creosote (Henningsson & Nilsson 1971).

The fungus has probably not been described earlier. It was first identified as a new *Phialocephala* sp. Then it was sent to Dr B. W. Kendrick in Canada and to Dr W. Gams, at CBS in Baarn. Both of them failed, however, to detect any sporulation of the fungus. On the basis of some micrographs sent to Dr Gams, he considered the fungus to be a *Phialophora* sp. rather than a species of *Phialocephala*.

Phialophora sp. C
Identical with *Phialophora* sp. I described by Gams and Domsch (1969).

Sepedonium chrysospermum (Bull. ex Fr.) Link
No clearing was obtained on the R-C medium.

Reese and Levinson (1952) found no cellulolytic activity while Domsch (1960) reported good utilization of cellulose.

Sporotrichum thermophile Apinis
Thermophilic soft rot.

Stilbella thermophila Fergus
Clearing was obtained on the R-C medium and the erosion type of attack was found in birch wood.

Fergus (1969) reported that filter paper was not degraded but the culture filtrates contained the Cx enzyme. Tansey (1971) using the technique of Rautela and Cowling (1966) obtained clearing of the cellulose.

Thermoascus aurantiacus (Miehe)
Thermophilic

Thermoascus thermophilus (Sopp) v. Arx
Syn.: Dactylomyces thermophilus Sopp
Thermophilic

Thermomyces languinosus Tsiklinsky
Syn.: Humicola languinosa (Griff. & Maubl.) Bunce
Thermophilic

Thielavia thermophila Fergus & Sinden
Thermophilic soft rot

Trichoderma spp.
Several strains of *Trichoderma* species have been tested. All produced clearing on the R-C medium and caused a slight erosion of the cell walls of birch wood. None of the tested strains formed soft rot cavities in birch wood.

Greaves and Savory (1965) found that *Trichoderma viride* cleared cellulose agar but no soft rot cavities were formed in birch wood.

In contrast, Liese and v. Pechman (1959) found soft rot cavities in birch wood attacked by *T. viride* and Courtois (1963 a) obtained cavities in beech wood. Merrill (1965) found cavity formation in a vessel of wood fiberboard. Levy (1967 and 1969) reported that one of eight isolates of *T. viride* (strain 69) was able to form cavities in birch (*Betula* sp.) and beech (*Fagus silvatica*) wood.

Discussion

The great number of fungi, belonging to more than sixty different genera, which have been found to be cellulolytic and wood-degrading indicate a very widespread occurrence of these activities among microfungi. It is interesting to note that some species, e.g. *Drechslera sorokiniana, Phialophora gregata* and *Stilbella thermophila,* which do not occur on wood substrates, were able to degrade wood. Levy (1969) and Findlay (1970) have demonstrated that fungi like *Ceratocystis piceae* and *Phialophora fastigiata,* which are considered to be typical blue stain fungi, are also capable of producing soft rot in wood. This was also confirmed in this investigation but it was found that several typical blue-stain fungi like *Aureobasidium pullulans,* several *Ceratocystis* species, *Discula pinicola, Dothichiza pityophila* and *Leptographium lundbergii* were unable to degrade wood.

Bergman and Nilsson (1966 and 1967) found that fungal degradation of wood could occur at higher temperatures than was expected before. They showed that several thermophilic fungi, some of them being able to grow even at 50 to 60°C, could produce soft rot in wood. Seven wood-degrading thermophilic fungi are included in the table presented here.

A prerequisite enabling fungus to degrade wood is the production of a cellulase which can accomplish a degradation of the wood cellulose. Reese et al. (1950) suggested that two different enzymes, called C_1 and C_x, are required for the breakdown of native cellulose. C_1 is generally considered to be required for native celluloses like cotton and wood cellulose, while the C_x enzymes attack degraded celluloses or substituted celluloses like carboxymethyl cellulose (CMC). The activity of the C_x enzymes are generally measured with CMC as substrate. In several papers the term "cellulase" has been used as synonymous with C_x enzymes but, as King and Vessal (1969) suggested, it would be preferable to reserve the term "cellulase" for the C_1—C_x complex.

Walseth cellulose was used in the assays of cellulolytic activity that was done here. The question is whether the dissolution of this cellulose can be accomplished by only C_x enzymes or if also C_1 enzymes are involved. Rautela and Cowling (1966) claimed that the dissolution of Walseth cellulose mainly involve C_x enzymes but C_1 enzymes might also be involved. According to my opinion, C_1 enzymes are necessary for dissolution of the Walseth cellulose and the following facts support this idea: Rösch et al. (1969) found that *Aureobasidium pullulans* and *Ceratocystis minor* produced CMC-degrading enzymes. These two species have also been tested here. Both failed to clear the cellulose in test tubes and produced no attack on wood. Rautela and Cowling (1966) and Levi and Cowling (1969) found that the brown rot fungi tested failed to produce clearing of the cellulose. For some of these brown rots, the production of C_x enzymes has been demonstrated by Reese and Levinson (1952), Lyr (1960) and by Keilich et al. (1969). If only C_x enzymes were necessary for the dissolution of Walseth cellulose, the two blue stain and the brown rot fungi would have produced clearing in the tube tests. Thus, it seems quite obvious that all fungi producing clearing of Walseth cellulose are equipped with C_1 enzymes. It has also been found that most of the species showing cellulolytic activity in the tube tests are able to degrade a native cellulose such as cotton (Nilsson, not published).

Bravery's (1968) finding that small amounts of alternative carbon sources can

inhibit the cellulolytic activity was confirmed in this investigation. Four of the fungi which produced clearing on the B-VII medium failed to clear the cellulose on the R-C medium. The cellulase production of these fungi thus appears to be inhibited by the small amounts of other carbon sources present in the R-C medium. The other fungi which gave clearing on both R-C and B-VII media do not seem to be influenced by small amounts of alternative carbon sources. All fungi were not tested on both media. It is possible that some of the species which failed to produce clearing on the R-C medium can do so on the B-VII medium.

Most of the results concerning the cellulolytic activity of those species which have also been studied by other workers agree with my results. As can be seen in the comments to Table 1, varying results have been published for some of the species. *Drechslera sorokiniana* (= *Helminthosporium sativum*) might be mentioned as an example. Evidence of cellulolytic activity of this fungus was found by Panasenko (1938) and Garrett (1963) and also in this investigation, while in a recent study Muse et al. (1972) failed to detect any cellulolytic activity. It is difficult to explain the results of King and Eggins (1972) who found that *Ceratocystis pilifera* and *Leptographium lundbergii* cleared cellulose agar. The strain of *Ceratocystis pilifera* tested here produced no clearing on the R-C medium nor on the B-VII medium. *Leptographium lundbergii* have not been tested on the B-VII medium and may possibly produce clearing on this medium.

It is evident that Type 1 and Type 2 attacks are quite different. The Type 2 attack must be regarded as the simplest. It only requires that a hypha should grow into the cell lumen where it produces wall-degrading enzymes which act directly upon the cell wall to give the typical erosion pattern (Fig. 3). It is likely that most species of microfungi with diffusable cellulases can produce this type of attack. The observations that in Type 2 attack the S_3 layer is often left and that the visible attack starts in the S_3 layer indicates a high resistance of the S_3 layer. If no submicroscopical attack occurs on the S_3 layer the enzymes will have to diffuse through this layer into the S_2.

It is difficult to explain the resistance of the S_3 layer in the hardwoods since very little is known of its composition. The S_3 layer in pine wood was found by Meier and Wilkie (1959) to contain a very high content of glucurono-arabinoxylan which might be resistant to attack. Sachs et al. (1963) and Parham and Côté (1971) found indications of a high concentration of lignin in the S_3 layer of *Pinus taeda* L.

Type 1 attack is more complicated than Type 2. Three steps can be distinguished in the process of cavity formation: 1) penetration into the cell wall by a hypha, 2) alignment of the hypha in the microfibrillar direction, either by "T-branching" (Corbett 1965) or by a change in the direction without branching, 3) production of enzymes which will dissolve the wall around the hypha. This decay pattern is thus restricted to a specialized group of fungi with the ability to grow within the wood cell walls in the direction of the microfibrils and to produce wall-degrading enzymes there. Several of the fungi which produce only Type 2 attack also often penetrate the cell walls but the hyphae do not grow in the microfibrillar direction; instead they grow through the whole cell wall to the neighbouring cell.

The results show that soft rot cavities are produced in all the wood species tested. All of the cavity-forming fungi which were tested on both birch and pine wood produced cavities in both of the wood species, although cavity formation was more rapid in the birch wood. Thus it is unlikely that any soft rot fungi exist which are restricted to hardwoods for cavity formation, as has been claimed by Levy (1969), Findlay (1970) and Casagrande and Ouellette (1971). Their failure to obtain cavities in softwoods might be explained by the use of different decay test methods. There might also be a variation between different strains of the fungi, so that some strains need an excep-

tionally long time for cavity formation in softwoods.

It is evident from the results that some correlation exists between the cellulolytic activity in the tube tests and the degradation of birch wood. The formation of clearing zones in the tube tests indicates that diffusible cellulases are produced by the fungi. It is likely that diffusable cellulases also will be produced in the wood cell lumina by hyphae of these fungi, giving rise to Type 2 attack. It was also found that 97 out of the 109 cellulolytic species produced Type 2 attack in the birch wood. The failure of the twelve species to attack the wood might be due to a lack of some other wall-degrading enzymes, such as xylanases or mannanases.

Another explanation might be that these fungi cannot degrade lignified cellulose. It is also possible that the S_3 layer represents a barrier which they could not degrade and through which their enzymes could not diffuse.

But all fungi which degraded birch wood did not show cellulolytic activity in the tube tests. Fifteen of the 120 wood-degrading species failed to produce clearing of the cellulose, thus indicating that diffusible cellulases were not produced. It is significant that all of these species produced only Type 1 attack in birch wood. An explanation as to why Type 2 attacks do not occur is that no diffusible or very small amounts of diffusible cellulases are produced by lumenal hyphae of these fungi. Cowling and Brown (1969) take cavity-producing soft rots as an example of microorganisms which have enzymes bound to their cell wall surfaces. It is possible in this case that all the "non-cellulolytic" fungi mentioned have cell-bound enzymes. But it would then be likely that hyphae lying close to the surface of the wood cell walls would produce some localized erosion. But this was not seen. Once inside the cell walls, the hyphae appears to be greatly stimulated to produce cellulases as indicated by the rapid production of cavities.

Kerner-Gang (1966) and Gersonde and Kerner-Gang (1968), who isolated microfungi from preservative-treated wood, discarded all isolates which failed to grow on a cellulose agar. These were not taken in consideration for the decay tests. This investigation clearly shows that growth on cellulose agar or clearing of cellulose in test tubes cannot be used as screening methods for soft rot fungi. Although it is likely that most of the fungi showing positive reactions also will degrade wood, a certain number of true soft rot species will be missed. This is serious since some of these species might be very common and probably important. Of the "non-cellulolytic" soft rots in this investigation, *Bispora betulina* and *Phialocephala* sp. A were very common in a pile of birch pulpwood chips, while the *Phialophora* sp. A (previously identified as *Phialocephala* sp.) is considered to be one of the most important soft rots in the degradation of preservative-treated timber in Sweden (Henningsson and Nilsson, 1971).

The results of the decay capacity tests show considerable variations in the aggressiveness of the species under the test conditions employed. Some indications of greater activity of fungi producing both Type 1 and Type 2 were seen but it must be remembered that the decay tests have been performed under standard conditions which might be far from optimal for several fungi. It is thus dangerous to draw any fargoing conclusions from the results presented here.

The considerable resistance of the softwoods against soft rot attack has been found by all earlier workers performing such tests. The resistance has been attributed to the higher lignin content of the softwoods compared with the hardwoods. It has been shown by Courtois (1963), Bailey et al. (1968), Nouvertné (1968) and Findlay (1970) that a rather slight delignification of softwood greatly increases its susceptibility to attack by some soft rot fungi.

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Sammanfattning

160 olika arter av mikrosvampar, de flesta isolerade från rötangripen ved, har undersökts med avseende på cellulolytisk aktivitet och förmåga att bryta ned ved.

Den cellulolytiska aktiviteten bestämdes genom att odla svamparna på ett cellulosa (Walseth cellulosa) agar medium i provrör. Klarning av cellulosan under de växande svamparna var en indikation på cellulolytisk aktivitet. Med användande av denna metod visade 109 av arterna cellulolytisk aktivitet.

Förmågan att bryta ned ved bestämdes mikroskopiskt på tunna snitt från träklotsar som angripits av svamparna. Träklotsarna rötades placerade på kulturer av svamparna vilka växte på maltextrakt eller cellulosa-agarmedium i snedagarrör. Angreppet på följande fem vedslag undersöktes: asp (*Populus tremula* L.), bok (*Fagus silvatica* L.), björk (*Betula verrucosa* Ehrh.), tall (*Pinus silvestris* L.) och gran (*Picea abies* (L.) H Karst.). De flesta studierna utfördes med björkved, som användes som "standard-ved", när jämförelser gjordes mellan angrepp på de olika vedslagen och när den cellulolytiska aktiviteten jämfördes med vednedbrytningsförmågan.

Två morfologiskt olika typer av aktiv nedbrytning av vedens cellväggar observerades. Den första typen (Typ 1) karaktäriserades av bildning av de typiska mögelrötekaviteterna inne i vedens cellväggar. Den andra typen (Typ 2) var en typ av erosion av cellväggen som börjar från lumen. S_3-skiktet i lövveden och speciellt i barrveden var mycket motståndskraftig mot båda typerna av angrepp.

120 av de undersökta arterna hade förmåga att bryta ned björkved. Dessa arter kunde med hänsyn till angreppstypen i björkved indelas i tre grupper: 1) tjugotre arter bildade endast mögelrötekaviteter; 2) femtiofyra arter hade förmåga att erodera cellväggarna; 3) fyrtiotre arter bildade kaviteter samtidigt som de åstadkom erosion.

Mögelrötekaviteter bildades i samtliga undersökta vedslag. Kavitetsbildningen i barrved var emellertid betydligt långsammare än i lövved. Samtliga kavitetsbildande arter som testades på både björk- och tallved bildade kaviteter i båda vedslagen.

Samtliga arter som åstadkom angrepp av Typ 2 eller Typ 1 + Typ 2 uppvisade cellulolytisk aktivitet i klarningsförsöken med cellulosa. Fyra av de cellulolytiska arterna kunde ej angripa björkved. Av de tjugotre som endast åstadkom angrepp av Typ 1 hade åtta cellulolytisk aktivitet medan femton arter inte åstadkom någon klarning av cellulosan. Av de senare odlades tretton på ett cellulosa-agarmedium som inte innehöll några andra kolkällor än cellulosa. Men inte heller på detta medium kunde de åstadkomma klarning av cellulosan. Oförmågan att åstadkomma klarning var således ej beroende på närvaron av alternativa kolkällor i agarmediet. Eftersom flera av de "icke-cellulolytiska" mögelrötesvamparna är vanliga i rötangripen ved är det uppenbart att den använda cellulosa-klarningsmetoden inte kan användas för att sålla fram mögelrötesvampar ur en samling isolat från rötangripen ved.

Rötförmågan (viktsförluster) hos de vednedbrytande svamparna har undersökts. Träklotsar av ovan nämnda fem vedslag användes. Träklotsarna rötades i tre månader i kolvar med vermiculit och en närlösning. Rötförmågan var mycket varierande hos de olika arterna. Stora variationer fanns också mellan svampar med samma nedbrytningsmönster. Viktsförlusterna hos lövved var generellt högre än viktsförlusterna hos barrved. Tre av vedslagen kunde ordnas efter ökande resistens i denna följd: asp — björk — tall.

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