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Comparison of wood decay among diverse lignicolous fungi

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Abstract: In decay tests with 98 isolates (78 species) of lignicolous fungi followed by chemical and anatomical analyses, the validity of the generally accepted, major decay types (white, brown, and soft rot) was confirmed, and no new major types proposed. We could distinguish soft rot from other decay types based on anatomical and chemical criteria, without reliance on cavities or recourse to taxonomy of causal agents. Chemically, soft rot of birch could be distinguished from white rot by lower Klason lignin loss, and from brown rot by much lower alkali solubility. Anatomically, erosion of birch fiber walls in soft rot was distinguished from that in white rot by the angular erosion channels, V-shaped notches and diamond-shaped, eroded pit apertures that predominated in the former and their rounded forms in the latter.

Substantial decay was caused by fungi representing eight orders in addition to the Aphyllophorales. Members of the Exidiaceae generally caused low weight losses and anatomical and chemical patterns of degradation characteristic of white rot. Isolates of *Auricularia auricula-judae* also caused a white rot, with high weight losses and unusual, branching microcavities that were oriented longitudinally in the S2 cell-wall layer. Ten species of the Dacrymycetales caused a brown rot like that caused by some Aphyllophorales; most caused high weight losses.

Among white-rot fungi on birch, a relationship was observed between strongly selective delignification and strongly selective utilization of mannose. Among brown-rot fungi on birch, the top two polyose sugars (not including glucose) in order of selectivity were galactose>mannose; among soft-rotters they were arabinose>xylose. On pine, distinctions were not so clear, but some differing trends were evident.

Previously unreported selective delignifiers were found in the Auriculariales, Agaricales, and in two orders of gasteromycetes. Selective delignification was most pronounced at low weight losses. Certain decay features similar to those in the Ascomycota were found in the Auriculariales, consistent with hypotheses that place that order near the phylogenetic root of Basidiomycota. A sequence of origins of decay types is proposed.

Key Words: Agaricales, Aphyllophorales, Auriculariales, brown rot, Dacrymycetales, Exidiaceae, phylogeny, soft rot, white rot, Xylariales

INTRODUCTION

Concepts of wood decay continue to be based largely on a limited range of lignicolous fungi, primarily in the families Polyporaceae, Hymenochaetaceae and Corticiaceae *sensu lato* of the order Aphyllophorales. Other basidiomycetes (Seifert, 1983) and nonbasidiomycetes (Duncan, 1960; Duncan and Eslyn, 1966; Merrill et al., 1964; Nilsson, 1973; Nilsson et al., 1989; Savory, 1954) cause substantial degradation of wood, but comprehensive studies on decay by such fungi are rare.

Three general types of decay are recognized (Blanchette, 1991; Eaton and Hale, 1993; Liese, 1970; Nilsson, 1988; Zabel and Morrell, 1992). In white rot, all cell-wall constituents are degraded. Two forms of white rot are distinguished. In selective delignification, polyoses (=hemicelluloses) and lignin are preferentially attacked, especially in early stages. The most remarkable anatomical effect is defibration by dissolution of the middle lamella. In simultaneous white rot, carbohydrates and lignin are attacked more or less uniformly. In this case, erosion of the cell wall from the lumen surface is a prominent anatomical feature. These two forms of white rot may be caused by one fungus in different portions of a piece of wood (Blanchette, 1991).

In brown rot, carbohydrates are extensively removed, but lignin is degraded only to a limited extent. Changes in birefringence can be observed in cell walls in polarized light, but microscopic changes are otherwise subtle until advanced stages (Wilcox, 1968).

Soft rot, the most recently described type of wood decay, has proven difficult to define and differentiate from other decays. It is caused by ascomycetes and

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deuteromycetes, and initially was characterized anatomically by longitudinal chains of cavities with conical tips in the S2 cell-wall layer (Savory, 1954). However, erosion at the lumen surface of hardwoods, similar to simultaneous white rot, sometimes occurs alone without the characteristic cavities (Courtois, 1963; Nilsson, 1973). Because features of the decays themselves were apparently not distinctive, the taxonomy of the causal agents has been used as a defining character (Nilsson, 1988). All cell wall constituents may be degraded during soft rot, but there is usually a preference for carbohydrates, especially in hardwoods (Eslyn et al., 1975; Nilsson et al., 1989).

A better understanding of the diverse kinds of wood-inhabiting fungi and their decay types will support efforts to prevent and control wood decay as well as recent efforts to find biotechnological applications of such fungi in the pulp and paper and other industries (Kirk and Chang, 1990). Such knowledge may also provide perspective in considering the evolution of wood-decay capability in various groups of fungi.

Our objectives were to 1) survey lesser-known and previously neglected lignicolous fungi for the ability to cause wood decay; 2) elucidate the macroscopic, microscopic, and chemical features of decay by such fungi in comparison with known decay types; 3) reassess decay classifications from the perspective of a broader range of lignicolous fungi, and; 4) assess the implications of decay features to fungal phylogeny.

MATERIALS AND METHODS

Fungal isolates.—Cultures were isolated by us or kindly provided by other workers (TABLE I). Deuteromycetes were chosen on the basis of previously known decay capability (Wang and Zabel, 1990; Zabel et al., 1991). Other isolates were chosen from those available to represent diverse groups of fungi associated with decay. Multiple isolates of some species were tested. Cultures isolated by us were tissue isolates from fruiting bodies collected in the field. When the fruiting structures were small and cultural characters unknown, spore isolations were also made for verification. Cultures were grown at 25°C on malt extract agar (1.25% malt extract, 1.5% agar) and stored at 4°C.

Decay tests.—Soil-block decay tests were conducted as described in a standard method (Anonymous, 1986a) except for the following details. Sapwood of yellow birch (*Betula alleghaniensis* Britton) and southern pine (*Pinus taeda* L.) was used. Test blocks were 20 mm (radial) × 10 mm (tangential) × 5 mm (longitudinal) and feeder strips were 25 mm × 33 mm × 3 mm (longitudinal). The soil was a loam whose moisture holding capacity was 34% and pH was 6.0. The appropriate amount of water followed by 120 mL of soil (approximately 96 g dry weight) was added to bottles with a capacity of 192 mL. A feeder strip of the same wood used for the blocks was soaked in deionized water for 5 min and placed on the soil. Bottles were capped, autoclaved for 75 min at 121°C, cooled, and inoculated with plugs (4 mm diam.) of mycelium and agar. After 20 d, blocks that had been oven-dried, weighed, soaked in deionized water for 5 min, then steamed at 100°C for 20 min were added aseptically, three per bottle. Usually four bottles were used per treatment for a total of 12 replicate blocks per fungus. Ten soil-block tests using about a dozen fungi each were conducted for this study.

After 12 wk (unless otherwise noted), blocks were removed. Observations were made of the nature and abundance of external mycelium and macroscopic appearance of the decayed wood. External mycelium was carefully removed. Blocks were oven dried and weighed, except that one block was placed in formalin-acetic acid without drying. The loss in dry weight was calculated as a percentage of the original dry weight. The corresponding figure for the uninoculated controls in each test (almost always between 1.0% and −1.0%) was then subtracted to arrive at a corrected percent weight loss.

To determine if certain fungal groups or decay types could be distinguished by the effects of nutrients on decay, soil-block tests with selected fungi were conducted with and without added nutrients. The nutrient solution of Worrall et al. (1991), but without glucose and thiamine, was used to moisten soil, feeder strips and blocks in place of water (which was used for controls) as described above. To permit study of early stages of decay, several experiments were conducted for periods shorter than 12 wk.

Soft-rot tests of two kinds were used because standard soil-block tests do not provide conditions suitable for all fungi. A vermiculite test was used in some cases (Worrall and Wang, 1991); an agar-block test was used in others (Worrall et al., 1991).

Macroscopic decay features.—When mean loss in dry weight exceeded 2% for a fungus, all replicate blocks were examined after drying and compared to controls with a stereomicroscope. Internal and external color changes and shrinkage were noted. Softness was judged after penetration with a blunt needle. Special features such as staining, loss of wood rays, resin canal enlargement, annual ring separations, and zone lines were noted also.

Chemical analyses.—Normally, four representative blocks were bulked for analysis from each treatment

that had mean weight loss ≥5%. Determination of acid-insoluble (Klason) lignin generally followed standard methods (Anonymous, 1991a; Effland, 1977). Analysis of wood sugars in the filtered hydrolyzate was by anion chromatography (Pettersen and Schwandt, 1991). Details of the hydrolysis and reproducibility are described elsewhere (Worrall and Anderson, 1993).

Acid-soluble lignin was measured in the filtrate from the hydrolysis (Anonymous, 1991b). After bringing the filtrate volume to 100 mL, absorbance was measured at 205 nm, using 1.44% H_2SO_4 (w/w) as a reference. Samples were diluted with 1.44% H_2SO_4 as necessary to get absorbance readings in the range 0.2 to 0.7.

Alkali solubility was determined generally according to established methods (Anonymous, 1986b). Six blocks not used for lignin and sugar analysis were ground and bulked for analysis. The procedure was scaled down for use of 750 mg sample.

Microscopy.—Slides were prepared from decayed blocks and examined with a Nikon Optiphot microscope when the mean weight loss for the treatment was > 2%. Tangential, radial and transverse sections (~17 μm) were cut with a sliding microtome, mounted in lactophenol/lactic acid, and observed with brightfield or Nomarski differential interference contrast microscopy. Principle features recorded were hyphal frequency and location, cell wall thinning, erosion channels and notches, pit erosion, frequency and size of transverse bore holes compared to diameters of lumen hyphae, destruction of ray parenchyma, cell separations, and longitudinal cavities in the S2. Erosion channels, also termed troughs, are localized, elongated areas of erosion on the lumen surface, usually associated with an overlying hypha. A notch is a V- or U-shaped point of erosion at the lumen surface seen in the tangential wall in a radial section or in the radial wall in a tangential section. A notch may represent a cross section of a horizontal channel or a point of bore hole or channel initiation.

Enzyme tests.—Polyphenol oxidases were detected by discoloration of gallic and tannic acid media after one week's growth of a test fungus (Davidson et al., 1938). Laccase, tyrosinase, and peroxidase were detected by media discoloration using drop tests (Stalpers, 1978). For use of the solutions, fungi were grown on malt extract agar (1.5% malt extract). Five wells (4 mm diam) were cut through the mycelial mat 1.5 cm from the margin. Two drops of a test solution or a control (water or 96% ethanol) were placed in each well. Color reactions were recorded at 1, 3, and 7 d. In the cases of fungi with black pigmentation, in both tests, a sterile film of cellophane was placed on the medium surface before inoculation and stripped off with the mycelium before reading (gallic and tannic acid) or adding solutions (drop tests). All tests were duplicated.

RESULTS

Weight loss.—Seventy (71%) of the isolates caused weight losses ≥2.0% in at least one test (TABLE I). High weight losses were caused, as expected, by many of the known decay fungi in the Aphyllophorales (TABLE I, FIG. 1). However, fungi in other groups of Basidiomycota also caused high weight losses (FIG. 1). Most species of the Dacrymycetales consistently caused high weight losses. In the Auriculariales, members of the Exidiaceae caused weight losses indicative of decay and *Auricularia auricula-judae* caused high weight losses. Also species in several orders of gasteromycetes and the Agaricales caused substantial weight losses. Among nonbasidiomycetes tested, some deuteromycetes, Xylariales, Sordariales and Diatrypales also caused substantial weight losses.

No further analysis was done with isolates that caused mean weight losses less than 2.0% (TABLE I) in all tests in which they were used. They included the few isolates in the Hypocreales and Ophiostomatales, two of the three Diaporthales, five of the six Pezizales, and all of the four members of the Tulasnellales. Other isolates that caused such low weight losses were scattered among most groups.

Effect of nutrients. Thirty-one species were tested for the effect of nutrients on decay. For analysis of variance, they were considered in the seven groups listed in TABLE II. The interaction of nutrient treatment and group was highly significant ($P < 0.001$) for both pine and birch, indicating that response to nutrients varied among the groups. All members of the Xylariales and Diatrypales showed significantly greater weight loss in the presence of nutrients ($P < 0.01$) on birch (TABLE II). Decay by two of the four members of Exidiaceae was also stimulated significantly on both woods ($P < 0.01$); the other two caused low weight losses throughout. No significant inhibition was observed in these groups.

In contrast, the Dacrymycetales and especially the Aphyllophorales/Agaricales had more cases of significant inhibition than stimulation by nutrients (TABLE II). Little or no effect was observed in the deuteromycetes, other Ascomycota, and gasteromycetes, where weight losses were lower.

Chemistry.—Fifty-nine (60%) of the isolates caused weight losses ≥5.0% in at least one test. Blocks from these tests were analyzed chemically.

Ratio of lignin loss to weight loss. The ratio between

TABLE I. Isolates used in the wood-decay experiments, supplier's isolate number, decay type based on our results, and mean weight losses on birch and pine in all experiments

Fungus[a]	Isolate number: supplier[b]	Type of decay[c]	Type and duration of test[d]	Mean weight loss (%)	
				Birch	Pine
DEUTEROMYCETES[e]					
Dematiaceous hyphomycetes—					
Cladosporium herbarum (Pers.: Fr.) Link	ED-132:1	S1, 2	+N	3.5	1.8
	ED-132:1	S1, 2	−N	2.2	2.5
Phialemonium dimorphosporum W. Gams & W.B. Cooke	ED-100:1	S1	A	17.4	3.7
Phialocephala dimorphospora W.B. Kendrick	P-109:1	S1	A	32.6	1.2
	P-109:1	S1	+N	16.4	1.7
	P-109:1	S1	−N	14.3	3.9
	P-109:1	S1	S	11.6	2.4
Phialophora melinii (Nannf.) Conant	P-850:1	S1	A	15.0	2.5
Phialophora parasitica Ajello, Georg & C.J.K. Wang	P-754:1	S1	A	13.5	1.6
Scytalidium lignicola Pesante	P-53:1	S2	V	6.5	2.4
Spegazzinia tessarthra (Berk. & M.A. Curtis) Sacc.	P-511:1	S2	A	10.0	2.6
	P-511:1	S2	+N	6.9	3.8
	P-511:1	S2	−N	3.2	2.9
Moniliaceous hyphomycetes—					
Acremonium sp.	1C:1	S1	+N	7.8	4.1
	1C:1	S1	−N	3.4	4.2
Arthrographis cuboidea (Sacc. & Ellis) Sigler	P-540:1	S2	V	9.6	2.8
	P-540:1	S2	+N	2.4	2.2
	P-540:1	S2	−N	1.3	0.8
Aspergillus terreus Thom	P-762:1	S2	A	8.9	4.2
ASCOMYCOTA					
Diaporthales—Diaporthaceae					
Cryphonectria cubensis (Bruner) C.S. Hodges	64159:2	—	S	0.5	0.9
Cryphonectria gyrosa (Berk. & Broome) Sacc.	48193:2	—	S	0.9	1.8
Cryphonectria parasitica (Murrill) M.E. Barr	EP-GY1:3	—	S	1.1	1.2
	EP-P1:3	S1, 2	S	2.5	1.6
	EP-P1:3	S1, 2	+N	1.9	2.6
	EP-P1:3	S1, 2	−N	1.6	2.6
Hypocreales—Hypocreaceae					
Nectria cinnabarina (Tode: Fr.) Fr.	N15	—	S	1.0	1.6
Nectria galligena Bres.	11684:2	—	S	−0.5	0.9
Leotiales—Leotiaceae					
Bisporella citrina (Batsch: Fr.) Korf & S.E. Carp.	N14	—	S	0.6	1.3
Bulgaria inquinans (Pers.: Fr.) Fr.	N13	S2	S	4.2	1.8
	N13	S2	S	2.2	1.9
Ophiostomatales—Ophiostomataceae					
Ophiostoma sp.	N8	—	−N	1.1	1.2
	N8	—	+N	0.7	1.5
Pezizales—Morchellaceae					
Morchella esculenta L.: Pers.	N21[f]	—	S	0.2	1.7
Morchella semilibera DC.	N22[f]	—	S	−0.2	1.1
Verpa bohemica (Krombh.) J. Schröt.	N23[f]	—	S	−0.1	1.8
	N24[f]	—	S	−0.4	0.7
Pezizales—Sarcoscyphaceae					
Sarcoscypha coccinea (Fr.) Lambotte	58028:2	—	S	0.4	−0.8
Urnula craterium (Schwein.: Fr.) Fr.	595:4	S2	S	3.4	1.7
	595:4	S2	−N; 8.7 wk	2.6	0.9
	595:4	S2	+N; 8.7 wk	0.7	1.1
Sordariales—Chaetomiaceae					
Chaetomium aureum Chivers	P-722:1	S1, 2	A; 10.5 wk	19.8	3.4
Chaetomium funicola Cooke	ED-189:1	S1, 2	A; 10.5 wk	12.7	2.5

TABLE I. Isolates used in the wood-decay experiments, supplier's isolate number, decay type based on our results, and mean weight losses on birch and pine in all experiments (Cont.)

Fungus[a]	Isolate number: supplier[b]	Type of decay[c]	Type and duration of test[d]	Mean weight loss (%)	
				Birch	Pine
Chaetomium globosum Kunze : Fr.	P-591:1	S1, 2	V; 8.4 wk	39.9	5.1
	P-591:1	S1, 2	+N	3.1	3.4
	P-591:1	S1, 2	−N	1.3	3.6
	P-591:1	S1, 2	S	0.2	3.5
	P-591:1	S1, 2	S	−0.4	1.8
Diatrypales—Diatrypaceae					
Cryptosphaeria lignyota (Fr. : Fr.) Auersw. (= *C. populina* Sacc.)	190-3:5	S2	S	6.0	2.0
Eutypella parasitica R. W. Davidson & Lorentz	N26	S2	+N	11.6	3.3
	N26	S2	−N	3.4	1.9
	N26	S2	S	1.8	1.8
Xylariales—Xylariaceae					
Daldinia concentrica (Bolton : Fr.) Ces. & De Not.	N7:6	S2	+N	38.6	2.7
	N7:6	S2	−N	22.6	2.8
	N7:6	S2	S	18.3	2.0
Hypoxylon atropunctatum (Schwein. : Fr.) Cooke	38987:2	—	S	0.4	0.8
Hypoxylon mammatum (Wahlenb.) J.H. Mill.	N25	S2	+N	14.2	3.3
	N25	S2	−N	4.6	2.7
	N25	S2	S	1.0	2.4
Rosellinia subiculata (Schwein. : Fr.) Sacc.	58850:2	—	S	1.3	1.0
Xylaria polymorpha (Pers. : Fr.) Grev.	N12	S1, 2	S	5.9	2.9
	N5	S1	+N	16.1	4.2
	N5	S1	−N	6.6	5.2
BASIDIOMYCOTA—TELIOMYCETES					
Platygloeales—Cystobasidiaceae					
Helicobasidium mompa Tanaka	11046:2	—	S	−0.5	−0.2
BASIDIOMYCOTA—HETEROBASIDIOMYCETES					
Auriculariales—Auriculariaceae					
Auricularia auricula-judae (Bull. : Fr.) J. Schröt.	11380:7	W	S	7.7	5.2
	617:8	W	S	39.5	25.3
	618:8	W	S	27.2	16.5
	619:8	W	S	37.8	14.9
	623:7	W	S	15.4	25.0
Auriculariales—Exidiaceae					
Basidiodendron cinereum (Bres.) Luck-Allen	1979:7	—	S	0.3	0.9
Basidiodendron eyrei (Wakef.) Luck-Allen	639:7	W	S	4.0	1.2
	639:7	W	+N; 8.7 wk	0.3	0.3
	639:7	W	−N; 8.7 wk	0.1	−0.4
Exidia crenata Schwein. : Fr. (*E. recisa* Ditmar : Fr. *sensu* most N. Amer. authors)	10688:7	W	+N; 8.7 wk	6.9	4.9
	10688.7	W	S	3.9	−0.9
	10688.7	W	−N; 8.7 wk	2.5	1.6
	580	W	S	4.0	6.2
Exidia glandulosa Bull. : Fr.	1966:7	W	S	5.9	5.4
	1967:7	W	S	3.3	4.8
	453	W	+N	10.2	10.6
	453	W	−N	3.7	4.7
	453	W	S	4.4	5.1
	453	W	S	3.3	3.7
Exidiopsis calcea (Pers. : Fr.) K. Wells *sensu* N. Amer. authors	1976:7	W	S	6.5	5.4
	1976:7	W	−N; 8.7 wk	2.5	0.8
	1976:7	W	+N; 8.7 wk	0.7	1.0

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Fungus[a]	Isolate number: supplier[b]	Type of decay[c]	Type and duration of test[d]	Mean weight loss (%)	
				Birch	Pine
Exidiopsis grisea (Pers.) Bourdot & L. Maire *sensu* N. Amer. authors	1978:7	W	S	4.9	5.6
Dacrymycetales—Dacrymycetaceae					
Calocera cornea (Batsch : Fr.) Fr.	440	B	+N	39.6	37.9
	440	B	−N	38.9	41.2
	440	B	S	22.2	25.3
Calocera viscosa (Pers. : Fr.) Fr.	11298:7	B	S	3.4	0.3
Dacrymyces capitatus Schwein.	48087:2	B	S	15.2	−0.5
Dacrymyces chrysospermus Berk. & M.A. Curtis [= *D. palmatus* (Schwein.) Bres.]	434	B	S	68.5	50.6
	434	B	S; 4.1 wk	10.9	5.6
	449	B	S	67.2	38.5
	449	B	S; 4 wk	9.6	21.0
	449	B	S; 4.1 wk	8.5	3.5
Dacrymyces dictyosporus G.W. Martin	46563:2	B	S	57.2	40.2
Dacrymyces minor Peck	429	B	S	25.2	18.6
	429	B	−N; 8.7 wk	20.6	18.6
	429	B	+N; 8.7 wk	19.1	17.6
Dacrymyces novae-zelandiae McNabb	48457:2	—	S	−0.7	−0.8
Dacrymyces punctiformis Neuhoff	1710:7	—	−N	1.6	1.4
	1710:7	—	+N	0.1	1.7
Dacrymyces stillatus Nees : Fr.	426	B	S	35.2	35.2
	426	B	S; 4.1 wk	5.0	2.2
	450	B	S	25.5	19.6
Dacryopinax spathularia (Schwein. : Fr.) G.W. Martin	439	B	+N	67.4	23.9
	439	B	S	67.0	31.1
	439	B	−N	55.7	41.2
	439	B	S; 4.1 wk	7.5	4.0
Tulasnellales—Tulasnellaceae					
Gloeotulasnella cystidiophora (Höhn. & Litsch.) Bourdot & Galzin	262-1:9	—	S	−0.7	−0.9
Tulasnella araneosa Bourdot & Galzin	123-17:9	—	S	−0.1	−0.1
Tulasnella pruinosa Bourdot & Galzin	9068:7	—	S	0.7	0.4
Tulasnella violea (Quél.) Bourdot & Galzin	31-1:9	—	S	−0.9	−0.6
BASIDIOMYCOTA—HOMOBASIDIOMYCETES					
Unknown	451	W	S	28.3	27.7
	2911:7	W	−N; 8.7 wk	6.1	4.3
	2911:7	W	S	6.0	5.3
	2911:7	W	+N; 8.7 wk	2.5	3.5
Agaricales—Tricholomataceae					
Armillaria gallica Marxm. & Romagn.	328	W	S	8.5	5.1
Armillaria calvescens Bérubé & Dessur.	509	—	S		1.7
	569	—	S	0.7	−0.2
Armillaria gemina Bérubé & Dessur.	559	W	S	5.6	2.0
Armillaria ostoyae (Romagn.) Herink	217	—	S	1.4	0.5
Armillaria sinapina Bérubé & Dessur.	B618:10	—	S	1.1	1.6
Agaricales—Xerulaceae					
Megacollybia platyphylla (Pers. : Fr.) Kotl. & Pouzar	464	W	S	14.5	16.6
	488	W	S	12.6	5.6
	508	W	S	16.1	4.7

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Fungus[a]	Isolate number: supplier[b]	Type of decay[c]	Type and duration of test[d]	Mean weight loss (%)	
				Birch	Pine
Mycena leaiana (Berk.) Sacc.	6113T2B:11	W	S	10.0	6.3
	6113T2B:11	W	+N; 8.7 wk	8.2	7.3
	6113T2B:11	W	−N; 8.7 wk	7.4	4.4
Aphyllophorales—Coniophoraceae					
Coniophora puteana (Schumach.: Fr.) P. Karst.	61	B	S	34.2	25.6
	61	B	−N; 8.7 wk	8.1	2.8
	61	B	+N; 8.7 wk	4.6	3.7
Aphyllophorales—Corticiaceae					
Phlebia tremellosa (Schrad.: Fr.) Nakasone & Burds.	25:12	W	S	53.4	30.7
	25:12	W	+N	27.1	17.4
	25:12	W	−N	18.4	29.8
	25:12	W	S; 4.1 wk	12.2	9.5
	25:12	W	S	11.2	5.4
Aphyllophorales—Hymenochaetaceae					
Phellinus pini (Thore: Fr.) A. Ames	19:12	W	S	10.2	19.4
	19:12	W	−N	5.6	22.0
	19:12	W	+N	1.8	20.5
Aphyllophorales—Polyporaceae					
Bjerkandera adusta (Willd.: Fr.) P. Karst.	F-58:13	W	S; 8.4 wk	51.3	28.1
	F-58:13	W	S	50.3	28.0
	F-58:13	W	S; 4.1 wk	8.5	5.8
Climacocystis borealis (Fr.) Kotl. & Pouzar	3	W	S	12.4	22.0
	3	W	S	6.8	23.3
Gloeophyllum trabeum (Pers.: Fr.) Murrill	32:13	B	S	57.5	59.8
	32:13	B	S; 4.8 wk	25.6	20.6
Heterobasidion annosum (Fr.) Bref.	32[f]	W	−N	1.6	8.9
	32[f]	W	+N	1.3	2.8
	32[f]	W	S; 4.1 wk	0.7	2.2
	33[f]	W	S; 4.1 wk	0.6	2.5
Oligoporus placentus (Fr.) Gilb. & Ryvarden	F-33:13	B	S	68.8	55.8
	F-33:13	B	S; 4.8 wk	41.4	29.5
Oligoporus fragilis (Fr.) Gilb. & Ryvarden	26	B	−N	7.9	6.2
	26	B	S	4.0	15.1
	26	B	+N	0.7	0.9
Trametes versicolor (L.: Fr.) Pilát	491:13	W	S	69.1	37.1
	491:13	W	S	64.3	40.2
	491:13	W	S; 8.4 wk	53.9	29.2
	491:13	W	S; 4.1 wk	26.3	11.3
	594	W	S	88.4	42.2
Trichaptum abietinum (Dicks.: Fr.) Ryvarden	7	W	S	2.3	1.3
Lycoperdales—Lycoperdaceae					
Lycoperdon perlatum Pers.	452	W	S	1.1	2.1
Lycoperdon pyriforme Schaeff.: Fr.	443	—	S	−0.2	0.6
	445	W	−N; 8.7 wk	0.7	−0.3
	445	W	+N; 8.7 wk	0.6	−0.1
	445	W	S	0.6	2.1
Nidulariales—Nidulariaceae					
Crucibulum laeve (Bull.) Kambly	444	W	+N	7.5	9.6
	444	W	−N	6.5	7.1
	444	W	S	4.5	3.8
Nidula sp.	4451:7	—	S	1.0	1.0

TABLE I. Isolates used in the wood-decay experiments, supplier's isolate number, decay type based on our results, and mean weight losses on birch and pine in all experiments (Cont.)

Fungus[a]	Isolate number: supplier[b]	Type of decay[c]	Type and duration of test[d]	Mean weight loss (%)	
				Birch	Pine
Sclerodermatales—Sphaerobolaceae					
Sphaerobolus stellatus Tode : Fr.	581	W	S	7.7	7.1
	581	W	S	5.8	6.9
	581	W	−N; 8.7 wk	3.7	3.5
	581	W	+N; 8.7 wk	2.7	4.9

[a] The classification follows Bandoni (1984) and Wells (1994) for the Heterobasidiomycetes and Hawksworth et al. (1995) for most other groups.

[b] Suppliers' isolate numbers are used and supplier is indicated by number following colon. Isolates were kindly supplied by: 1, C. J. K. Wang, SUNY College of Environmental Science and Forestry, Syracuse (ESF); 2, American Type Culture Collection; 3, W. A. Powell, ESF; 4, F. Tainter, Clemson University (our isolate number); 5, P. Manion, ESF; 6, K. Hammel, U.S. Forest Products Lab., Madison (FPL) (our isolate number); 7, H. H. Burdsall, Center for Forest Mycology, FPL; 8, K. Wells, Hot Springs NC (dikaryon synthesized by us from two isolates; our isolate number); 9, K. Wells; 10, T. C. Harrington, University of Iowa, Ames; 11, T. Baroni, SUNY College at Cortland; 12, R. A. Blanchette, Univ. Minnesota, St. Paul; 13, stock culture collection of ESF. Others were isolated by us from nature. All cultures were from North America except 262-1 from Germany, 11684 from England, 48457 from New Zealand, and 11046 which is of uncertain geographic origin. Some isolates are represented more than once when tested multiple times in different experiments or for different lengths of time.

[c] Decay type. S = soft rot; W = white rot; B = brown rot; "—" = no decay (mean weight loss < 2.0% in all tests). The numbers 1 and 2 refer to anatomical evidence of soft rot types 1 and 2.

[d] S refers to the standard, 12-wk soil-block test. +N and −N refer to treatments with added nutrients and controls from the same experiments, respectively. A and V refer to agar-block and vermiculite tests, respectively, both of which contained added nutrients. Experiments shorter than standard are indicated by the number of weeks.

[e] Asexual fungi with uncertain or unknown teleomorphs. Most are presumably asexual ascomycetes.

[f] Single-spore isolate.

the percentages of lignin loss and weight loss of analyzed blocks (L/W) was calculated and used in subsequent comparisons (TABLE III, FIG. 2). In wood decayed by typical white-rot fungi in the Aphyllophorales and members of the Agaricales, several orders of gasteromycetes, and the Auriculariales, L/W ranged from 0.8 to 4.4. Wood decayed by typical brown-rot fungi of the Aphyllophorales, all members of the Dacrymycetales, and all members of the Ascomycota and deuteromycetes, which include the typical soft-rot fungi, was associated with L/W <0.8.

When isolates were tested and analyzed at different weight losses, it was possible to observe the trend of delignification at successive stages of decay (TABLE III). When L/W was >0.8, as in white-rot fungi, L/W decreased at the higher weight loss in most cases, indicating greater attack of lignin in early stages. When L/W was <0.8, as in brown- and soft-rot fungi, it increased at the higher weight loss in all cases, indicating that delignification (loss of Klason lignin) increased with weight loss.

Alkali solubility. The alkali solubility of sound wood samples (mean of nine analyses ± standard error) was 20.9±1.4% for birch and 16.1±1.1% for pine. Alkali solubility of decayed samples ranged up to 80% on birch and 67% on pine. Generally, samples with higher weight losses had higher alkali solubilities (FIG. 2). This trend was greater for brown-rotted samples with L/W <0.8, especially on pine.

The nonbasidiomycetes, which include the known soft-rot fungi, could be clearly distinguished from typical brown-rot fungi. Alkali solubility of blocks decayed by nonbasidiomycetes was much lower than is typical for brown rot and also generally lower than for white rot (FIG. 2). Alkali solubility was measured on many additional samples decayed by nonbasidiomycetes and generally was below 30% for birch and 20% for pine (data not shown). Complete chemical analyses of decays by ascomycetes and deuteromycetes were done only on birch because those fungi caused generally low weight losses of pine in these experiments.

Major decay types. We provide here operational definitions of the three major decay types for use in presentation of the remaining results. The definitions are quantitative with respect to our data, and the values used may not apply in other studies. White rot is a decay in which L/W is 0.8 or greater. Both brown rot and soft rot are characterized by L/W less than 0.8. In brown rot, alkali solubility is above 30% in pine and 35% in birch; in soft rot, alkali solubility is below those values (FIG. 2).

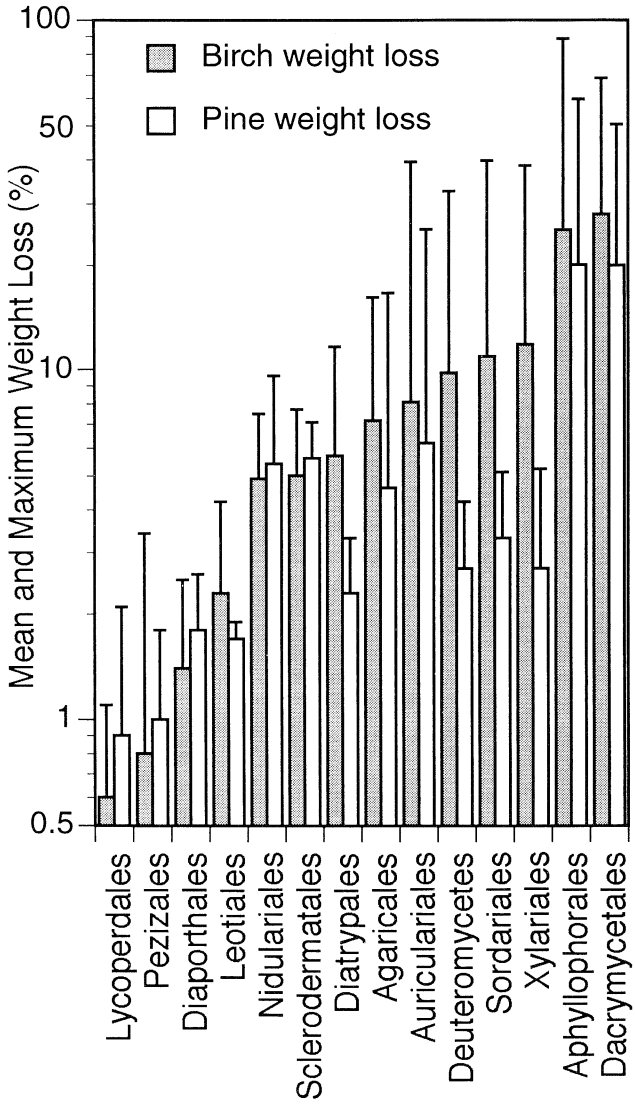


FIG. 1. Mean and maximum percent weight loss of birch and pine caused by fungi in all tests in each order and in the deuteromycetes. Means include isolates that caused no detectable decay. Three orders (Hypocreales, Ophiostomatales and Tulasnellales) are not shown; all weight losses were less than 2%.

Polyose utilization. Weight losses of the polyose monomers were expressed as a percent of the monomer amount in sound wood. Selective use of a sugar is indicated when its weight loss is substantially greater than that of other sugars.

In birch, selective use of mannose was associated with selective delignification (TABLE III). Among all birch samples analyzed, mannose loss was at least 10% greater than that of the other polyose sugars in 11 cases; all were white rot with average L/W of 2.3. Selectivity for mannose was so great in early stages of selective delignification that mannose was frequently used in greater absolute amounts than even xylose, which is present in sound wood in amounts over ten times those of mannose. When L/W exceeded 1.5, mannose was used most preferentially in 11 of 17 cases. White-rotters with L/W < 1.5 showed no strong pattern of selectivity.

Among birch samples characteristic of brown rot as defined above, galactose was used preferentially in 14 of 17 cases and was within 10% of the most selectively used sugar in the remaining cases (TABLE III; data on minor sugars not shown). Mannose, in turn, was used more selectively than xylose except at highest weight losses (TABLE III).

Among 15 soft-rot samples on birch, arabinose was most selectively used in 10 cases, xylose in 3 cases and galactose in 2 (TABLE III; data on additional sugars not shown). Xylose was consistently used more selectively than mannose.

On pine, the fungi varied in monomer use and no clear relationship between L/W or decay type and selective usage was apparent (TABLE III and data on additional sugars not shown). Overall, however, loss of arabinose exceeded loss of weight (both as percents of original amounts) in 37 of the 41 cases analyzed chemically. Arabinose was preferentially used in 22 of those cases. Xylose and mannose utilization was not consistently different, but usually exceeded glucose utilization.

Acid-soluble lignin. On birch, a loss of acid-soluble lignin (ASL) was the general rule, but white-rotters at low weight losses caused an increase (TABLE III). On pine, ASL almost always increased. The increase was generally much greater for white-rotters than for brown-rotters.

Morphology.—Macroscopic features of decay generally were distinct only at high weight losses. In some cases, blocks with weight losses as high as 12% appeared macroscopically sound. Conversely, in blocks with localized decay zones, some features were detectable at low weight losses. Two general patterns of features could be discerned in dried blocks at the higher weight losses, one typified by the white-rot fungi and the other by the brown-rot fungi.

In the white-rot pattern, blocks were often bleached both externally and internally, birch more so than pine. Internally, they became soft and fibrous. Block shrinkage was moderate, uniform, and generally first detected above 50% weight loss. Annual ring separations were caused by some selective delignifiers.

In the brown-rot pattern, blocks generally became light brown both internally and externally. Blocks were softened but less fibrous than in white rot. Block shrinkage (detected at weight losses as low as 25%) was severe, irregular, and characterized by collapsed

TABLE II. Number of species in seven groups for which the addition of nutrients caused a statistically significant increase, decrease or no significant effect on wood decay as measured by weight loss[a]

	Number of species					
	Birch			Pine		
	Increase	No effect	Decrease	Increase	No effect	Decrease
Deuteromycetes	1	4	0	0	5	0
Other Ascomycota	0	4	0	0	4	0
Xylariales/Diatrypales	4	0	0	0	4	0
Exidiaceae	2	2	0	2	2	0
Dacrymycetales	1	3	0	0	2	2
Aphyllophorales/Agaricales	1	2	4	1	3	3
Gasteromycetes	0	3	0	0	3	0

[a] Significance was tested by ANOVA, $\alpha = 0.05$. See Table I for species and mean weight losses of nutrient-treated and control blocks.

zones and surface checking. In the Dacrymycetales, severe shrinkage at higher weight losses was often accompanied by collapsed zones several millimeters in size that were filled with mycelial tufts.

Wood decayed by many soft-rot fungi did not clearly conform to either pattern. Gray or black sapstains developed in wood decayed by dematiaceous hyphomycetes. In the Xylariales, blocks were often bleached as in white rot. No soft-rot fungi caused the fine surface checking characteristic of advanced soft rot in the field.

Anatomy.—Microscopically, several patterns were apparent with combinations of erosion channels and notches in the wood cell wall, wall thinning, erosion of pits, and additional features as described below.

Soft rot. Soft-rotters caused two or more of the above features in conjunction with transverse bore holes that were narrower than lumen hyphae. In pine, where weight losses were low, neither cell-wall thinning, channels nor notches were observed. The distinctive cavities (longitudinal bore holes) characteristic of soft-rot type 1 were observed in just over half of cases of soft-rot (FIG. 3), including *Chaetomium* spp., *Xylaria polymorpha, Cryphonectria parasitica,* all but two dematiaceous hyphomycetes (not *Scytalidium lignicola, Spegazzinia tessarthra*), and several other species. Some species on birch caused both cavities and erosion at the lumen surface (type 2 soft rot), while others caused only type 2. In birch, erosion channels were generally angular and notches were V-shaped (FIG. 4). Sometimes the erosion channels had serrated edges (FIG. 5). Eroded pits (radial section) also were commonly angular or diamond-shaped (FIG. 6).

White rot. White rot usually had all of the features above and transverse bore holes that were the same size as or wider than lumen hyphae. Bore holes were usually frequent in white rot; their size corresponded with degree of decay, reaching up to 8 μm diam. In contrast to soft rot, white-rot erosion was evident as rounded channels and U-shaped notches (FIG. 7). Pit erosion was rounded or oval also (FIG. 8). Several fungi for which chemical data were not available (*Armillaria gemina, Basidiodendron eyrei*) or anomalous (*Exidiopsis calcea* on pine) were classified as white-rotters based on these rounded features. Several specimens decayed by fungi characterized chemically as white-rotters showed only one of the characteristic anatomical features of white rot described above. These were associated with low weight losses (around 5%) and most were in the Exidiaceae. Some specimens decayed by members of the Exidiaceae also differed in having narrow bore holes. However, some members of the Exidiaceae, e.g. *Exidia glandulosa* and *Exidiopsis calcea,* produced well-developed erosion channels (FIG. 9).

Two additional features were sometimes observed among fungi causing the white-rot pattern of degradation. One was cell separation in connection with degradation of the middle lamella. This feature was associated with selective delignification and was caused by *Phellinus pini, Phlebia tremellosa, Mycena leaiana,* Unknown #2911, *Exidia glandulosa* #453, *Exidiopsis calcea,* and *Auricularia auricula-judae* #11380, #617 and #618.

The second distinctive feature was numerous longitudinal microcavities in the secondary wall (FIGS. 10, 11). Only isolates of *A. auricula-judae* caused such degradation and did so in both birch and pine. The microcavities arose from numerous t-branching hyphae, which in turn arose from transverse bore holes. Widening (up to 2.1 μm) of the transverse bore holes was observed; such widening was not observed in soft rot. One isolate of *Auricularia auricula-judae* (617) caused only narrow bore holes on pine. Microcavities were initially extremely narrow (<0.5 μm) and gen-

erally remained fairly small, though some became as much as 2.1 μm diam. They occurred in dense patches and were much branched but largely parallel. Widening of microcavities was not oscillatory but fairly uniform along the length; chains of cavities were never observed. Otherwise, decay by *A. auricula-judae* followed the white-rot pattern, with wall thinning, rounded channels and notches, erosion of pits, and enlarged, transverse bore holes. Wall thinning was inconsistent in pine.

Brown rot. Fungi that caused brown rot caused none or rarely one of the features described above. No erosion channels were seen. Erosion of pits was found only at high weight losses. Even at high weight losses, bore holes were usually infrequent or, especially in the Dacrymycetales, rare, and at most only slightly wider than lumen hyphae. In the Dacrymycetales, numerous irregular collapsed zones were associated with deteriorated rays and resin canals in pine and vessels and associated parenchyma in birch.

Ray parenchyma. Substantial degradation of ray parenchyma was observed microscopically in all pine samples, regardless of decay type, except those with low weight losses where no other decay features were observed. In birch, brown-rot fungi caused no visible degradation of ray parenchyma, but white- and soft-rot fungi often did (24 of 56 cases), especially at higher weight losses.

Enzyme tests.—The phenoloxidase reactions fell into several common patterns that were generally characteristic of taxonomic groups and decay types, although there were exceptions. The patterns were as follows (data not shown):

1. Gallic/tannic acid (GTA), laccase and peroxidase positive. This pattern was most common (27 fungi) and included the typical white-rotters, all Exidiaceae (except *Exidia crenata,* which was GTA negative), six ascomycetes (three in the Xylariales), two gasteromycetes, and *Scytalidium lignicola.*

2. Negative for all enzymes. This pattern was also common (14 fungi). It characterized several typical brown-rotters (e.g., *Gloeophyllum trabeum, Oligoporus placentus*), all members of Dacrymycetales tested, *Eutypella parasitica,* and *Phialemonium dimorphosporum.* However, one brown rotter (*Oligoporus fragilis*) was laccase positive.

3. GTA and laccase positive, peroxidase negative. This occurred in 5 soft-rot fungi, mostly type 1 (*Phialocephala dimorphospora, Phialophora melinii, Chaetomium aureum, Chaetomium globosum, Arthrographis cuboidea*). *Daldinia concentrica* was GTA positive but negative for other enzymes.

4. GTA negative, laccase and peroxidase positive. This pattern was unique to *Auricularia auricula-judae.* Isolates from the Center for Forest Mycology Research were tyrosinase negative; those from K. Wells were tyrosinase positive.

Positive tyrosinase reactions were infrequent. They occurred in four white-rotters (*Armillaria gemina, Phlebia tremellosa, Trametes versicolor, Auricularia auricula-judae*) and one soft rotter (*Arthrographis cuboidea*).

DISCUSSION

As the deuteromycetes used in this study are probably all derived from the Ascomycota, caused the same decay type and responded similarly to nutrients, in this discussion both groups will be subsumed under the Ascomycota.

Weight loss.—Our results indicate that the capacity to cause wood decay occurs in many groups of fungi and is not limited to a few orders of Basidiomycota. A weight loss of 2% was considered the threshold for decay since the woods we used contain several percent of low-molecular-weight constituents that fungi might consume without decaying cell wall polymers (Fengel and Wegener, 1984). Fungi that caused weight losses below 2% in these tests may not be decayers, instead functioning as mycoparasites or scavengers, but there are other explanations. Some may require unusual conditions for decay, the decay may develop slowly, or some cultures may have been debilitated.

Major decay types.—All cases of wood decay observed in this study could be considered white, brown, or soft rot, the previously recognized decay types. However, as detailed below, some distinctions and features of those types are now more clearly elucidated.

Soft rot vs. white and brown rots. The clear distinction of soft rot from the white and brown rots has been problematic, as discussed above. Our results permit their separation by both chemical and anatomical criteria without reliance on taxonomy.

Chemically, soft rot differed from white rot in that lignin degradation was relatively low. Although this difference is useful as a generality, a threshold value of L/W=0.8 may not be universally applicable. For instance, although most have found, as we have, that lignin loss lags considerably behind weight loss during soft rot (Eslyn et al., 1975; Levi and Preston, 1965; Savory and Pinion, 1958; Seifert, 1966), lignin loss sometimes exceeded weight loss in a study of the Xylariales (Nilsson et al., 1989). Also, L/W may be greater with soft rot of softwoods than of hardwoods (Eslyn et al., 1975). In our study, soft rot of pine was below the weight-loss threshold for chemical analysis.

In all cases, soft rot differed chemically from brown rot in that alkali solubility of wood (AS) remained

TABLE III. Lignin/weight loss ratio (L/W)[a] and percentage loss of glucose, xylose, mannose and acid-soluble lignin during decay of birch and pine[b]

	Birch						Pine					
		Weight loss (% original weight)[c]						Weight loss (% original weight)				
Fungus	L/W	Blocks[d]	Glu	Xyl	Man	ASL[e]	L/W	Blocks	Glu	Xyl	Man	ASL
Ascomycota and deuteromycetes												
Arthrographis cuboidea P-540[f]	0.4	10	9	31	8							
Aspergillus terreus P-762[g]	0.3	10	6	26	−1							
Phiale. dimorphosporum ED-100[g]	0.3	19	24	31	−36							
Phialo. dimorphospora P-109	0.0	12	27	20	−3	55						
Phialo. dimorphospora P-109[g]	0.1	33	46	51	17							
Phialophora melinii P-850[g]	0.2	15	23	21	−15							
Phialophora parasitica P-754[g]	0.3	13	27	25	−31							
Scytalidium lignicola P-53[f]	0.2	6	4	20	−27							
Spegazzinia tessarthra P-511[g]	0.8	11	14	27	−41							
Chaetomium aureum P-722[g,h]	0.2	20	27	32	−23							
Chaetomium funicola ED-189[g,h]	0.0	13	10	20	−38							
Chaetomium globosum P-591[f,i]	0.5	40	50	52	33							
Cryptosphaeria lignyota 190-3	0.4	5	11	10	−106	−3						
Daldinia concentrica N7	0.7	18	24	18	−87	19						
Xylaria polymorpha N12	0.5	6	17	16	−84	20						
Auriculariaceae												
Auricularia auricula-judae 617	1.0	39	47	43	55	12	1.1	25	28	30	26	−139
Auricularia auricula-judae 618	1.3	23	25	28	18	−3	1.3	18	17	27	11	−115
Auricularia auricula-judae 619	1.1	35	40	37	39	21	1.4	15	15	20	19	−189
Auricularia auricula-judae 623	3.8	11	8	7	70	−22	1.5	24	16	29	28	−109
Auricularia auricula-judae 11380	1.5	8	16	12	37	−7	1.4	5	2	−4	3	−148
Exidiaceae												
Exidia crenata 580							2.0	6	−6	8	−19	−103
Exidia crenata 10688[i,j]	1.9	7	4	9	45							
Exidia glandulosa 453[j]	1.2	13	15	15	25	10	1.4	11	10	8	17	−124
Exidia glandulosa 1966	3.0	6	5	3	76	−5	0.9	6	1	4	−4	−72
Exidiopsis calcea 1976	3.3	6	9	1	62	−4	0.3	5	2	2	−1	−34
Exidiopsis grisea 1978							1.2	6	2	6	−2	−53
Dacrymycetales												
Calocera cornea 440	0.3	32	42	47	86	9	0.4	24	32	46	45	−26
Calocera cornea 440[j]	0.4	39	53	59	66	28	0.5	45	54	69	67	−44
Dacrymyces capitatus 48087	0.3	18	21	35	48	−1						
Dacrymyces chrysospermus 434[k]	0.0	11	15	27	77	14						
Dacrymyces chrysospermus 434	0.3	68	88	90	78	54	0.4	46	61	72	73	−28
Dacrymyces chrysospermus 449[k]	0.0	8	12	27	71	−3						
Dacrymyces chrysospermus 449	0.3	67	88	90	41	52	0.3	38	52	56	60	9
Dacrymyces dictyosporus 46563	0.3	59	80	81	87	44	0.2	41	57	55	67	−57
Dacrymyces minor 429	0.2	27	28	56	100	28	0.6	22	23	45	41	−14
Dacrymyces stillatus 426	0.0	37	39	60	74	25	0.2	34	46	68	70	−76
Dacrymyces stillatus 450	0.0	27	40	55	64	32	0.4	22	28	44	38	−15
Dacryopinax spathularia 439[k]	0.1	8	13	18	60	7						
Dacryopinax spathularia 439	0.4	67	84	90	48	66	0.5	31	37	56	36	−22
Agaricales/Aphyllophorales												
Armillaria gallica 328	1.4	9	14	−4	32	−7	0.8	6	1	7	−5	−5
Megacollybia platyphylla 464	2.2	14	4	21	39	−17	1.1	16	18	20	3	−53
Megacollybia platyphylla 488	2.1	14	8	10	52	−15	1.1	9	13	12	14	−59
Mycena leaiana 6113T2B	3.6	12	0	7	654	−11	1.6	7	1	6	15	−114
Mycena leaiana 6113T2B[i,j]	4.4	9	−6	14	25							

TABLE III. Lignin/weight loss ratio (L/W)[a] and percentage loss of glucose, xylose, mannose and acid-soluble lignin during decay of birch and pine[b] (Cont.)

	Birch						Pine					
		Weight loss (% original weight)[c]						Weight loss (% original weight)				
Fungus	L/W	Blocks[d]	Glu	Xyl	Man	ASL[e]	L/W	Blocks	Glu	Xyl	Man	ASL
Bjerkandera adusta F-58	1.2	52	42	64	44	43	1.2	28	26	46	21	−72
Bjerkandera adusta F-58[k]	2.3	9	4	13	62	27	1.7	5	1	13	−9	−63
Climacocystis borealis 3	1.6	12	17	−2	41	−13	1.1	23	22	28	12	−68
Climacocystis borealis 3	1.3	9	12	10	36	0	1.1	23	25	27	24	−117
Coniophora puteana 61	0.1	26	24	49	52	21	0.2	26	28	45	60	−38
Gloeophyllum trabeum F-32	0.3	64	81	84	86	56	0.3	60	82	87	86	−41
Oligoporus fragilis 26	0.0	8	15	16	35	2	0.0	15	21	23	51	−56
Oligoporus placentus F-33	0.2	69	92	92	100	56	0.3	55	75	81	82	−78
Phellinus pini 19	2.2	13	14	5	66	−13	1.7	18	14	25	10	−79
Phlebia tremellosa 25	1.1	55	57	70	20	4	1.1	33	33	35	50	−274
Phlebia tremellosa 25[k]	2.3	13	11	19	28	−12	2.2	11	9	16	−12	−63
Trametes versicolor F-491	0.9	65	69	67	39	57	1.0	36	42	52	47	−112
Trametes versicolor F-491[k]	1.6	24	23	25	15	9	1.9	13	11	22	−9	−47
Unknown 451	1.2	33	41	30	69	16	1.1	24	26	26	31	−124
Unknown 2911	3.3	6	7	10	−22	−13	2.1	5	−2	−8	−3	−98
Unknown 2911[i]	3.8	7	−7	9	3							
Gasteromycetes												
Crucibulum laeve 444	2.8	6	0	8	−84	−4	1.9	4	6	−2	13	−96
Crucibulum laeve 444	2.6	6	7	7	−13	1	2.2	8	2	13	0	−122
Sphaerobolus stellatus 581	4.0	8	4	−2	26	−20	2.1	8	−4	8	10	−93

[a] L/W = The ratio between the percentages of lignin loss and weight loss of analyzed blocks.

[b] Mean percentages of components in sound birch were: glucose 46.4%, xylose 22.8%, mannose 1.8%, galactose 1.1%, arabinose 0.7%, Klason lignin 22.1%, acid-soluble lignin 3.6%. Mean percentages of components in sound pine were: glucose 48.2%, xylose 7.7%, mannose 12.5%, galactose 2.3%, arabinose 1.5%, Klason lignin 29.0%, acid-soluble lignin 0.71%. Sugar values were not corrected for water of hydrolysis.

[c] The corresponding figure for lignin can be determined by multiplying the columns 'L/W' and 'Blocks.'

[d] For accuracy of calculations, the mean weight loss of only those blocks analyzed was used rather than overall mean weight loss.

[e] ASL = acid-soluble lignin.

[f] Vermiculite test.

[g] Agar-block test.

[h] Decay period 10.5 wk.

[i] Decay period 8.7 wk.

[j] Nutrients added.

[k] Decay period 4.1 wk.

low during soft rot. Alkali-soluble materials are largely oligosaccharides. Brown-rot fungi have a mechanism for rapidly depolymerizing carbohydrates throughout the wall, while white-rot fungi tend to consume depolymerized carbohydrates before further depolymerization (Kleman-Leyer et al., 1992). Low AS of wood decayed by *Chaetomium globosum* in comparison to the large increase during brown rot has been noted previously (Henningsson, 1967; Seifert, 1966).

Anatomically, erosion found in white rot differed from that found in soft rot type 2. In white rot, features consistently had rounded edges, while in soft rot the features were angular. The angular erosion of type 2 soft rot, especially the chains of diamond-shaped figures on the lumen surface, are suggestive of type 1 soft rot. Such angular erosion has been noted for several fungi previously (Eaton and Hale, 1993; Francis and Leightley, 1984). These observations suggest that mechanisms of soft rot erosion are more closely aligned to type 1 soft rot than to white rot, as chemical analysis confirms.

White rot vs. brown rot. Although early studies suggested that Klason lignin is not lost during brown rot, modern studies often show substantial loss (Blanchette et al., 1994). Likewise, we observed loss of Kla-

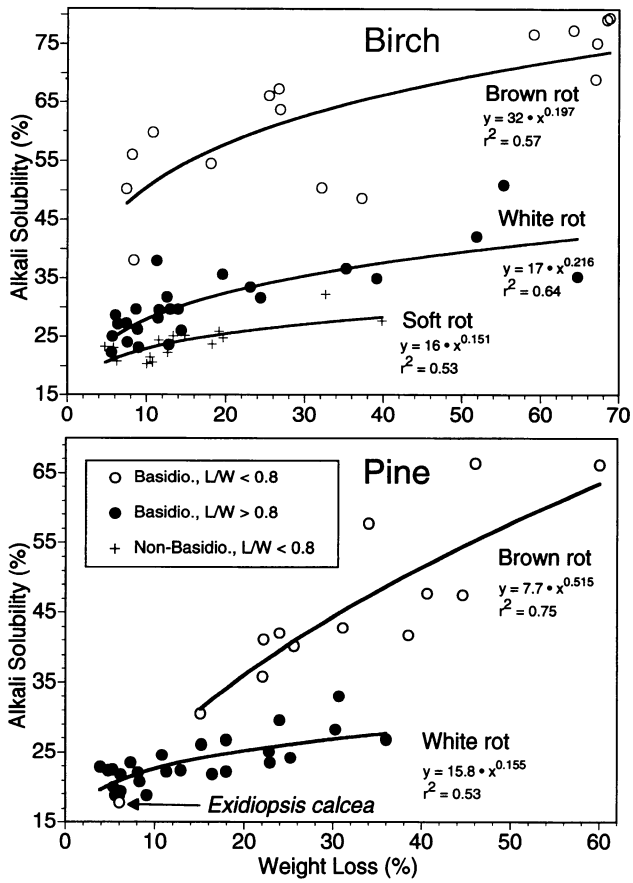


FIG. 2. Weight loss vs. alkali solubility. Weight loss is the mean weight loss of those blocks ground for analysis of lignin and sugars. L/W is the ratio of the percentages of lignin loss to weight loss. Mean alkali solubility for sound birch and pine were 20.9 and 16.1%, respectively. The formula and correlation coefficient are indicated for each fitted curve.

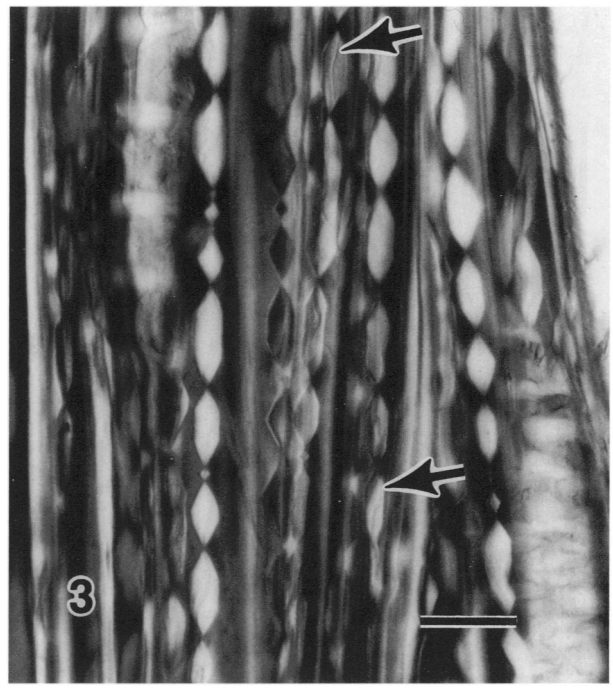


FIG. 3. Soft rot type 1 in birch caused by *Phialophora melinii* P-850. Chains of diamond-shaped cavities extend longitudinally through the S2 cell wall layer. Hyphae are evident within the cavities (arrows). Tangential section. Bar = 25 μm.

son lignin during brown rot as high as 26% in birch and 21% in pine. The difference may be due to filtering methodology. Various porous crucibles or asbestos mats were used earlier (Effland, 1977), but glass fiber filters are often used today (Worrall and Anderson, 1993; R. Pettersen, U.S. Forest Products Laboratory, pers. comm.). Lignin may not be significantly mineralized during brown rot, but modified such that particles will pass through a glass fiber filter and not an asbestos mat.

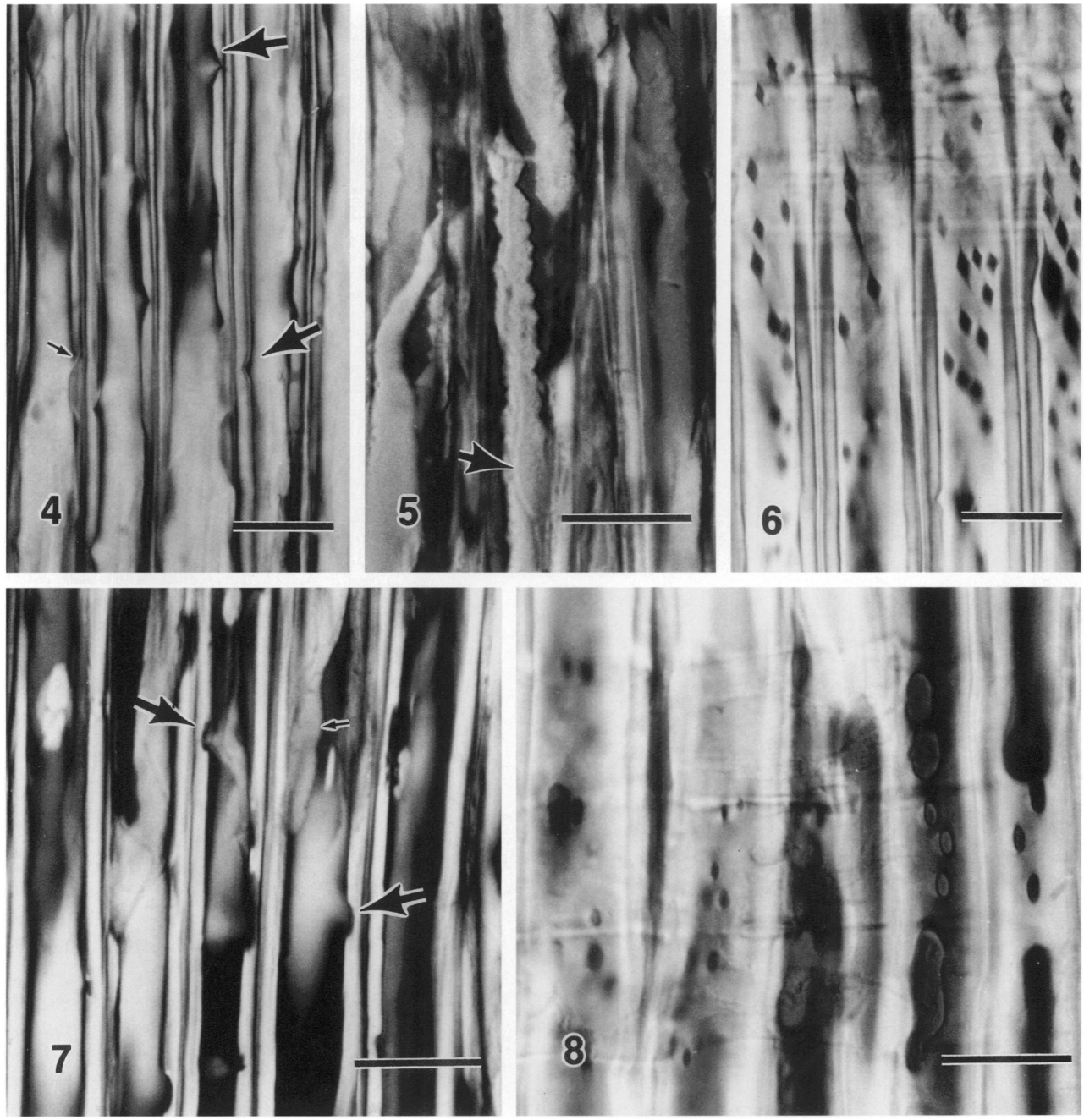
Our data suggest that such lignin loss increases at later stages of brown rot. During white rot, on the other hand, delignification is most selective at lower weight losses. This is consistent with fundamentally different mechanisms of lignin modification. Acid-soluble lignin tended to be higher following white rot than brown rot in early stages. The rapid decrease of Klason lignin during white rot may be expected to result in an accumulation of soluble lignin residues.

Anatomically, we observed ray parenchyma in pine attacked in both white and brown rots, but only white- (and soft-) rotters caused visible damage to rays in birch. Wilcox (1968) also found that ray cells of hardwood were resistant during brown rot, suggesting that hardwood rays may have a unique chemistry that makes them resistant to brown rot, but not to white or soft rot.

Although frequency of bore holes varies considerably among brown-rot fungi and with stage of decay (Cowling, 1961; Eaton and Hale, 1993; Wilcox, 1993), our data indicate that white-rot fungi generally produce more and larger bore holes than do brown-rotters.

Polyose utilization. Polyose loss during decay has been of interest because their utilization may be a necessary first step that could be targeted to prevent decay (Highley, 1987a). Patterns of polyose loss may also reflect ecological niches of the fungi (Lewis, 1976) and better characterize decay types. As do previous studies (Eslyn et al., 1975; Highley, 1987b; Highley and Illman, 1990; Kirk and Highley, 1973), our data suggest that selectivity can vary not only with wood and decay type, but also with fungus and stage of decay.

Our data for birch indicate selectivity for mannose by white- and brown-rot fungi, particularly at low to



FIGS. 4–8. Types of erosion in soft rot (4–6) and white rot (7–8). 4. V-shaped notches (large arrows) and angular erosion channel (small arrow) in soft rot type 2 of birch caused by *Daldinia concentrica* N7. Tangential section. 5. Soft rot type 2 of birch caused by *Eutypella parasitica* N26. Extensive erosion is evident in the form of erosion channels with serrated edges. A hypha is visible within a channel (arrow). Tangential section. 6. Diamond-shaped pit erosion in a radial pit field in soft rot of birch caused by *Daldinia concentrica* N7. Radial section. 7. Rounded erosion channels (small arrow) and U-shaped notches (large arrows) in white rot of birch caused by Unknown isolate 451. Radial section. 8. Rounded pit erosion in white rot of birch by *Megacollybia platyphylla*. Radial section. Bars = 25 μm.

moderate weight losses and in association with selective delignification. This supports the conclusions of Highley (1987b) and Highley and Illman (1990). In white-rotted pine, we found, as did Highley and Illman (1990), that xylose was more selectively utilized than glucose and mannose, but the differences were usually small. In brown-rotted pine, our results agree with those of Kirk and Highley (1973), showing that mannose and xylose were usually used more selectively than glucose.

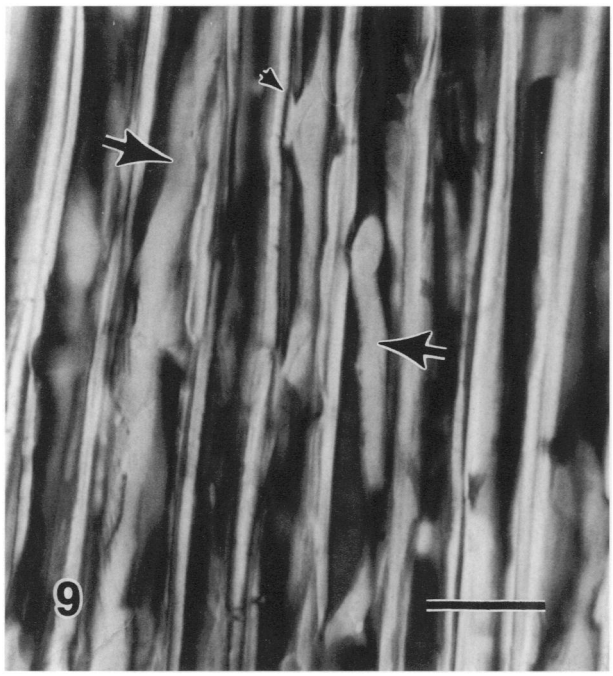


FIG. 9. White rot caused by *Exidia glandulosa* 589. Extensive erosion is evident in the form of rounded channels (large arrows), sometimes extending into the middle lamella (small arrow). This fungus had a very high L/W ratio (3.0) indicating preferential delignification. Radial section. Bar = 25 μm.

Two minor sugars, arabinose and galactose, were usually utilized more quickly or earlier in decay than the sugars discussed above. Although not quantitatively important constituents of the cell wall, their early selective removal may be necessary before depolymerization of the more abundant sugars can proceed. Previous studies generally did not consider these minor sugars. The minor sugars should be considered with caution since sugars of fungal origin may substantially affect analyses (Jones and Worrall, 1995). For example, some soft-rot fungi on birch in this study caused an increase in mannose as has been reported previously (Eslyn et al., 1975).

Decay features of higher taxa.—Ascomycota. Weight losses caused by members of Ascomycota were generally moderate to low, but in the Xylariales and Sordariales approached 40%. Decay capability in these groups is well established (Duncan and Eslyn, 1966; Merrill et al., 1964; Nilsson, 1973). All ascomycetes that caused weight loss exceeding 2% caused decay features characteristic of soft rot (type 1, type 2, or both).

Cryphonectria parasitica, Cryptosphaeria lignyota, and *Bulgaria inquinans* have not been previously shown to cause wood decay. None of the Morchellaceae caused decay in our tests. They are not reported as lignicolous fungi; they were tested because they are often associated with dying and recently killed trees but their natural nutritional sources are unknown.

Exidiaceae. Relatively low weight losses were caused by members of the Exidiaceae, although weight losses of individual blocks were as high as 16%. These fungi are thus capable of utilizing wood as a nutritional source. We are not aware of previous reports of wood decay in the Exidiaceae. Although many members fruit on wood, their mode of nutrition has been uncertain. The known mycoparasitism of many Tremellales, some of which also fruit on wood and with which the Exidiaceae was thought to be closely related until recently (Bandoni, 1984; Wells, 1994) makes clear that a variety of nutritional modes are available to fungi that fruit on wood.

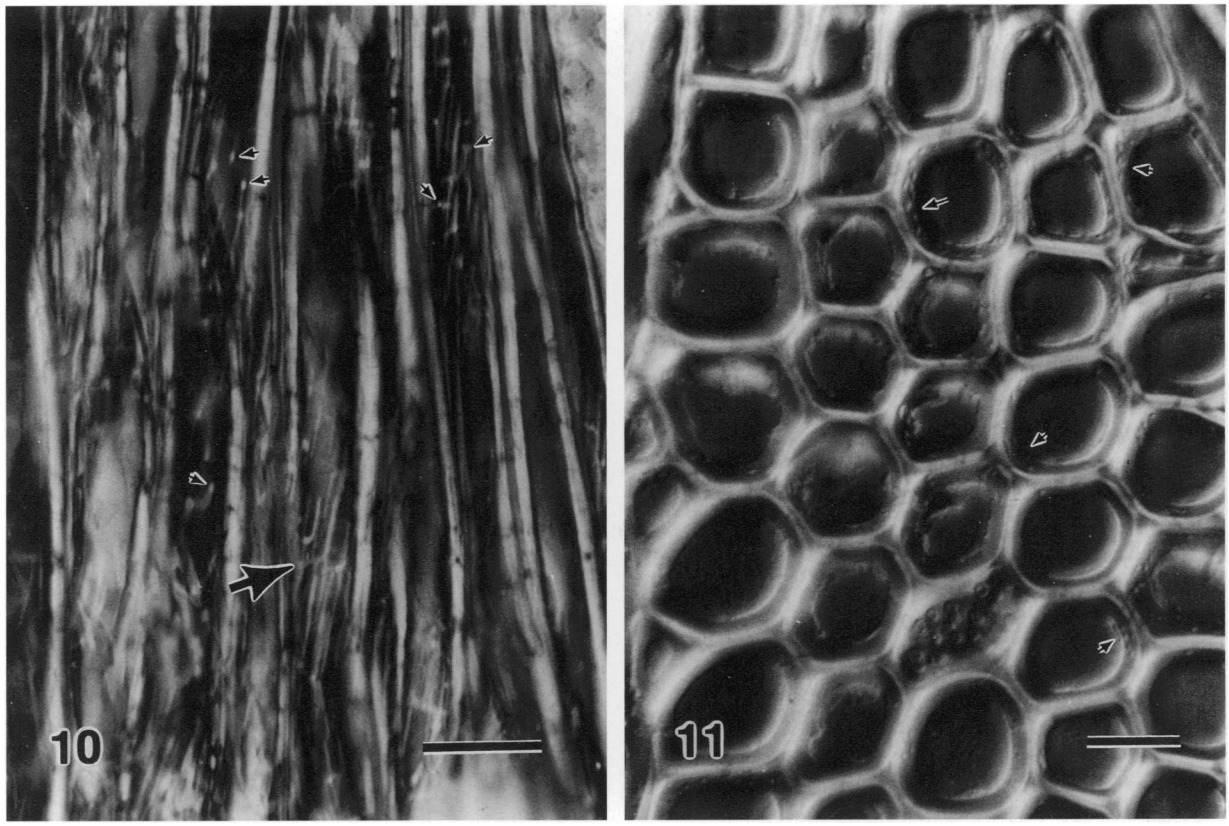
Members of Exidiaceae caused white rot. In some cases, especially on birch, selective delignification was evident. Anatomically, the decay differed from that caused by typical white-rotters in the Aphyllophorales in that wall thinning and channels and notches were rare and bore holes sometimes narrower than lumen hyphae.

Auriculariaceae. Auricularia auricula-judae, the only representative of the Auriculariaceae, proved to be a major decayer, causing a white rot. Anatomical features of typical white-rot fungi in the Aphyllophorales, including enlarged transverse bore holes, were almost invariably present. Although *A. auricula-judae* is known as an edible fungus grown commercially on woody substrates, we are aware of only one previous test of decay capability in this family (Tanesaka et al., 1993). The difference in decay type between *Auricularia auricula-judae* and *Helicobasidium corticioides,* a brown rotter (Davidson and Hinds, 1958) formerly placed in the Auriculariaceae, is consistent with their reclassification (Bandoni, 1984).

The branching, parallel microcavities, initiated by t-branches, were unique in this study. They differ from cavities characteristic of type 1 soft rot in size, branching, uniformity of diameter (no chains of cavities), and in their rounded rather than angular ends. Longitudinal growth of hyphae inside woody cell walls has been reported rarely in basidiomycetes (Daniel et al., 1992; Duncan, 1960; Nilsson and Daniel, 1988; Schwarze et al., 1995), but such cases require confirmation and further documentation.

Tulasnellales. Although many members of the Tulasnellales occur on wood (Ginns and Lefebvre, 1993), none of the four species tested here caused decay. They may be mycoparasitic like the Tremellales or they may scavenge soluble products released by decay fungi, etc.

Dacrymycetales. The Dacrymycetales caused weight losses comparable to the major decay fungi in the



FIGS. 10, 11. Cavities in the S2 layer of birch caused by the white-rot fungus, *Auricularia auricula-judae* 11380. Cavities appear light against the dark cell wall. 10. Longitudinal view of cavities. Bore holes from penetrating hyphae are obvious (small arrows) and cavities are often highly branched (large arrow). Tangential section. 11. Transverse view of cavities within the S2 cell wall layer (arrows). Bars = 25 μm.

Aphyllophorales. These levels of decay are generally similar to those reported previously for the Dacrymycetales (Seifert, 1983), but in some cases are higher, especially for *Calocera cornea, Dacrymyces chrysospermus* and *Dacryopinax spathularia.*

Decay caused by all the Dacrymycetales in our tests was clearly characterized by chemistry, anatomy, and/or morphology as brown rot. *Calocera viscosa,* which was reported to cause white rot (Seifert, 1983), caused weight loss below our threshold for chemical analysis (as it did in the previous study), but morphology and anatomy in discrete zones of decay had the hallmarks of brown rot: external and internal browning, shrinkage, and lack of wall thinning and erosion in the presence of hyphae. Basidiomes of *C. viscosa* in a specimen from our Herbarium were also associated with brown rot.

Gasteromycetes. Low levels of decay (2–10%) were caused by fungi in the gasteromycetous orders of the Homobasidiomycetes. Such decay was indistinguishable from that caused by typical white-rot fungi. There are previous reports of wood decay in the gasteromycetes but they are not well documented (Shields and Shih, 1975). The marine gasteromycete *Nia vibrissa* reportedly causes white rot but no weight loss could be detected in laboratory tests (Leightley and Eaton, 1979).

Other Homobasidiomycetes. As expected, members of the Aphyllophorales generally caused high weight losses and both white and brown rot occurred, even among fungi that are usually classified in the same family. The few members of the Agaricales tested here caused white rot.

Selective delignification.—Fungi that selectively degrade lignin (L/W > 1) have potential for applications such as biopulping. Among the most selective delignifiers in this study, only *Phlebia tremellosa* has been well studied in this regard. However, others, previously unreported as selective delignifiers, were similarly or even more selective. On pine, *Crucibulum laeve* and *Sphaerobolus stellatus,* both gasteromycetes, and *Exidia crenata* #580 were highly selective. On birch, *Mycena leaiana* (an agaric), several members of the Auriculariales, and *S. stellatus* were highly selective for lignin.

Wood decay and fungal phylogeny.—Wood is the most abundant form of fixed carbon in forested ecosys-

tems, but the ability to quickly decay wood is not widespread among decomposers. This, and the apparent complexity of the process (Zabel and Morrell, 1992), suggest that wood is a recalcitrant substrate for most decomposers and that efficient decay mechanisms evolved infrequently. Thus, although decay capability may have evolved independently in several of the groups of fungi treated here, it is also possible that the capability was maintained and enhanced as some groups arose from earlier ones. If so, features of decay may contribute clues to phylogeny.

Effect of nutrients. Evidence suggests that efficient utilization of mineral nutrients, especially nitrogen, by conservation and recycling is a specialized adaptation of some Aphyllophorales to the mineral-poor environment of wood (Cowling and Merrill, 1966). Our finding that decay by such fungi was usually inhibited and rarely increased by added nutrients supports that hypothesis. The Dacrymycetales showed a similar response.

A corollary of the above hypothesis is that less highly adapted decay fungi, or those similar to the earliest wood-decay fungi, would be less efficient with nutrients and therefore stimulated by added amounts. The Xylariales, Diatrypales and the Exidiaceae showed such stimulation and no inhibition by added nutrients. The deuteromycetes and other Ascomycota also generally showed stimulation by nutrients but, as decay levels were relatively low in soil-block tests, it was rarely significant. Soft-rot fungi in general, including others that did not cause substantial decay in this experiment, are known to be stimulated by nutrients (Worrall and Wang, 1991).

Thus, with respect to the effect of nutrients, wood-decaying Ascomycota and the Exidiaceae are similar and behave as might be expected of the earliest fungi capable of decaying wood. The Aphyllophorales/Agaricales and the Dacrymycetales, which have mechanisms for efficiently utilizing low levels of nutrients, would thus represent more advanced wood-decay fungi.

Soft-rot and white-rot fungi. The earliest fossil record of wood decay is from stems of *Callixylon* in the Devonian, 395 million years before present (Stubblefield et al., 1985). Cavities and erosion were associated with septate but unclamped hyphae, which could represent ascomycetous or basidiomycetous fungi. The decay features were unclear, but consistent with soft rot. The first record clearly indicating decay by a basidiomycete (white pocket rot), is from *Vertebraria* in the Permian, 280 million years before present (Stubblefield and Taylor, 1986).

Soft-rot fungi, although apparently well adapted for adverse environments (Duncan, 1960), seem to be less well adapted for rapid wood decay than white- and brown-rot fungi. Soft-rot fungi are found on a wide array of lignocellulosic substrates, such as herbaceous plant debris, whereas basidiomycetous decayers are usually restricted to wood. Most ascomycetes that decay wood do so slowly. Most data, including ours, indicate that they degrade relatively less lignin than do white-rot fungi. Thus, they may have inefficient mechanisms for degrading lignin, which protects carbohydrates from enzymes. Their reliance on high levels of mineral nutrients (see above) also suggests a limited degree of adaptation to the wood environment. Furthermore, as suggested above, soft rot may precede basidiomycetous decays in the limited fossil record.

Physiological similarities between soft and white rot suggest that the causal fungi may be related. For instance, many ascomycetous decayers have a complete cellulase system like white-rot fungi, but others lack exo-1,4-β-glucanase as do most brown-rot fungi (Ljungdahl and Eriksson, 1986). In our study, several ascomycetes, such as some Xylariales, had the same complement of tested phenoloxidase activities (gallic and tannic acid, laccase, and peroxidase) as did typical white-rot fungi. Thus, if basidiomycetes arose from ascomycetes (Bartnicki-Garcia, 1987; Bruns et al., 1991), it seems likely that some components of the early decay apparatus, such as cellulases and phenoloxidases, were maintained during that transition.

Members of the Xylariaceae and Chaetomiaceae and a few additional species showed other advanced decay features in our study, including relatively high weight loss and lignin degrading ability. Moreover, decay by the Xylariaceae and Diatrypaceae as encountered in the field is different from other soft-rot fungi. Other soft-rot fungi are often active only on the wood surface or mixed with other fungi. The decayed wood tends to be brown and may have surface cross-checking similar to that in brown-rotted wood. Decayers in the Xylariaceae and Diatrypaceae (which are sometimes grouped in the same order), in contrast, may colonize large volumes of wood in what appears to be a pure colony. The decayed wood appears bleached white and often has zone lines. Thus, these higher ascomycetes have decay features that are similar to those of white-rotting basidiomycetes. Indeed, the decay is sometimes referred to as white rot (Eaton and Hale, 1993). This is not to suggest that such an extant group gave rise to the Basidiomycota, but that ascomycetes in general possess physiological capabilities that could have developed into decay mechanisms very similar to those of white-rotting basidiomycetes.

Some groups of white-rotting Heterobasidiomycetes, on the other hand, showed relatively primitive

decay features. As discussed above, anatomical features and nutrient effects in the Exidiaceae were similar to those in the Ascomycota. Members of the Auriculariaceae caused intrawall, longitudinal cavities, although they were different from those formed by soft-rot fungi. Thus the Auriculariales may be close to the first white-rot fungi that developed from ascomycetous ancestors.

Several phylogenetic schemes consider the Basidiomycota to be rooted near the Auriculariales (Jülich, 1981; Savile, 1968) Our results are consistent with that hypothesis. A progenitor group with transversely septate basidia (or asci) and primitive decay features may have given rise to the order, in part by conversion to longitudinal septation (Exidiaceae) and increases in the efficiency of decay mechanisms (Auriculariaceae). It is not essential to this hypothesis that all transitional taxa decay wood; nondecaying transitional fungi may have retained many of the genes necessary for soft rot, which later became more useful as basidiomycetes began to utilize woody substrata.

An obvious difference between soft rot and white rot is the common presence of longitudinal cavities in soft rot. The tertiary wall or warty layer at the lumen surface often has a high phenolic content, at least in softwoods (Fengel and Wegener, 1984). This layer may be difficult for soft-rot fungi to erode, as they can degrade lignin to only a limited extent. Cavity formation may be a means to colonize less lignified portions of the wall. As fungi became better able to degrade lignin (white rot), perhaps cavities were no longer a necessary strategy.

Brown-rot fungi. Although relatively few fungi cause brown rot, they are widely, if unevenly, distributed among groups of basidiomycetes. Brown rot is widespread, if not universal, in the Dacrymycetales. It also has been confirmed in an unrelated member of the Heterobasidiomycetes, *Helicobasidium corticioides* (Davidson and Hinds, 1958), now placed in the Platygloeales (Bandoni, 1984; Ginns and Lefebvre, 1993). Some known or suspected brown-rot fungi not tested by us are usually classified in the Agaricales, where there are many white-rotters (Redhead and Ginns, 1985).

The Aphyllophorales is the only order in which two major types of decay occurred in this study. In the polypores, white and brown rot are interspersed within groups of apparently closely related fungi. Several genera of the Corticiaceae are associated with brown rots (Gilbertson, 1980; Ginns and Lefebvre, 1993). The Coniophoraceae, where brown rot appears to be a consistent feature, is placed by some authors in the Boletales (Ginns and Lefebvre, 1993).

Gilbertson (1980) developed a convincing argument that brown-rot fungi evolved from white-rot fungi recently and independently in a number of groups. Most have a unifactorial mating system, which is considered to be derived by simplification of the bifactorial system more common in white-rot fungi. This may increase the inbreeding level, which would be advantageous during speciation. Gilbertson considered brown-rot fungi better adapted to coniferous habitats than white-rot fungi and generally more efficient in obtaining energy from wood.

Although the mechanisms of wood decay are not entirely clear, there are two important differences between white and brown rot. First, white-rot fungi degrade lignin extensively, which apparently facilitates enzyme access to carbohydrates. Brown-rot fungi do not cause such an extensive loss of Klason lignin, and usually lack the extracellular phenoloxidases that are characteristic of white-rot fungi. Second, whereas white-rot fungi degrade carbohydrates enzymatically at an exposed surface, brown-rot fungi apparently have a non-enzymatic oxidative mechanism for initial depolymerization of carbohydrates, and usually lack exo-1,4-β-glucanase.

Thus, development of a brown-rot fungus from a white-rot fungus would be characterized, in large part, by simplification: conversion from bifactorial to unifactorial mating system and loss of extracellular phenoloxidase and exoglucanase. Development of the nonenzymatic mechanism of depolymerization would be necessary, but current hypotheses suggest that it involves in part simple, inorganic products. Once that mechanism was in place, extensive delignification and fully enzymatic depolymerization would no longer be necessary and those characters would eventually be lost. However, some brown-rot fungi, such as *Oligoporus fragilis,* still produce what may be "vestigial" extracellular phenoloxidases. Lack of such oxidases may be an advanced feature rather than a primitive one as has been suggested (Nobles, 1958). Members of the Coniophoraceae still have an exo-1,4-β-glucanase (Highley, 1975).

Thus, the ability to decay wood probably evolved slowly, beginning with soft-rot fungi in the Ascomycota. White-rot fungi in the Basidiomycota probably evolved from fungi causing a soft-rot type of decay, and may have arisen independently along several lines in the Basidiomycota. Once white-rot fungi were highly specialized for the wood environment, brown-rot fungi apparently arose from them in many groups, most especially in the polypores. If so, it is ironic to consider that only when fungi had conquered lignin, the great barrier to wood decomposition, via white rot, did they find a way to largely circumvent it via brown rot.

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