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Screening Wood Decayed by White Rot Fungi for Preferential Lignin Degradation†

ROBERT A. BLANCHETTE

Department of Plant Pathology, University of Minnesota, St. Paul, Minnesota 55108

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A screening procedure in which scanning electron microscopy was used indicated that 26 white rot fungi selectively removed lignin from various coniferous and hardwood tree species. Delignified wood from field collections had distinct micromorphological characteristics that were easily differentiated from other types of decay. The middle lamella was degraded, and the cells were separated from one another. Secondary cell wall layers that remained had a fibrillar appearance. Chemical analyses of delignified wood indicated that the cells were composed primarily of cellulose. Only small percentages of lignin and hemicellulose were evident. Delignified wood was not uniformly distributed throughout the decayed wood samples. White-pocket and white-mottled areas of the various decayed wood examined contained delignified cells, but adjacent wood had a nonselective removal of lignin where all cell wall components had been degraded simultaneously. This investigation demonstrates that selective delignification among white rot fungi is more prevalent than previously realized and identifies a large number of fungi for use in studies of preferential lignin degradation.

Microbial degradation of lignin has received considerable attention in recent years. Fungi that selectively remove lignin without loss of appreciable amounts of cellulose are extremely attractive for use in biological pulping processes, to improve the digestibility of highly lignified plant residues, and for bioconversion of lignocellulosics into industrial products (3, 7, 19). There are hundreds of white rot fungi in North America alone (12), and only a few have been selected for studies involving preferential lignin degradation.

A simple technique to select microorganisms that can preferentially utilize lignin in wood is not available (23). Various laboratory tests have been used to evaluate white rot fungi for their ability to delignify wood (3, 11, 20, 23). The results of these assays have been difficult to interpret since delignification may vary depending on the techniques used (7). In a recent study (R. A. Blanchette, L. Otjen, M. J. Effland, and W. E. Eslyn, Wood Sci. Technol., in press), different delignification capacities were evident when wood degraded in the laboratory was compared with field-decayed samples.

Histological examination of white rots by Hartig (13) over a century ago led him to suggest that some white rot fungi may preferentially degrade lignin from wood. Recent investigations have demonstrated the capacity of several white rot fungi to selectively remove lignin (4, 5, 21). Chemical, micromorphological, and ultrastructural studies (5; Blanchette et al., in press) demonstrated that two distinct types of decay patterns are found in white-rotted wood: (i) a simultaneous removal of all cell wall components and (ii) a selective removal of lignin and hemicellulose. Delignified wood observed with a scanning electron microscope had micromorphological characteristics that could be easily differentiated from those of white-rotted wood where all cell wall components are degraded simultaneously or from those of other decay types (4, 5, 5a, 21, 22; Blanchette et al., in press).

The investigations reported here evaluated, by direct observation of decayed wood, scanning electron microscopy as a method to select microorganisms with the capacity to preferentially degrade lignin.

MATERIALS AND METHODS

A few white rot fungi that caused white-mottled and white-pocket rots have been previously found to remove lignin preferentially from wood (4, 5, 21, 22; Blanchette et al., in press). White rot fungi that caused a white-mottled or white-pocket appearance in wood were selected from field collections and from herbarium specimens of decayed wood that was collected along with sporophores. The fungi responsible for the decayed wood used in this study are presented in Tables 1 and 2. Isolations were made from all samples collected in the field to ensure the presence of only one decay fungus.

Radial and tangential sections of wood were cut from each collection of decayed wood and mounted on aluminum stubs. The sections were dried in a desiccator and coated with 40% gold–60% palladium in a vacuum evaporator. Specimens were observed with a Philips 500 scanning electron microscope. Lignin and wood sugar analyses were made on several field-collected samples. Areas of delignified wood, appearing as white zones, were removed from the samples with fine-pointed forceps. Samples were ground to pass through a 40-mesh screen, and the wood meals were analyzed for sulfuric acid lignin (8) and individual wood sugars by high-pressure liquid chromatography (Blanchette et al., in press).

RESULTS

The macroscopic appearance of white zones differed among the different types of decayed wood examined (Fig. 1a, c, and e). Micromorphological characteristics of the white zones, however, were similar in wood decayed by those fungi listed in Table 1. White tissues contained cells that lacked middle lamellae. Individual tracheids in coniferous wood and fibers, parenchyma cells, and vessels in hardwoods separated from one another (Fig. 1b, d, and f). Despite the many different types of wood examined and the various species of fungi responsible for the degradation (Table 1), a general defibration of cells had occurred (Fig. 1b, d, and f). The degradation was not localized to a specific

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TABLE 1. Fungi that selectively remove middle lamellae and defibrate cells

Fungus[a]	Location	Host
Bjerkandera adusta (*Polyporus adustus*)	Minnesota	*Betula papyrifera*
Cerrena unicolor (*Daedalea unicolor*)	Minnesota	*Betula papyrifera*
Dichomitus squalens (*Polyporus anceps*)	Minnesota	*Pinus bankisana*
Dichomitus squalens	Minnesota	*Pinus resinosa*
Dichomitus squalens FP 58543	Colorado	*Pinus ponderosa*
Dichomitus squalens FP 100565	New Hampshire	*Picea rubens*
Dichomitus squalens FP 313	Chihuahua, Mexico	*Pinus arizonica*
Ganoderma applanatum	Minnesota	*Betula papyrifera*
Ganoderma applanatum	Minnesota	*Acer saccharum*
Ganoderma applanatum	Minnesota	*Quercus alba*
Ganoderma lobatum FP 18692	Virginia	*Acer saccharinum*
Ganoderma lobatum FP 18679	Arkansas	*Quercus lyrata*
Ganoderma oregonense	Alaska	*Tsuga heterophylla*
Ganoderma oregonense	Washington	*Tsuga heterophylla*
Ganoderma tsugae	Wisconsin	*Tsuga canadensis*
Hapalopilus croceus (*Polyporus croceus*) FP 46228	Virginia	*Castanea dentata*
Hapalopilus croceus FP 12503	New York	*Castanea dentata*
Heterobasidion annosum (*Fomes annosus*)	Michigan	*Pinus resinosa*
Heterobasidion annosum	Utah	*Picea engelmannii*
Heterobasidion annosum	West Germany	*Picea abies*
Inonotus dryadeus FP 36133	Washington, D.C.	*Quercus digitata*
Inonotus dryophilus (*Polyporus dryophilus*)	Minnesota	*Quercus alba*
Inonotus dryophilus	Minnesota	*Quercus macrocarpa*
Inonotus dryophilus	Massachusetts	*Quercus rubra*
Inonotus ludovicianus FP 18695	Florida	*Quercus catesbaei*
Inonotus rheades Strid-1076	Sweden	*Populus tremula*
Inonotus texanus FP 94178	Texas	*Prosopis* sp.
Inonotus tomentosus	Minnesota	*Picea glauca*
Ischnoderma resinosum	Minnesota	*Betula papyrifera*
Laurilia sulcata (*Stereum sulcatum*) FP 105104	Colorado	*Picea* sp.
Perenniporia medulla-panis (*Poria medulla-panis*)	Minnesota	*Betula papyrifera*
Perenniporia subacida (*Poria subacida*)	Minnesota	*Abies balsamea*
Perenniporia subacida FP 94346	South Carolina	*Pinus* sp.
Phellinus sp.	Hawaii	*Acacia koa*
Phellinus fastuosus FP 21778	Florida	*Exothia paniculata*
Phellinus nigrolimitatus (*Fomes nigrolimitatus*)	Utah	*Picea engelmannii*
Phellinus nigrolimitatus	Idaho	*Larix occidentalis*
Phellinus pini	Minnesota	*Pinus banksiana*
Phellinus pini	Minnesota	*Pseudotsuga menziesii*
Phellinus pini	Wisconsin	*Tsuga canadensis*
Phellinus viticola (*P. isabellinus*) FP 4250	Montana	*Pinus contorta*
Xylobolus frustulatus (*Stereum frustulatum*)	Minnesota	*Quercus rubra*
Xylobolus frustulatus	Minnesota	*Quercus alba*
Xylobolus subpileatus (*Stereum subpileatum*) FP 18502	Arkansas	*Quercus texana*
Xylobolus subpileatus FP 12703	Arkansas	*Quercus alba*

[a] Numbers after fungus names are identification codes for herbarium collections.

TABLE 2. Fungi that cause a simultaneous removal of all cell wall components (simultaneous white rot)

Fungus[a]	Location	Host
Coriolus versicolor	Minnesota	*Betula papyrifera*
Fomes fomentarius	Minnesota	*Betula papyrifera*
Fomes fomentarius	Wisconsin	*Betula papyrifera*
Ganoderma applanatum	Wisconsin	*Acer saccharum*
Ganoderma applanatum	Minnesota	*Populus alba*
Ganoderma applanatum	Colorado	*Populus tremuloides*
Ganoderma curtisii FP 81809	South Carolina	*Quercus rubra*
Ganoderma lucidum	Louisiana	*Quercus niger*
Ischnoderma resinosum	Minnesota	*Populus deltoides*
Phellinus robustus	Minnesota	*Quercus rubra*
Phellinus robustus	Minnesota	*Populus grandidentata*
Phellinus robustus	Minnesota	*Populus tremula*
Phellinus igniarius	Minnesota	*Betula papyrifera*
Unknown FP 12783	Florida	*Quercus virginiana*

[a] Numbers after fungus names are identification codes for herbarium collections.

area of a cell as observed in previous studies (5; Blanchette et al., in press) of white rot fungi that removed all cell wall components simultaneously (simultaneous white rot). The patterns of cell wall attack also were different. Holes and erosion troughs in the cell walls, typical of a simultaneous white rot, were not observed. Degradation of the middle lamella without substantial attack of other cell wall layers was apparent. Hyphae were observed in the cell lumens.

Although the gross patterns of delignification appeared similar among the various samples investigated, differences in the fine detail of the cell walls were evident. The range of patterns observed are presented in Fig. 2a to d. Fungi such as *Ischnoderma resinosum* and *Phellinus viticola* that delignified birch and pine, respectively, removed lignin from the wood and left cells that had a relatively smooth appearance (Fig. 2a and b). Only slight alteration of the secondary wall was evident. Balsam fir wood decayed by *Perenniporia subacida* and the *Phellinus* sp. on *Acacia koa* caused more obvious degradation of the remaining cell wall layers (Fig. 2c

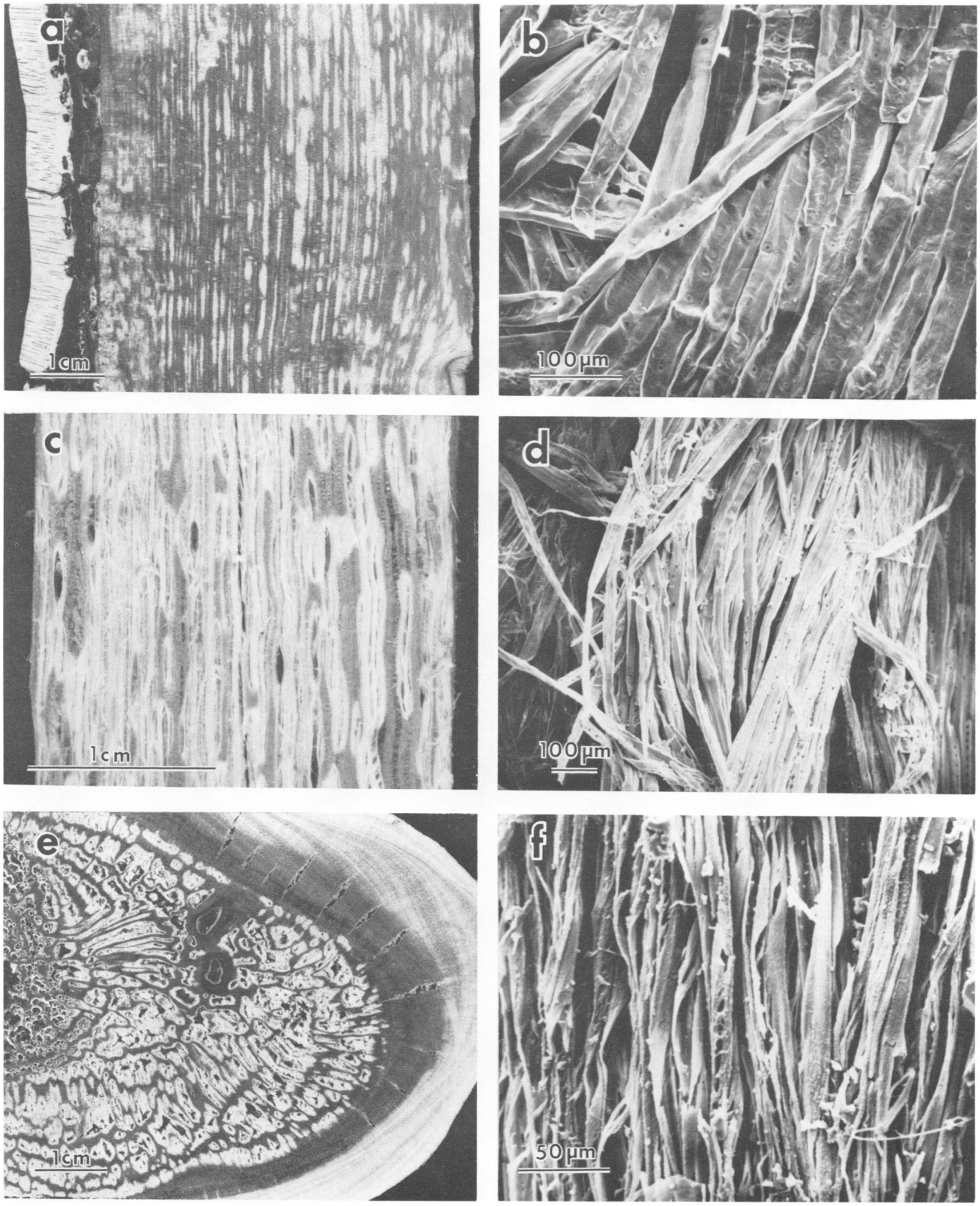

FIG. 1. Macroscopic appearance of wood decayed by *D. squalens* (a, radial cut through a log with sporophore on outer edge), *Hapalopilus croceus* (c, tangential section of wood), and *Phellinus fastuosus* (e, transverse section of wood) from *Pinus banksiania*, *Castanea dentata*, and *Exothia paniculata*, respectively. Scanning electron micrographs of white areas from wood degraded by *D. squalens* (b), *Hapalopilus croceus* (d), and *Phellinus fastuosus* (f) showed delignified cells that lacked middle lamellae and separated from one another.

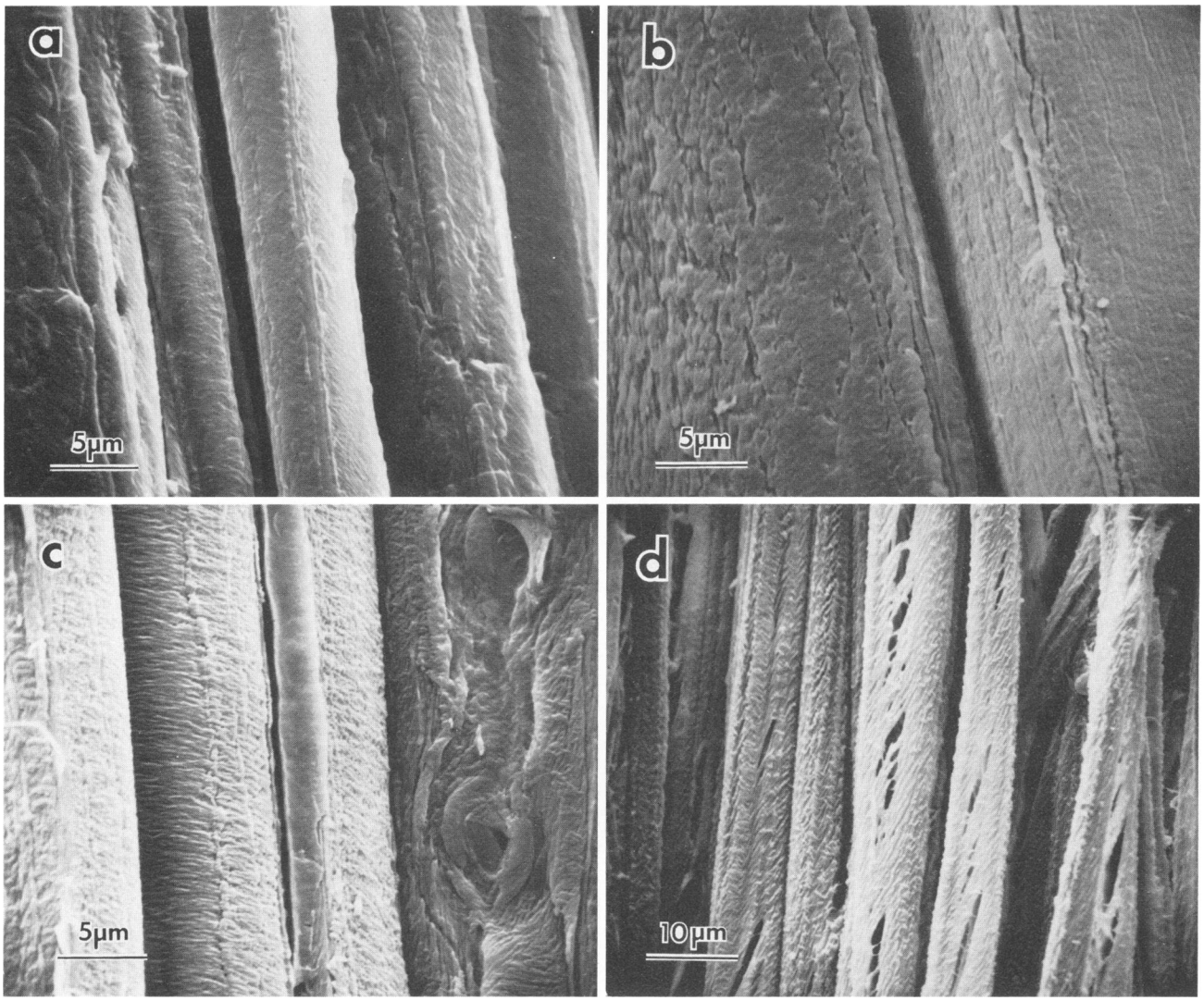

FIG. 2. Scanning electron micrographs of cells from *Betula papyrifera* delignified by *Ischnoderma resinosum* (a) and of cells of *Pinus contorta* delignified by *Phellinus viticola* (b) showed slight alteration of cell wall layers. No middle lamella was evident. *Picea balsamea* (c) and *Acacia koa* (d) delignified by *Perenniporia subacida* and *Phellinus* sp., respectively, also lacked middle lamellae, but cell wall layers had a distinct fibrillar structure.

and d). A distinct fibrillar structure was apparent that gives the cells a rough appearance.

Chemical analyses of white tissues confirmed the micromorphological observations that lignin had been preferentially removed (Table 3). White tissues, removed from the decayed wood, contained small amounts of lignin, xylose, and mannose when compared with those from sound wood. Glucose concentrations, however, were exceedingly high, suggesting that the cells that remained were composed primarily of cellulose.

Not all white-mottled and white-pocket rots selected for study contained selectively delignified wood. In many samples (Table 2), the white areas consisted of fungal mycelium and not delignified cells. White pockets were evident in a cross section of oak decayed by an unknown basidiomycete in herbarium sample FP 12783 (Fig. 3a). Scanning electron micrographs of these areas, however, showed them to consist of large holes filled with mycelia (Fig. 3b and c). No delignified cells were present.

The mottled and pocket rots that had zones of delignified cells (Table 1) also had a simultaneous white rot pattern of decay in other parts of the wood. An example of this situation can be seen in Fig. 3d and e. *Ganoderma lobatum* caused a mottled type of rot in maple (Fig. 3d). The white zones consisted of delignified cells (Fig. 3e), but wood immediately adjacent to the delignified areas contained a simultaneous white rot (Fig. 3f). Zones of delignified cells were not uniformly distributed throughout the wood. Delignified cells and simultaneous white-rotted cells were always separated spatially within the decayed wood (Fig. 3c).

The fungi listed in Table 2 caused only a simultaneous white rot. However, *Ganoderma applanatum* and *Ischnoderma resinosum* are also listed in Table 1 and were capable of causing a selective delignification when found on other tree species.

When decayed wood from field collections was cultured on artificial media, only one basidiomycete was isolated from each sample. Isolates were identified, using cultural

TABLE 3. Percent lignin and wood sugars in sound and decayed wood from white-mottled and white-pocket areas

Wood	%			
	Lignin	Glucose	Xylose	Mannose
Bjerkandera adusta (birch)	2.48	77.45	6.96	Trace
Cerrena unicolor (birch)	1.83	81.12	6.06	1.12
Ganoderma applanatum (birch)	1.08	80.55	9.32	1.97
Ganoderma applanatum (oak)	1.78	89.54	4.97	0.85
Ganoderma tsugae (hemlock)	1.37	86.04	2.45	4.70
Heterobasidion annosum (red pine)	1.61	77.91	1.27	4.09
Ischnoderma resinosum (birch)	2.47	73.98	9.72	1.74
Inonotus dryophilus (oak)	2.59	82.58	3.34	0.91
Perenniporia medulla-panis (birch)	2.79	78.32	8.16	1.37
Perenniporia subacida (balsam fir)	1.49	77.42	2.19	6.28
Phellinus pini (Douglas fir)	0.21	83.31	0.69	5.08
Sound birch[a]	20.18	44.10	22.66	2.70
Sound hemlock[a]	32.35	47.96	4.18	13.83
Sound oak[a]	31.04	37.39	22.01	1.10
Sound balsam fir[a]	31.20	49.03	6.13	13.33

[a] Percent lignin and wood sugars in sound wood is presented for comparative purposes.

characteristics, as the same fungus found sporulating on the living or dead tree. Bacteria, yeasts, and various deuteromycetes were also isolated from some of the samples.

DISCUSSION

Scanning electron microscopy can be used to readily identify selectively delignified wood. The results demonstrated that 26 different fungi in diverse substrates caused selective delignification. Many of the decayed wood samples examined had extensive areas of delignification, whereas others contained only small localized pockets. In addition to the areas of preferential lignin degradation, a simultaneous removal of all cell wall components was also evident in adjacent wood. Although the factors responsible for regulat-

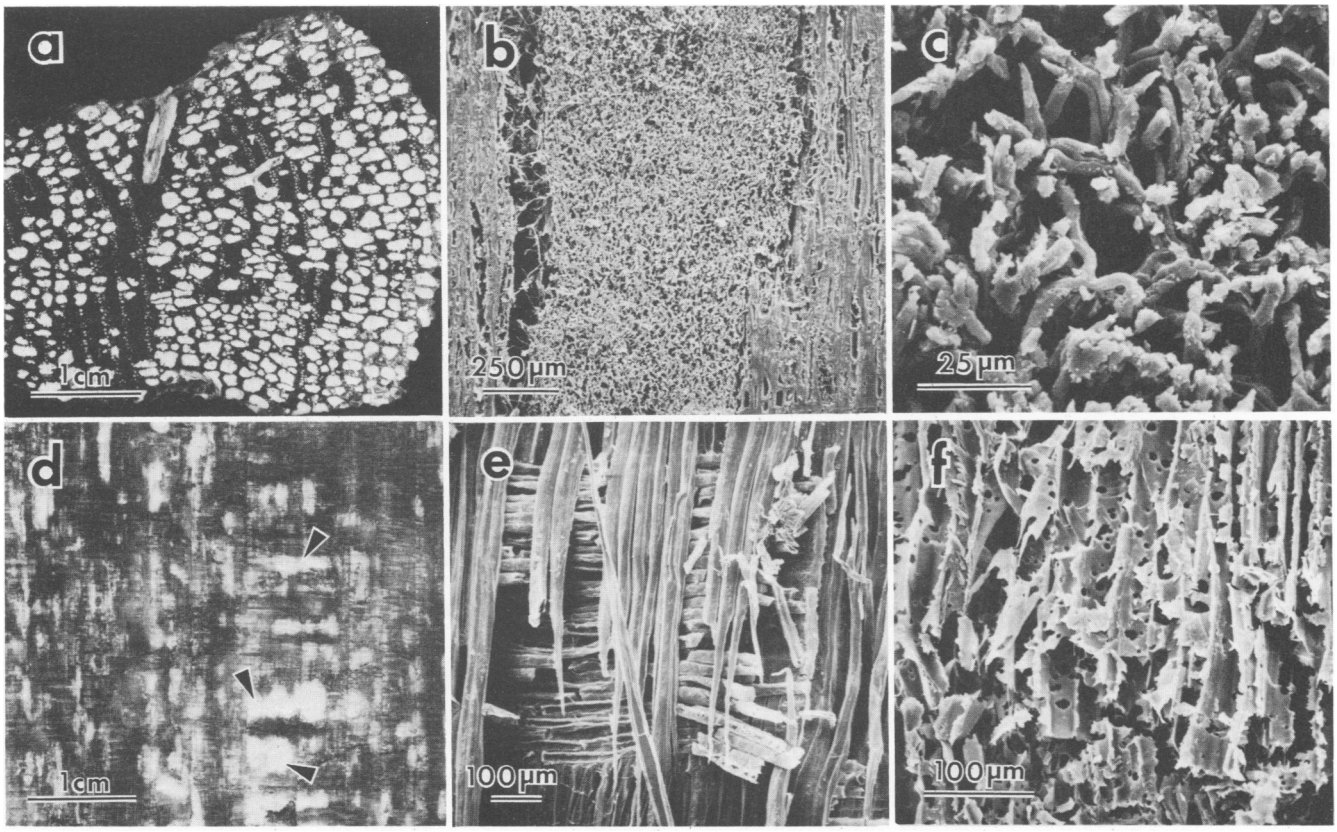

FIG. 3. White-pocket appearance of *Quercus virginiana* decayed wood (transverse section, herbarium sample FP 12783) (a). White pockets were composed of mycelial masses that filled vessels and large holes within the wood (b). Fungal mycelium was present in the white areas, but no delignified cells were found (c). White-mottled rot of *Acer saccharinum* caused by *G. lobatum*, shown in radial section (d), exhibited delignified cells (white areas in d, arrowheads) that lacked middle lamellae (e) and a simultaneous white rot (dark areas in d) where all cell wall components were removed in approximately equal proportions (f). Holes and erosion troughs were evident.

ing the delignification process are not known, some fungi have a preference for certain cell types. *Dichomitus squalens* appeared to delignify earlywood cells, whereas *Phellinus pini* showed a preference for latewood. In contrast, decay by the *Phellinus* sp. in *Acacia koa* contained a white-pocket rot composed of delignified cells, but no annual rings were present in this tropical hardwood. A previous study of decay patterns in oak caused by *Inonotus dryophilus* demonstrated that this fungus has a preference for earlywood fibers and parenchyma cells but not medullary rays or latewood fibers (21).

The study presented here also indicates that wood from various trees may be degraded differently by the same fungus. This may be due to particular substrate characteristics of a tree species, nutrient availability, environmental conditions, or variation among isolates. Recently, high concentrations of manganese have been found associated with delignified wood (5a). Fungi such as *Heterobasidion annosum*, *G. applanatum*, and *Ganoderma tsugae* have large manganese deposits in delignified tissues. Moisture content, temperature, and other environmental factors also appear to be important since laboratory decay tests, using many of the fungi listed in Table 1, have not shown selective delignification (3, 18, 21, 23). Bacteria, yeasts, and other microorganisms may also have significant effects on wood decayed by basidiomycetes (6).

Several fungi from Table 1 have been previously suggested to selectively degrade lignin. Eriksson (9) showed *Phellinus viticola* (as *Phellinus isabellinus*) to specifically degrade lignin in birch wood. Kawase (16) found that *Ischnoderma resinosum* caused extensive delignification of spruce wood. He also examined many other types of decayed wood but found most of them to have a ratio of cellulose to lignin similar to that of sound wood. Since many of these fungi cause delignification in isolated areas, assaying the simultaneous rotted wood with delignified wood can alter the ratio of carbohydrates to lignin. The amount of delignified wood and simultaneous rotted wood within a sample is also an important consideration in laboratory wood block decay tests. If entire blocks of wood are ground for analyses, the delignification capacity, although only in small areas, may be masked. The large differences reported among white rot fungi in selectivity toward lignin could be due to the intermittent nature of the delignification process in laboratory-decayed wood.

The list of fungi in Table 1 is not a complete tabulation of all fungi with specificity for lignin degradation. Many additional fungi also may have this capacity. Henningsson et al. (14) isolated a fungus that appeared to selectively remove lignin from birch wood. Highley et al. (15) and Kirk and Moore (20) also found white rotters with good specificity toward lignin. The fungi listed in Table 2 of this study also may have the potential to delignify wood. Additional samples from a wide variety of substrates and environments need to be examined before eliminating them. Herbarium sample FP 12783 is an example in which a fungus caused large white pockets in oak. These pockets, however, were filled with mycelium and not delignified cells. In another investigation involving *Xylobolus frustulatus* (22) the cellulose that remained in delignified pockets was subsequently depleted by the same fungus. A similar process could have occurred with FP 12783. Samples of incipient stages of decay must be examined to evaluate this fungus adequately.

The data presented in Table 3 indicate that hemicellulose was removed in addition to lignin. Other researchers (1, 2, 9, 18) have demonstrated that at least one of the polysaccharides in wood must be degraded simultaneously with lignin. The recently developed cellulaseless mutants also removed hemicellulose when lignin was degraded (10). The preference for hemicellulose may be due to the close spatial relationship of lignin and hemicellulose within the cell wall (17). After the lignin and hemicellulose matrix is degraded by chemical pulping, ribbon-like structures of cellulose fibrils bond in their radial planes to form lamellae. Examination of cells in wood delignified by fungi also demonstrated a similar fibrillar structure. The macrofibrillar structure of cellulose observed in this study appears to support the model of Kerr and Goring (17) for the arrangement of cell wall components.

A recent ultrastructural study of delignified wood also demonstrated the removal of lignin from specific cell wall layers (Blanchette et al., in press). The loss of middle lamellae without significant alteration of the S_2 layer occurred at considerable distances from fungal hyphae. The study reported here confirms the removal of extensive amounts of lignin from the middle lamella region when hyphae were located in cell lumens. In contrast, simultaneous white-rotted wood had a localized degradation pattern that was apparent immediately around the hyphae.

Direct observations of decayed wood by scanning electron microscopy identified a large number of fungi that have the capacity to selectively remove lignin from wood. Investigations are now needed to elucidate the mechanisms involved in lignin degradation during a simultaneous white rot and also during selective delignification so that a more complete understanding of these processes can be realized.

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LITERATURE CITED

1. **Ander, P., and K.-E. Eriksson.** 1975. Influence of carbohydrates on lignin degradation by the white-rot fungus *Sporotrichum pulverulentum*. Sven. Papperstidn. **78**:643–652.
2. **Ander, P., and K.-E. Ericksson.** 1976. The importance of phenol oxidase activity in lignin degradation by the white rot fungus *Sporotrichum pulverulentum*. Arch. Microbiol. **109**:1–8.
3. **Ander, P., and K.-E. Eriksson.** 1977. Selective degradation of wood components by white rot fungi. Physiol. Plant. **41**:239–248.
4. **Blanchette, R. A.** 1980. Wood decomposition by *Phellinus (Fomes) pini*: a scanning electron microscopy study. Can. J. Bot. **58**:1496–1503.
5. **Blanchette, R. A.** 1984. Selective delignification of eastern hemlock by *Ganoderma tsugae*. Phytopathology **74**:153–160.

5a. **Blanchette, R. A.** 1984. Manganese accumulation in wood decayed by white rot fungi. Phytopathology **74**:725–730.

6. **Blanchette, R. A., and C. G. Shaw.** 1978. Associations among bacteria, yeasts and basidiomycetes during wood decay. Phytopathology **68**:631–637.
7. **Crawford, R. L.** 1981. Lignin biodegradation and transformation. John Wiley & Sons, Inc., New York.
8. **Effland, M. J.** 1977. Modified procedure to determine acid-

soluble lignin in wood and pulp. Tappi **60:**143–144.
9. **Eriksson, K.-E.** 1978. Enzyme mechanisms involved in cellulose hydrolysis by the rot fungus *Sporotrichum pulverulentum*. Biotechnol. Bioeng. **20:**317–332.
10. **Eriksson, K.-E., A. Grunewald, and L. Vallander.** 1980. Studies of growth conditions in wood for three white-rot fungi and their cellulase-less mutants. Biotechnol. Bioeng. **22:**363–376.
11. **Eslyn, W. E., and T. L. Highley.** 1976. Decay resistance and susceptibility of sapwood of fifteen tree species. Phytopathology **66:**1010–1017.
12. **Gilbertson, R. L.** 1980. Wood rotting fungi of North America. Mycologia **72:**1–49.
13. **Hartig, R.** 1878. Die zersetzungserscheinungen des holzes der nadelholzebaume und der eiche in forstlicher botanischer und chemischer richtung. Springer-Verlag, Berlin.
14. **Henningsson, B., M. Henningsson, and T. Nilsson.** 1972. Defibration of wood by the use of a white-rot fungus. Swedish Royal College of Forestry Research Notes NR78. Royal College of Forestry, Stockholm.
15. **Highley, T. L., S. S. Bar-Lev, T. K. Kirk, and M. J. Larsen.** 1983. Influence of O_2 and CO_2 on wood decay by heartrot and saprot fungi. Phytopathology **73:**630–633.
16. **Kawase, K.** 1962. Chemical components of wood decayed under natural conditions and their properties. Hokkaido Daigaku Sapporo J. Fac. Agric. **52:**186–245.
17. **Kerr, A. J., and D. A. I. Goring.** 1975. The ultrastructural arrangement of the wood cell wall. Cellul. Chem. Technol. **9:**563–573.
18. **Kirk, T. K., and T. L. Highley.** 1973. Quantitative changes in structural components of conifer woods during decay by white- and brown-rot fungi. Phytopathology **63:**1338–1342.
19. **Kirk, T. K., T. Higuchi, and H. M. Chang.** 1980. Lignin biodegradation: summary and perspectives, p. 235–244. *In* T. K. Kirk, T. Higuchi, and H.-M. Chang (ed.), Lignin biodegradation: microbiology, chemistry and potential applications. CRC Press, Inc., Boca Raton, Fla.
20. **Kirk, T. K., and W. E. Moore.** 1972. Removing lignin in wood with white rot fungi and digestibility of resulting wood. Wood Fiber **4:**72–79.
21. **Otjen, J., and R. A. Blanchette.** 1982. Patterns of decay caused by *Inonotus dryophilus* (Aphyllophorales: Hymenochaetaceae), a white-pocket rot of oaks. Can. J. Bot. **60:**2270–2279.
22. **Otjen, L., and R. A. Blanchette.** 1984. *Xylobolus frustulatus* decay of oak: patterns of selective delignification and subsequent cellulose removal. Appl. Environ. Microbiol. **47:**670–676.
23. **Setliff, E. C., and W. E. Eudy.** 1980. Screening white-rot fungi for their capacity to delignify wood, p. 135–149. *In* T. K. Kirk, T. Higuchi, and H.-M. Chang (ed.), Lignin biodegradation: microbiology, chemistry and potential applications. CRC Press, Inc., Boca Raton, Fla.