# Influence of $O_2$ and $CO_2$ on Wood Decay by Heartrot and Saprot Fungi

T. L. Highley, S. S. Bar-Lev, T. K. Kirk, and M. J. Larsen

Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, maintained in cooperation with the University of Wisconsin at Madison.

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## ABSTRACT

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The effect of various partial pressures of $O_2$ (0.01, 0.1, 0.2, and 0.4 atm) and $CO_2$ (0.004, 0.1, and 0.2 atm) on decay in sapwood and heartwood by four heartrot fungi (*Phellinus everhartii*, *Ph. igniarius*, *Ph. ferrugineofuscus*, and *Inonotus glomeratus*) and three saprot fungi (*Ph. ferreus*, *Ph. ferruginosus*, and *Poria medulla-panis*) was studied to determine whether heartrot fungi possess ligninolytic and cellulolytic systems tolerant of low $O_2$ and high $CO_2$ levels. Decay caused by both groups of fungi was reduced by low $O_2$ (0.01 and 0.1 atm) and high $CO_2$ (0.1 and 0.2 atm). Increasing $O_2$ partial pressures above 0.1 atm enhanced decay by the saprot more than by the heartrot fungi. The saprot fungi were generally more selective in lignin removal than were the heartrot fungi. It is concluded that the unique ecology of the heartrot fungi is not attributable to an unusual ability to decompose wood at the high $CO_2$ and low $O_2$ concentrations found in the hearts of living trees.

*Additional key words:* lignin biodegradation, paper birch, sugar maple, sweetgum, white oak, white spruce.

Of the several thousand species of fungi known to decay wood, only a few hundred cause decay in the heartwood of living trees (17). The unique features that enable some decay fungi to cause heartrot are not known, but their wood degradative mechanisms apparently are not unique (7). It has been suggested that heartrot fungi may simply be more tolerant than saprot fungi of the chemical and physical environment within the heartwood of living trees (7). Constraints that are obviously suspect in this regard are the levels of $O_2$ and $CO_2$.

Heartrot fungi can grow in a nearly anaerobic atmosphere containing high levels of $CO_2$. Concentrations of $O_2$ <1% of the volume of gases in tree trunks are common (11), and $CO_2$ concentrations as high as 20% have been reported (8). Hintikka and Korhonen (8) reported that heartrot fungi are more tolerant of high $CO_2$ than are saprot fungi.

Recent studies have shown that the partial pressure of $O_2$ strongly influences the rate of degradation of wood by some decay fungi (14,18). The saprot fungus *Phanerochaete chrysosporium* Burds. (= *Sporotrichum pulverulentum* Nov.) degraded lignin and carbohydrates in alder thermomechanical pulp much faster in $O_2$ than in air (18). Reid and Seifert (14) found that degradation of lignin and carbohydrates in aspen wood was faster in $O_2$ than in air for seven (including *P. chrysosporium*) of nine saprot fungi. They did not examine low concentrations of $O_2$. Differences in growth rate in air and $O_2$ were insignificant and could not explain the stimulation of decomposition by $O_2$ (14). Both ligninolytic (13) and cellulolytic (4) systems of *P. chrysosporium* were stimulated by $O_2$.

Unpublished results from this laboratory have shown that cellulose degradation by the brownrot fungus *Poria placenta*, which causes a saprot, also is stimulated markedly by increasing the partial pressure of $O_2$.

The purpose of this study was to test the hypothesis that heartrot and saprot fungi differ in decay-causing capacities in the presence of different concentrations of $O_2$ and $CO_2$. Decay rates were assessed for selected fungi in cultures maintained at various partial pressures of these two gases.

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## MATERIALS AND METHODS

**Wood samples and decay.** Blocks of sapwood and heartwood measuring 18 × 18 × 3 mm, with the small dimension in the grain direction, were cut from white oak (*Quercus alba* L.), paper birch (*Betula papyrifera* Marsh.), sugar maple (*Acer saccharum* Marsh.), and white spruce (*Picea glauca* [Moench.] Voss.). Sapwood blocks also were cut from sweetgum (*Liquidambar styraciflua* L.). All blocks were subjected to decay in 125-ml Erlenmeyer flasks according to the ASTM soil-block procedure (1). Flasks were incubated at 21 C under intermittent light. Percentage of weight loss, which is the measure of decay, was calculated from the weights of decayed blocks after equilibration at 70% RH and 27 C. Original weights had been recorded after similar equilibrations. All decay was conducted under a total pressure of 1 atm. Four replications were used in each treatment.

In the first part of the study, sweetgum sapwood blocks were decayed at four $O_2$ concentrations (0.01, 0.1, 0.2, and 0.4 atm) by three heartrot fungi, *Phellinus igniarius* (L.:Fr.) Quél., *Ph. everhartii* (Ell. et Gall.) Pilát, *Ph. ferrugineofuscus* (Karst.) Bourd., and by two saprot fungi, *Ph. ferruginosus* (Schrad.:Fr.) Bourd. et Galz., and *Poria medulla-panis* (Jacq.:Fr.) Cke. In addition, sweetgum blocks were decayed by these fungi under 0.01 and 0.1 atm of $O_2$ with 0.004, 0.1, and 0.2 atm of $CO_2$.

The effects of $O_2$ on decay were also studied when fungi were matched with heartwood and sapwood of the wood species that these fungi normally degrade in nature. The heartrot fungus, *Inonotus glomeratus* (Pk.) Murr., and the saprot fungus, *Ph. ferreus* (Pers.) Bourd. et Galz., were included in this segment of the study.

In all tests, the decay test flasks were flushed every 2 or 3 days with the appropriate $O_2$/$CO_2$ mixture in $N_2$ for 15 min with 100 ml of gas mixture per minute. On several occasions the $O_2$ concentrations were measured 3 days after flushing. In all cases, the reduction in $O_2$ concentration was less than 25% of the original concentration (ie, the 0.1 atm concentration was never less than 0.075 atm after 3 days).

**Lignin and carbohydrate determinations.** Decayed and control blocks were ground to pass a screen (40-mesh), and the wood meal was dried in a vacuum oven at 45 C. The wood meals were analyzed, without extraction, for sulfuric acid lignin and for total reducing sugars in acid hydrolysates (determined colorimetrically as glucose) (3). Results are expressed on the basis of the original dry weights.

## RESULTS

**Decay of sweetgum sapwood.** In the first experiments, the decay of sweetgum sapwood by the various fungi was assessed in cultures maintained at different partial pressures of $O_2$ and $CO_2$. High $CO_2$ markedly inhibited decay by both heartrot and saprot fungi (Table 1). At 0.01 atm of $O_2$, decay was completely inhibited by 0.1 atm of $CO_2$; at 0.1 atm of $O_2$, decay was suppressed 60% or more by 0.1 atm of $CO_2$. The most $CO_2$-tolerant fungi were *Ph. everhartii* (heartrot) and *P. medulla-panis* (saprot). Because the heartrot fungi did not exhibit any particular tolerance to $CO_2$, further study focused on the effect of $O_2$ concentration.

The partial pressure of $O_2$ strongly influenced the sweetgum decay rate by both heartrot and saprot fungi (Table 2). Under 0.01 atm of $O_2$, all of the fungi caused only a slight weight loss (3–6%). Increasing the $O_2$ pressure to 0.1 and 0.2 atm allowed progressively more weight loss. At 0.4 atm (included to clarify the influence of $O_2$), decay by the two saprot fungi was further stimulated, while decay by the three heartrot fungi was similar to that at 0.2 atm. Decay by the other two heartrot fungi, *Ph. igniarius* and *Ph. everhartii*, was somewhat slower under 0.4 atm than under 0.2 atm of $O_2$. *Ph. ferrugineofuscus* (heartrot) and *P. medulla-panis* (saprot) responded the most to increased $O_2$.

Both lignin and carbohydrate were degraded by both groups of fungi. Neither group showed a uniform pattern in selecting one component over the other (Table 2). The ratios of percent loss in carbohydrates to percent loss in lignin varied from 0.43 to 1.45.

**Decay of host woods.** Because decay rates vary greatly with wood species, the fungi were next matched with their normal host woods—both heartwood and sapwood—and the influence of $O_2$ on decay was assessed. Two additional fungi were included, *I. glomeratus* (heartrot) and *Ph. ferreus* (saprot), and $O_2$ partial pressures of 0.1, 0.2, and 0.4 atm were evaluated.

Similar to sweetgum, the partial pressure of $O_2$ markedly influenced decay rates by both the heartrot and saprot fungi (Table 3, Fig. 1). With the exception of heartwood decay by *I. glomeratus*, decay by the fungi was enhanced by increasing the partial pressure of $O_2$ from 0.1 to 0.2 atm. Decay by the three saprot fungi was further stimulated by increasing the partial pressure of $O_2$ to 0.4 atm. Again, the heartrot fungi responded variably to the increase from 0.2 to 0.4 atm, but sometimes their decay was suppressed. The effect on heartwood decay was not always the same as on sapwood decay. Thus, *Ph. ferrugineofuscus* caused lower weight losses in spruce heartwood at 0.4 atm than at 0.2 atm of $O_2$, but in spruce sapwood the weight loss was higher at 0.4 atm.

In general, the saprot fungi were more selective for lignin than the heartrot fungi (Table 3). The average ratio of percent loss of carbohydrates to percent loss in lignin was 0.47 for all wood samples decayed by the saprot fungi. The corresponding ratio for the heartrot fungi was 0.94. Only *Ph. igniarius* in maple heartwood

TABLE 1. Percent weight loss in sweetgum sapwood exposed to decay for 8 wk with low $O_2$ and high $CO_2$[a]

| | 0.01 atm $O_2$ | | | 0.1 atm $O_2$ | | |
|---|---|---|---|---|---|---|
| Fungus | 0.004 atm $CO_2$ | 0.1 atm $CO_2$ | 0.2 atm $CO_2$ | 0.004 atm $CO_2$ | 0.1 atm $CO_2$ | 0.2 atm $CO_2$ |
| Heartrot | | | | | | |
| *Phellinus igniarius* | 3.1 ± 0 | 0 | 0 | 9.7 ± 3.5 | 1.5 ± 0.52 | 0 |
| *Ph. everhartii* | 3.8 ± 0.30 | 0 | 0 | 25.5 ± 2.9 | 9.7 ± 1.6 | 6.3 ± 2.9 |
| *Ph. ferrugineofuscus* | 4.0 ± 0.75 | 0 | 0 | 23.5 ± 9.5 | 0 | 0 |
| Saprot | | | | | | |
| *Ph. ferruginosus* | 6.1 ± 0.35 | 0 | 0 | 20.2 ± 5.6 | 3.0 ± 0.72 | 3.7 ± 1.9 |
| *Poria medulla-panis* | 4.8 ± 0.36 | 0 | 0 | 22.2 ± 5.0 | 7.4 ± 5.0 | 6.6 ± 1.4 |

[a] Average of four replications with standard deviation.

TABLE 2. Effect of oxygen concentration on decay of sweetgum sapwood by heartrot and saprot fungi[a]

| Fungus | Decay time (wk) | Oxygen concentration (atm) | Weight loss (%) | Lignin loss (%) | Carbohydrate loss (%) | Ratio of carbohydrate loss to lignin loss |
|---|---|---|---|---|---|---|
| Heartrot | | | | | | |
| *Phellinus igniarius* | 8 | 0.01 | 3.1 ± 0 | 1.0 | 1.4 | 1.40[b] |
| | 10 | 0.1 | 17.8 ± 3.4 | 17.4 | 18.4 | 1.05 ± 0.19 |
| | 10 | 0.2 | 28.5 ± 6.4 | 27.9 | 29.2 | 1.04 ± 0.10 |
| | 10 | 0.4 | 21.7 ± 3.8 | 22.3 | 21.4 | 0.94 ± 0.09 |
| *Ph. everhartii* | 8 | 0.01 | 3.8 ± 0.30 | 2.0 | 2.9 | 1.45[b] |
| | 8 | 0.1 | 30.0 ± 2.9 | 34.1 | 29.3 | 0.86 ± 0.48 |
| | 8 | 0.2 | 42.4 ± 7.2 | 43.7 | 46.6 | 1.06 ± 0.07 |
| | 8 | 0.4 | 36.1 ± 4.0 | 35.6 | 32.6 | 0.91 ± 0.17 |
| *Ph. ferrugineofuscus* | 8 | 0.01 | 4.0 ± 0.75 | 3.6 | 1.6 | 0.44[b] |
| | 10 | 0.1 | 32.0 ± 9.4 | 56.6 | 25.4 | 0.45 ± 0 |
| | 10 | 0.2 | 56.4 ± 8.3 | 71.4 | 54.8 | 0.76 ± 0.77 |
| | 10 | 0.4 | 58.9 ± 2.7 | 70.0 | 47.5 | 0.67 ± 0.14 |
| Saprot | | | | | | |
| *Ph. ferruginosus* | 8 | 0.01 | 6.1 ± 0.35 | 6.5 | 3.5 | 0.54[b] |
| | 8 | 0.1 | 24.2 ± 4.1 | 45.2 | 19.4 | 0.43 ± 0.48 |
| | 8 | 0.2 | 45.3 ± 11.6 | 61.0 | 42.1 | 0.69 ± 0.14 |
| | 8 | 0.4 | 49.3 ± 1.5 | 56.4 | 37.9 | 0.67 ± 0.08 |
| *Poria medulla-panis* | 8 | 0.01 | 4.8 ± 0.36 | 2.4 | 3.0 | 1.25[b] |
| | 6 | 0.1 | 22.2 ± 10.2 | 32.8 | 22.3 | 0.68 ± 0.29 |
| | 6 | 0.2 | 39.8 ± 3.3 | 52.4 | 41.4 | 0.79 ± 0.08 |
| | 6 | 0.4 | 52.0 ± 6.0 | 55.3 | 45.2 | 0.82 ± 0.18 |

[a] Average of four replications with standard deviation.
[b] Replications combined for analysis.

exhibited selectivity toward lignin comparable to that of the saprot fungi. The saprot fungus, *Ph. ferreus*, was exceptionally selective for the lignin component in both sapwood and heartwood.

## DISCUSSION

**Unique features of heartrot fungi.** This study shows that high $CO_2$ and low $O_2$ levels relative to the normal atmosphere reduce wood decay by both heartrot and saprot fungi. Thus, the heartrot fungi possess no unique tolerances to high $CO_2$ or low $O_2$. Such tolerance was considered to be the most probable common feature of heartrot fungi, if any exists, explaining their ability to decay heartwood of living trees (7). Other environmental factors that differ between the heartwood of living trees and downed timber, such as the presence of volatile tree metabolites (6) and slower temperature fluctuations in the former (10), do not provide a firm basis for a general hypothesis. We suggest, therefore, that no such general features exist. Instead, it would appear more probable that each heartrot fungus has become adapted to the peculiar environmental constraints imposed by its host or hosts. Such adaptation must include primarily a tolerance for heartwood extractives and volatile metabolites, for peculiar conditions of pH, moisture and competing microorganisms, and perhaps for other unknown factors (7).

Many heartrot fungi are unable to continue decay when the host tree dies naturally or is harvested. In laboratory tests, such fungi produce little or no decay in the host heartwood. For example, incense cedar and black locust are severely decayed by the heartrot fungi *Tyromyces amarus* (Hedge.) Lowe and *Phellinus robiniae* (Murr.) Ames, respectively, in living trees, but are decay-resistant after harvest (7). The heartrot fungi in our study produced significant weight losses in the laboratory soil-block tests, although they generally degraded wood more slowly than did the saprot fungi. Heartwood was generally degraded more slowly by both types of fungi.

Our data support Jensen's (9) proposal that heartrot fungi may remain active only when the infection court is open, and that once this has healed the decay column becomes inactive because of reduced $O_2$ and increased $CO_2$ levels. This is also supported by the fact that heartrot fungi cannot decay wetwood of cottonwood, apparently owing to nearly anaerobic conditions in the wetwood (16). Thacker and Good (15) and Jensen (9) found that high $CO_2$ suppressed the growth of various heartrot fungi. Thus, the inhibitory effect of $CO_2$ noted here was probably not specifically on decay. Nevertheless, because the fungi were established in culture flasks under atmospheric conditions prior to insertion of wood samples, the effects noted were not on growth alone.

**Influence of $O_2$ on wood decay.** Our results provide more information about the strong influence that molecular $O_2$ has on metabolism of wood and wood components. Surprisingly, this influence has received very little attention until recently. Indeed, it was only recent findings that prompted us to include the hyperatmospheric concentration of 0.4 atm of $O_2$ in this investigation. Eriksson (5) reports that cellulose hydrolysis by culture filtrates of *Sporotrichum pulverulentum* (=*Phanerochaete chrysosporium*) is twice as fast under air as under $N_2$. This was later found to be caused by an influence of $O_2$ on the activity of cellobiose oxidase (4). This enzyme presumably relieves product inhibition of the endoglucanases by cellobiose. Molecular $O_2$ has a dual stimulatory influence on lignin degradation by *P. chrysosporium*: increasing the partial pressure of $O_2$ increases the titer of the ligninolytic system that is formed in the cultures, and also increases the rate of lignin oxidation to $CO_2$ by the system after it is formed (2). Reid and Seifert (14) have shown that degradation of $^{14}$C-lignin-labeled aspen wood to $^{14}CO_2$ by several wood-decay fungi was faster under $O_2$ than under air. With all of the fungi, degradation of the carbohydrate component was also faster in $O_2$. Interestingly, Reid and Seifert (14) found that the fungi grew on chemically delignified wood at equal rates in air and $O_2$, and concluded that growth of these fungi on wood in air is limited by the

TABLE 3. Effect of oxygen concentration on decay of host heartwood and sapwood by heartrot and saprot fungi[a]

| | | | Heartwood | | | | Sapwood | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fungus | Wood species | Oxygen concentration (atm) | Weight loss (%) | Lignin loss (%) | Carbohydrate loss (%) | Ratio of carbohydrate loss to lignin loss | Weight loss (%) | Lignin loss (%) | Carbohydrate loss (%) | Ratio of carbohydrate loss to lignin loss |
| Heartrot | | | | | | | | | | |
| *Phellinus igniarius* | Sugar maple | 0.1 | 15 ± 1 | 24.2 | 12.7 | 0.52 ± 0 | 23 ± 6 | 31.0 | 22.5 | 0.73 ± 0.04 |
| | | 0.2 | 16 ± 5 | 26.3 | 16.9 | 0.64 ± 0.20 | 37 ± 4 | 35.2 | 40.3 | 1.14 ± 0.02 |
| | | 0.4 | 9 ± 2 | 23.0 | 5.8 | 0.25 ± 0.09 | 26 ± 8 | 29.3 | 27.5 | 0.94 ± 0.14 |
| *Ph. everhartii* | White oak | 0.1 | 10 ± 2 | 9.8 | 10.0 | 1.02 ± 0.06 | 25 ± 6 | 26.1 | 22.7 | 0.87 ± 0.05 |
| | | 0.2 | 17 ± 5 | 19.8 | 16.5 | 0.83 ± 0.02 | 35 ± 2 | 34.6 | 34.5 | 1.00 ± 0.05 |
| | | 0.4 | 20 ± 6 | 22.3 | 21.6 | 0.97 ± 0.11 | 36 ± 5 | 38.6 | 34.5 | 0.89 ± 0.14 |
| *Inonotus glomeratus* | Paper birch | 0.1 | 12 ± 3 | 12.4 | 14.0 | 1.13 ± 0.58 | 20 ± 7 | 30.5 | 18.0 | 0.59 ± 0.28 |
| | | 0.2 | 11 ± 8 | 8.9 | 10.0 | 1.12[b] | 27 ± 10 | 36.3 | 25.8 | 0.71 ± 0.31 |
| | | 0.4 | 19 ± 1 | 21.4 | 22.9 | 1.07 ± 0.36 | 23 ± 4 | 24.5 | 28.5 | 1.16 ± 0.50 |
| *Phellinus ferrugineofuscus* | White spruce | 0.1 | 8 ± 13 | 9.3 | 9.4 | 1.01 ± 0.23 | 18 ± 11 | 14.7 | 15.2 | 1.03 ± 0.35 |
| | | 0.2 | 28 ± 10 | 28.6 | 31.7 | 1.10 ± 0.12 | 22 ± 6 | 27.3 | 24.0 | 0.88 ± 0.17 |
| | | 0.4 | 18 ± 13 | 19.5 | 21.4 | 1.09 ± 0.02 | 33 ± 14 | 36.2 | 35.6 | 0.98 ± 0.29 |
| Saprot | | | | | | | | | | |
| *Ph. ferreus* | Sugar maple | 0.1 | 15 ± 4 | 38.3 | 3.4 | 0.09 ± 0.06 | 23 ± 3 | 47.3 | 12.2 | 0.25 ± 0.10 |
| | | 0.2 | 19 ± 7 | 45.5 | 7.1 | 0.15 ± 0.10 | 33 ± 5 | 64.7 | 21.0 | 0.32 ± 0.05 |
| | | 0.4 | 28 ± 13 | 50.0 | 16.4 | 0.33 ± 0.11 | 39 ± 4 | 70.1 | 27.5 | 0.39 ± 0.06 |
| *Ph. ferruginosus* | Sugar maple | 0.1 | 16 ± 5 | 34.1 | 8.8 | 0.26 ± 0.18 | 30 ± 6 | 39.9 | 16.6 | 0.42 ± 0.30 |
| | | 0.2 | 33 ± 13 | 50.9 | 27.5 | 0.54 ± 0.27 | 32 ± 12 | 58.2 | 24.4 | 0.42 ± 0.15 |
| | | 0.4 | 42 ± 15 | 55.2 | 35.5 | 0.64 ± 0.10 | 43 ± 16 | 64.9 | 36.1 | 0.56 ± 0.06 |
| *Poria medulla-panis* | Sugar maple | 0.1 | 19 ± 4 | 31.3 | 17.3 | 0.55 ± 0.06 | 18 ± 4 | 28.1 | 17.5 | 0.62 ± 0.20 |
| | | 0.2 | 29 ± 4 | 43.9 | 25.3 | 0.58 ± 0.12 | 37 ± 3 | 47.4 | 37.3 | 0.79 ± 0.06 |
| | | 0.4 | 48 ± 6 | 56.6 | 47.0 | 0.83 ± 0.06 | 45 ± 10 | 56.2 | 43.3 | 0.77 ± 0.22 |

[a] Exposed 10 wk, average of four replications with standard deviation.
[b] Replications combined for analysis.

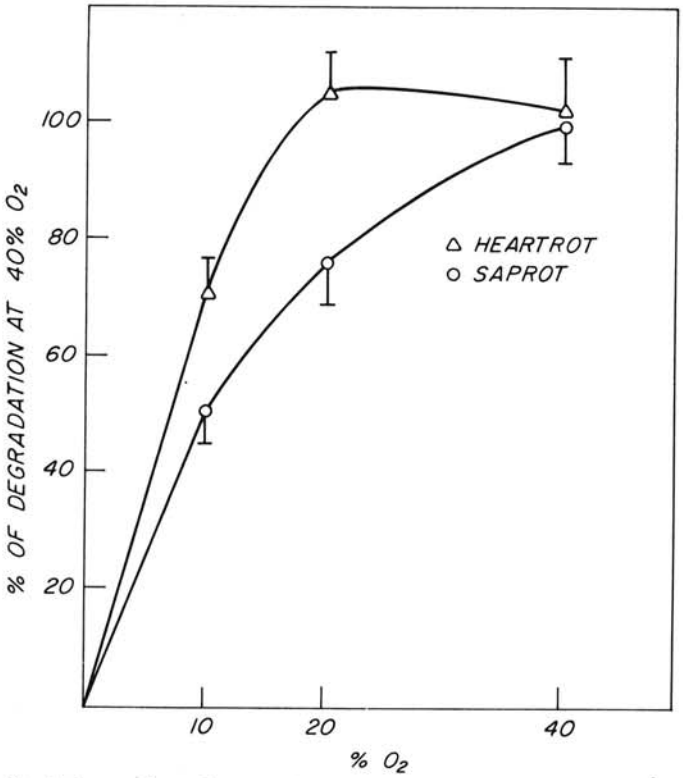


**Fig. 1.** Comparison of average decay rates in heartwood and sapwood by four heartrot and three saprot fungi with increased $O_2$ concentration. The average weight loss at 40% $O_2$ for each fungus was taken to be 100%; loss at 10 and 20% was calculated as a percent of that value. The incubation time was 10 wk.

rate of lignin degradation. All of the saprot fungi and two of the heartrot fungi examined in this study decayed wood (including the lignin) faster when partial pressures of $O_2$ were increased from 0.1 to 0.4 atm. Probably the lowest $O_2$ concentration used with sweetgum (0.01 atm) was too low for normal respiration.

**Competitive degradation of lignin and carbohydrate.** The fungi exhibited great variation in selectivity toward lignin and carbohydrate. The saprot fungi showed greater selectivity for decaying lignin that did the heartrot fungi, except for *Ph. igniarius* and *I. glomeratus*, which degraded the lignin selectively in maple heartwood and birch sapwood, respectively. Examination of additional heartrot and saprot fungi would be required to determine how general is the greater selectivity of saprot fungi for lignin degradation.

In any case, the results agree with previous work showing large variation among white-rot fungi in selectivity toward lignin (12). At least one of the fungi studied here, *Ph. ferreus*, deserves further study for potential application in biodelignification.

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