

Consumption of Sound and Decayed Ponderosa Pine and Douglas-Fir by *Reticulitermes* spp. (Isoptera: Rhinotermitidae) from Northern California

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ABSTRACT Survival, amount of wood consumed, and the feeding rate of workers of western subterranean termites, *Reticulitermes* spp., were assessed on sapwood blocks of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws, and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, that were sound or decayed by 1 of 2 brown-rot fungi, *Gloeophyllum trabeum* (Fr.) Murr. or *Postia placenta* (Fr.) M. Lars & Lomb. Groups of 200 workers were confined separately on combinations of each wood and fungal species for 28 d. Mean survivorship of 2 colonies was 89.5 and 96.1%, and were not significantly different, whereas 1 of these suffered significantly greater mortality when fed wood of either species decayed by *G. trabeum*. Groups of workers consumed an average of 293 mg or 25.5% of wood during the test period. The amount and percentage of wood consumed by termites was significantly greater when decayed by either fungus; however, 1 colony consumed significantly more wood of both species when decayed by *G. trabeum*. When corrected for mortality over the length of the test, feeding (milligrams wood per worker per 28 d) was not significantly different between colonies or wood species. Wood of either species was consumed at a significantly greater rate if decayed by *G. trabeum* (1.77 mg per termite per 28 d) than by *P. placenta* (1.55 mg per termite per 28 d); wood decayed by either fungus was consumed at a significantly greater rate than nondecayed wood (1.25 mg per termite per 28 d).

KEY WORDS *Reticulitermes*, *Gloeophyllum trabeum*, *Postia placenta*, wood consumption

FACTORS AFFECTING THE selection of a food source by termites in nature include species of termite, type of wood, the moisture content of the wood, type and amount of extractives in wood, differences between heartwood and sapwood, hardness of the wood, and the extent of any previous attack by fungi or other insects (Kofoid and Bowe 1934). In North America, wood-rotting fungi are estimated to comprise 1,700 species (Gilbertson 1980). Based on the type of decay they cause, these fungi usually are referred to as white-rot or brown-rot fungi. Brown-rot fungi make up $\approx 6\%$ of the total species of wood-rotting Basidiomycetes in North America (Gilbertson 1981). They degrade cellulose and hemicellulose, leaving a residue of lignin. Wood with a high lignin content that is highly resinous can be termite resistant (Breznak and Brune 1994). Gilbertson (1984) has suggested that the greater rates of survival and development of termites in decayed wood were caused by both the increased nutritional value and the breakdown of some toxic substances.

For the decomposition of cellulose, termites rely primarily on the symbiotic relationship of bacteria and protozoa in their gut. It has been shown that termites can have a mutualistic relationship with fungi outside of the gut. Because energy is required for the break-

down of the stable cellulose molecule, fungal degradation of this carbohydrate is beneficial to termites (Gilbertson 1984). The amount of time termites and fungi interact and the species of termite and fungus all appear to affect the attraction, repellency, and palatability of wood to termites (Amburgey and Smythe 1977a; Becker 1971, 1976; Esenther and Coppel 1964; Gilbertson 1984).

Smythe et al. (1971) demonstrated that *Reticulitermes flavipes* (Kollar) workers consumed twice the amount of decayed ponderosa pine when compared with nondecayed wood. Termites survived better on ponderosa pine when it was oven dried, decayed wood compared with nondried, decayed wood. In another study, *R. flavipes* and *R. virginicus* (Banks) failed to survive on decayed ponderosa pine that was either oven dried or nondried (Smythe and Carter 1970). Becker (1948) indicated in choice tests that *R. lucifugus* (Rossi) consumed more pine sapwood when decayed by *Gloeophyllum trabeum* (Fr.) Murr. than nondecayed sapwood. Termites fed on wood decayed by *G. trabeum* and *Postia placenta* (Fr.) M. Lars & Lomb survived longer than on nondecayed controls (Lund 1960).

Sample size and species of wood also plays a role in consumption rates. Waller (1988) found that when given a choice of sound wood, *Reticulitermes* spp. collected from logs in northern Virginia consumed

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more Douglas-fir than ponderosa pine. Termites also ingested more wood from larger blocks than smaller blocks of Douglas-fir, but ate similar amounts from both large and small blocks of ponderosa pine. Waller (1988) further speculated that other factors affecting wood consumption and host choice may include the availability of food sources.

The nutritional value of some wood can be either increased or decreased by brown-rot fungi, depending on the species. *R. flavipes* consumed more *Pinus elliotii* Engelm. decayed in the range of 5–20% weight loss than wood with a greater amount of decay (Becker 1965, 1976; Lenz et al. 1991). However, *R. flavipes* consumed a greater amount of *Pinus ponderosa* Dougl. ex Laws with up to 30% weight loss from decay by *G. trabeum* or *Meruliporia (Poria) incrassata* (Berk. & Curt.) Murr., than nondecayed wood (Amburgey and Smythe 1977b). Wood decayed by *G. trabeum* in the range of 6–12% weight loss resulted in greater amounts of wood removed by *R. lucifugus* (Rossi) and *R. lucifugus santonensis* Feytaud in choice tests than in tests with <6% weight loss from decay (Becker 1965). These studies demonstrate that the amount of wood removed by termites can be variable and may be affected positively or negatively by decay or the degree of decay.

There is an increasing awareness of the high incidence of 2 brown-rot fungi [*Gloeophyllum trabeum* (Fr.) Murr. (formerly *Lenzites trabea*) and *Postia placenta* (Fr.) M. Lars & Lomb. (formerly *Poria monticola*)], in wooden structures in California (Wilcox and Dietz 1997). The relationships among a species of *Reticulitermes*, these brown-rot fungi, and 2 wood species commonly used in buildings [*P. ponderosa* and *Pseudotsuga menziesii* (Mirb.) Franco], was investigated in this study. The current study differs from earlier works in that it attempts to determine whether differences in wood and fungal species affect the amount of wood removed by one of the common *Reticulitermes* in northern California.

Materials and Methods

Wood. Ponderosa pine and Douglas-fir used in this study were obtained from the Forest Products Laboratory, University of California, in collections from northern California. Three hundred and twenty-two sample blocks of each species were cut tangentially into pieces 2 by 2 by 0.5 cm. To reduce variation within a wood species and to facilitate uniform decay of the wood, all blocks were cut from the same log. The blocks were stored on an open surface in a conditioning room at 12% moisture content, 20°C, and 66% RH. Four days later, blocks were individually weighed in the conditioning room to obtain an initial weight.

Decaying Process. Decay chambers were prepared using polystyrene petri dishes (100 by 15 mm), each containing an agar medium. Agar medium was prepared using 20 g of malt extract, 15 g of agar, and 1,000 ml of distilled water, then autoclaved at 120°C for 20 min. Seventy-five agar plates were prepared in a sterile room at the Forest Products Laboratory. Approxi-

mately 15 ml of the prepared agar was poured into each plate and allowed to set for 24 h. Two separate groups were inoculated, 1 with *G. trabeum* and the other with *P. placenta*. The inoculated plates were allowed to incubate for 10–14 d at 27°C in a sterile, dark chamber until mycelial growth had spread over at least half of the agar surface.

The test blocks were wrapped in aluminum foil and autoclaved at 120°C for 20 min, then soaked in similarly autoclaved distilled water. Ponderosa pine and Douglas-fir blocks were exposed separately to either of 2 species of decay fungi. Four wood samples were placed in each agar dish on top of a 2-mm polyethylene mesh that was placed, in turn, on top of the mycelia. The decay chambers and test blocks were allowed to incubate for 4–8 wk in a dark room at 27°C. Wood decayed by *G. trabeum* required ≈4 wk to reach 10–15% weight loss, whereas *P. placenta* required ≈8 wk. One block was randomly selected from each dish and removed periodically over each of the following weeks to determine weight losses caused by decay. When weight loss on a test block reached 10–15%, all blocks were removed from the decay chambers. Hyphae were removed from test blocks by using a small toothbrush, and the blocks were returned to the conditioning room for 48 h to equilibrate to a uniform moisture content, temperature, and relative humidity before weighing.

Feeding Interaction Tests. Termite workers used in this study were collected from the Eddy Arboretum in the western portion of the U.S. Forest Service, Pacific Southwest Research Station's Institute of Forest Genetics, near Placerville, CA. The Institute is located between Placerville and Camino, CA, at an elevation of ≈775 m (≈2,500 ft). Based on the accepted biogeographical information, only *R. hesperus* occurs in the Sierra Nevada (Nutting 1990). However, 3 distinct cuticular hydrocarbon phenotypes (A, B, and C) occur in this site. The termites used in this study are all of 1 phenotype (A) as characterized by their integumental hydrocarbons (Haverty and Nelson 1997). Because we are uncertain of the exact species designation, we refer to these insects as *Reticulitermes* spp. Three distinct colonies, at least 200 m apart, were tested and determined to be cuticular hydrocarbon phenotype A (Haverty and Nelson 1997).

Round polystyrene containers (3 cm high, 4 cm diameter) filled with a mixture of sand, vermiculite, and water (1:1:1 vol:vol:vol) served as feeding chambers (Haverty 1979). Forty grams of the above mixture (without water) were placed in each sample container; the appropriate amount of water was added later. A decayed wood block soaked in distilled water for 2 min and 200 termite workers were added to complete the experimental unit. The experimental units were kept in a dark chamber for 4 wk at ambient laboratory conditions (≈24°C). Nondecayed blocks were submitted to the same procedures but without exposure to fungi and were used as controls.

Test containers were set up to allow continuous observation without significant disturbance to the termites during the 28-d testing period. Many of the

termites had built up sand and vermiculite over the wood block. This behavior obstructed most of the view of the wood sample within the test container. At the end of 4 wk, the wood blocks were removed, placed in the 12% conditioning room, and the remaining live termites were counted. The wood blocks were cleaned of sand and termite carton after 48 h and returned to the 12% conditioning room for another 48 h. They were subsequently weighed and the amount of wood loss determined.

Experimental Design, Response Variables, and Statistical Analysis. The experimental design was a 3 by 2 by 3 factorial, with colony, wood species, and fungal treatment as the main effects. The 4 response variables (percentage of survival, milligrams of wood removed by termites, percentage of wood removed by termites, and feeding rate) were used to assess the main effects. The feeding rate was determined to compensate for the effect of mortality over the duration of the test. The feeding rate was calculated from the average number of termites that were alive during the test period. The following formula was used: feeding rate = mg of wood removed over 28 d / ([initial number of termites + final number of termites] \times 0.5). Each treatment combination (3 colonies \times 2 wood species \times 3 fungal treatments [*G. trabeum*, *P. placenta*, none]) was replicated 6 times.

For each response variable, an analysis of covariance (ANCOVA) (SAS Institute 1985) was conducted to assess the potential influence of the covariates as follows: (1) wood weight before feeding, (2) percentage of weight loss of wood during the decay process, and (3) weight of wood before decay. Because there were 2 significant covariates (1 and 3) for percentage of wood removed by termites, an additional ANCOVA using these 2 covariates was conducted to adjust for these factors with this response variable. Of these 2 covariates, initial weight of wood before feeding was found to have the most significant *F* value, and the ANCOVA for this covariate was used to assess the main effects and interactions for percentage of wood removed. The initial wood weight before decay was used to assess the main effects and interactions for the feeding rate. No significant covariate was found for percentage of survival or milligrams of wood removed. For these response variables, an analysis of variance (ANOVA) was used to assess the significance of the main effects. For ANCOVA and ANOVA, significance of the *F*-statistic was tested at the $\alpha = 0.05$ level.

Therefore, in these cases, although the effect on the response variable from wood species could be described by a simple main effect, the main effects of colony and fungal treatment do not provide an adequate description. Response means of each combination of colony and fungal treatment were required and compared statistically. For the feeding rate there were no significant interactions, thus only main effects of all factors were necessary to describe adequately the effects on feeding rate.

Results and Discussion

Colony Mortality. Termites built foraging tunnels (galleries) along the edges and bottom of the containers and were seen moving through the tunnels. However, it was not uncommon during the test period to find few to no termites present in these galleries, and it was assumed termites were deeper in the substrate or in or on the wood and out of view. After 14 d, termites in colony 2 were not visible upon daily inspection. Termites in both colonies 1 and 3 could be seen in at least 1 or more experimental containers on inspection.

After the termites fed for 28 d, they were removed and the number of survivors counted. Colonies 1 and 3 were found to have a high mean survival of 96.1 and 89.5%, respectively (Table 1), whereas colony 2 experienced significantly higher mortality ($F = 730.61$; $df = 2, 93$; $P < 0.0001$), with a mean survival of 10.9%. In most instances, colony 2 test containers had no survivors and evidence of the dead termites was not apparent. Colony 2 exhibited high mortality in all treatment combinations.

There is no clear-cut evidence of what factor or combination of factors may have caused the rapid mortality of test colony 2. Because of this excessive mortality and the potential for aberrant results, colony 2 was removed from the final data set.

Survival. There was a statistically significant interaction between colony and fungal treatment ($F = 5.53$; $df = 2, 62$; $P < 0.0062$). Wood species had no statistically significant effect on survival (Table 1). Survival of colonies 1 and 3 was 94.7 and 92.8%, respectively, when fed nondecayed blocks. Survival was 96.2 and 96% for colonies 1 and 3 when fed blocks decayed by *P. placenta*. The highest survival (97.5%) was colony 1 on *G. trabeum*-decayed wood. In contrast, colony 3 termites fed blocks decayed by *G. trabeum* elicited a statistically significantly lower survival (79.8%). This is likely the reason for the overall lower survival (88.6%) for the main effect of *G. trabeum* (Table 1).

Weight of Wood Consumed. There was a statistically significant interaction between colony and fungal treatment ($F = 5.77$; $df = 2, 62$; $P < 0.0050$). Wood species had no statistically significant effect on milligrams of wood consumed (Table 1). The least amount of wood was consumed from nondecayed blocks; colony 1 consumed an average of 236.7 mg and colony 3 consumed 238.3 mg (Table 1). When fed on wood decayed by *P. placenta*, termites in both colonies consumed the same average amount of wood (306.7 mg) during the test. The amount of *G. trabeum*-decayed wood consumed by termites from colony 1 (358.3 mg) was significantly greater than that for termites from colony 3 (310.8 mg) confined to the same fungal treatment ($F = 5.77$; $df = 2$; $P < 0.0050$). These wood consumption results are probably caused by differences in survival between the 2 colonies feeding on *G. trabeum*-decayed wood.

Percentage of Wood Consumed. A significantly greater percentage of ponderosa pine (27%) was consumed than Douglas-fir (24.1%) (Table 1). There was

Table 1. Mean \pm SE percentage of survival, milligrams of wood consumed, percentage of wood removed, and feeding rate (milligrams of wood per termite per 28 d) of *Reticulitermes* spp.

	% survival ^{a,b}	Wood removed mg ^{a,b}	% wood removed ^{a,b}	Feeding rate ^a
Colony (n = 36)				
Colony 1	96.1 \pm 1.67	300.6 \pm 4.74	26.4 \pm 0.46	1.52 \pm 0.028 ^a
Colony 3	89.5 \pm 1.67	285.3 \pm 4.74	24.6 \pm 0.46	1.53 \pm 0.028 ^a
Wood species (n = 36)				
Ponderosa pine	94.5 \pm 1.67 ^a	290.0 \pm 4.74 ^a	27.0 \pm 0.85 ^a	1.58 \pm 0.051 ^a
Douglas-fir	91.2 \pm 1.67 ^a	295.8 \pm 4.74 ^a	24.1 \pm 0.85 ^b	1.46 \pm 0.051 ^a
Fungal treatment (n = 24)				
<i>Gloeophyllum trabeum</i>	88.6 \pm 2.05	334.6 \pm 5.81	29.2 \pm 0.55	1.77 \pm 0.034 ^a
<i>Postia placenta</i>	96.1 \pm 2.05	306.7 \pm 5.81	27.8 \pm 0.55	1.55 \pm 0.034 ^b
Control	93.7 \pm 2.05	237.5 \pm 5.81	19.4 \pm 0.57	1.25 \pm 0.035 ^c
Interactions ^b (n = 12)				
Colony 1 \times <i>Gloeophyllum trabeum</i>	97.5 \pm 2.90 ^a	358.3 \pm 8.22 ^a	31.5 \pm 0.78 ^a	1.77 \pm 0.050
Colony 1 \times <i>Postia placenta</i>	96.2 \pm 2.90 ^a	306.7 \pm 8.22 ^b	28.3 \pm 0.77 ^b	1.54 \pm 0.048
Colony 1 \times control	94.7 \pm 2.90 ^a	236.7 \pm 8.22 ^c	19.5 \pm 0.78 ^c	1.24 \pm 0.049
Colony 3 \times <i>Gloeophyllum trabeum</i>	79.8 \pm 2.90 ^b	310.8 \pm 8.22 ^b	26.9 \pm 0.83 ^b	1.76 \pm 0.047
Colony 3 \times <i>Postia placenta</i>	96.0 \pm 2.90 ^a	306.7 \pm 8.22 ^b	27.5 \pm 0.79 ^b	1.56 \pm 0.047
Colony 3 \times control	92.8 \pm 2.90 ^a	238.3 \pm 8.22 ^c	19.4 \pm 0.79 ^c	1.26 \pm 0.048

Experimental groups of 200 workers of 1 of 2 colonies fed 1 of 2 species of wood undecayed or decayed by 1 of 2 brown-rot fungi. Duration of test was 28 d. Each combination of factors (colony \times wood species \times fungal treatment) was replicated 6 times. Means within a category (i.e., colony, wood species, or fungal treatment) followed by the same letter are not significantly different ($P < 0.05$) by the Tukey procedure (SAS Institute 1985).

^a Analysis of covariance indicated a statistically significant influence ($P < 0.05$) of wood weight before feeding for percentage of wood removed and initial wood weight for feeding rate. No significant covariate was found for percentage of survival or milligrams of wood removed. The reported means for percentage of wood removed and feeding rate are reported at the overall average of the covariate.

^b Statistically significant interactions ($P < 0.05$) for colony and fungal treatment were found for these variables. With a significant interaction, significance of the differences between or among main effect means was not tested.

a significant interaction between colony and fungal treatment ($F = 3.83$; $df = 2, 61$; $P < 0.0271$). Colonies 1 and 3 removed a similar percentage of wood decayed by *P. placenta* (28.3 and 27.5%, respectively). However, there was a significant difference when both colonies were confined on *G. trabeum*-decayed wood, (i.e., colony 1 removed 31.5%, whereas colony 3 removed only 26.9%). There was no significant difference in the amount of wood removed by colony 3 confined to *G. trabeum*-decayed wood, and colony 3 and colony 1 confined to *P. placenta*-decayed wood. These results are generally consistent with the lower survival percentage in colony 3 confined on *G. trabeum*-decayed blocks.

Feeding Rate. There were no significant interactions for the feeding rate. However, there was a significant difference in wood consumption rate among fungal treatments ($F = 62.80$; $df = 2, 62$; $P < 0.0001$) (Table 1). There was a significant difference in feeding rate between each of the 2 fungal treatments and the nondecayed wood treatment. The feeding rate was significantly greater for *G. trabeum*-decayed wood (1.77 mg per termite per 28 d) than *P. placenta*-decayed wood (1.55 mg per termite per 28 d). A significantly lower feeding rate (1.24 mg per termite per 28 d) was recorded for termites feeding on nondecayed wood.

Differences in feeding rate may be caused by numerous factors, including wood anatomy or chemistry, amounts of nitrogen found in wood, extent of degradation, or the presence of fungi and their metabolites. Even a slight amount of deterioration by fungi may increase the nutritional value of wood for insects

(Becker 1971, Light and Weesner 1947). Results from our study clearly demonstrate that more wood per termite was consumed when wood had been decayed by either of 2 fungi compared with nondecayed wood. This difference in wood consumption could be the result of a fungus-induced increase in nitrogen in the wood, partial degradation or depolymerization of cellulose molecules, or production of phagostimulants by the fungi (La Fage and Nutting 1978). Conversely, the increased feeding also could occur in response to lower nutrient quality of the wood, requiring a greater amount of wood to be consumed for the same nutrient value. The exact reason is limited to speculation because our study was not designed to determine preferences (a choice test would be needed) nor was the chemical nature of the various woods characterized.

Significant interactions between decay fungal treatments and colonies of the same termite species were found in our study. Thus, the results reinforce the need to examine numerous colonies of 1 species before generalizing on the effect of fungal treatments. Even with the differences in survival of termite colonies feeding on *G. trabeum*-decayed wood, this study reinforces, for yet another species of *Reticulitermes*, the enhancement of wood consumption when wood is decayed by an acceptable brown-rot fungus. Continuation of this research to include other species of wood, extent of decay, and effect of temperature would enhance our understanding of the role of these termites in wildland ecosystems, as well as provide improvements in baiting technology for control of *Reticulitermes*.

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