The Role of Decay Fungi and Wood Species on the Wood Consumption Rates of *Reticulitermes hesperus* Banks (Isoptera: Rhinotermitidae)

by

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B.S. (University of California, Berkeley) 1992

A thesis submitted in partial satisfaction of the

requirements for the degree of

Master of Science

in

Wood Science and Technology

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA, BERKELEY

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Spring 1997

ABSTRACT

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Survival, amount of wood removed, and the feeding rate of *Reticulitermes hesperus* workers were assessed on *Pseudotsuga menziesii* and *Pinus ponderosa* sapwood blocks that were decayed by the brown-rot fungi, *Gloeophylum trabeum* and *Postia placenta*. Groups of termites were confined separately on combinations of each wood and fungal species for 28 days. Three colonies were tested. Mean survivorship of two colonies fed both species of wood and fungi was 89.5% and 96.1% and not significantly different, while one of these suffered significantly greater mortality when fed wood decayed by *G. trabeum*. The third colony tested had a mean survival rate of approximately 10%, irrespective of the wood or fungal species. The amount of wood of both species removed by termites was significantly greater when decayed by either fungus. However decayed *P. ponderosa* was consumed at a higher rate than decayed *P. menziesii* or non-decayed controls. More non-decayed *P. menziesii* was removed than non-decayed *P. ponderosa*. A proportionally greater amount of wood was removed by termites as block size increased. Although colony differences were found, *R. hesperus* consumed more wood when it was decayed by either of these fungi.

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Introduction

Factors thought to affect the selection of a food source by termites in nature include both the species of wood and termite, as well as the moisture content, 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). Responses of species to environmental cues such as temperature and humidity may also be important variables. There is an increasing awareness of the high incidence of two fungi (i.e. *Gloeophylum trabeum* (Fr.) Murr. (formerly *Lenzites trabea*) and *Postia placenta* (Fr.) M. Lars and Lomb. (formerly *Poria monticola*) (Wilcox and Dietz 1997)), in wood structures in California (Wilcox and Dietz 1977). The relationships among *Reticulitermes hesperus* (Banks), these brown-rot fungi, and two wood species commonly used in buildings (i.e. *Pinus ponderosa* (Dougl. ex Laws) and *Pseudotsuga menziessi,* (Mirb.) Franco), was investigated in this study.

In North America wood-rotting fungi are estimated to comprise 1,700 species (Gilbertson 1980a). According to the type of decay they cause, they can also be separated into two groups, usually referred to as white-rot fungi and brown-rot fungi. Brown-rot fungi make up about 6 percent of the total species of wood-rotting Basidiomycetes in North America (Gilbertson 1981). Their basic role is the recycling of carbon from the atmosphere. They also 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 (1980b) has suggested that the greater rates of survival and development of termites in decayed wood were due to 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/or protozoa in their gut. It has been shown that termites can have a mutualistic relationship with fungi outside of the gut. Since energy is required for the break down of the stable cellulose molecule, fungal degradation of this carbohydrate has proven beneficial to termites (Gilbertson 1980b). How long the termite and fungus interact, and the species of termite and fungi all appear to affect the attraction, repellency and palatability of certain woods to the termites (Amburgey and Smythe 1977a; Becker 1971, 1976; Esenther and Coppel 1964; Gilbertson 1980b).

There may also be benefits to the fungi in their relationship with termites. Hendee (1933) proposed that termites are probably disseminators of fungi and their hyphae. In a study by Zoberi and Grace (1990), in which they tested forty species of fungi isolated from *R. flavipes* (Kollar) they found that termites passing through the soil, having body contact with other colony members, and through grooming or feeding behavior, could become contaminated with fungal propagules, and thus pass them on to other colony members. In addition, Lund (1960a) demonstrated that *Reticulitermes* spp. are able to infect sound wood with wood-rotting fungi.

Behavioral habituation, which "refers to a decrease in response to a stimulus occurring as the result of repeated or continuous exposure to that stimulus", may be a factor in the relationship between termites and fungi (Grace 1989). In a study of paper disks treated with extracts of *G. trabeum*, *R. flavipes* (Kollar) responded less over time to the semiochemical produced by *G. trabeum*, although the loss of chemical intensity was not a factor. Apparently, behavioral habituation of the termites resulted in a reduced response to the extract (Grace 1989).

Temperature appears to affect survival and the amount of decayed wood removed by termites (Lenz et al. 1982). Research generally indicates that the highest optimal temperature for *Heterotermes aureus* (Snyder) is 28°C (Haverty and Nutting 1974); however, the optimum may be as low as 20°C (Gilbertson 1980a). Lenz et al. (1991), found the optimal range to be 25°C to 27°C for *R. flavipes* while Becker (1969) indicates that, with few exceptions a temperature between 26°C and 28°C is, in general, most favorable for testing consumption rates of termites of decayed wood.

Species of wood and degree of decay also appear to affect termite growth. Hendee (1934, 1935) found that *R. hesperus* fed decayed Douglas-fir appeared "healthier" than those fed filter paper or sound Douglas-fir. In contrast to this finding, Smythe et al. (1971) demonstrated that *R. flavipes* workers fed ponderosa pine removed almost twice as much when fed non-decayed wood as compared to decayed wood. Survival on ponderosa pine was better when termites fed on oven-dried decayed wood compared to non-dried decayed wood. In another study, *R. flavipes* and *R.virginicus* (Banks) failed to survive on decayed ponderosa pine that was either oven-dried or non-dried (Smythe and Carter 1970). Becker (1948) indicated in choice tests, that *R. lucifugus* consumed more pine sapwood when decayed by *G. trabeum* than non-decayed sapwood. Termites fed on wood decayed by *G. trabeum* and *P. placenta* survived longer than on non-decayed controls (Lund 1960b).

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 more Douglas-fir than ponderosa pine. Termites also removed 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 further suggests that there are many factors at work during host choice and wood consumption, including 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. Lenz et al. (1991) and Becker (1965, 1976) discovered that *Pinus elliottii* Engelm., decayed in the range of 5% to 20% weight loss, was removed more by *R. flavipes*, than wood with a greater amount of decay. However, *R. flavipes* removed a larger amount of *P. ponderosa* with up to 30% weight loss due to decay by *G. trabeum* or *Poria incrassata* (Berk. and Curt.) Burt., than non-decayed wood (Amburgey and Smythe 1977b). Wood decayed by *G. trabeum* in the range of 6% to 12% weight loss, resulted in larger amounts of wood removed by *R. lucifugus* and *R. santonensis* in choice tests than in tests with less than 6% decay (Becker 1965). These studies demonstrate that the amount of wood removed by termites is variable and may or may not be associated with decay or the amount of decay.

Based on the accepted biogeographical information that only *R. hesperus* occurs in the Sierra Nevada (Nutting 1990), termites used in this study are all of one phenotype as characterized by their integumental hydrocarbons (Haverty and Nelson 1997). The present 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 termites determined to be *R. hesperus* by their cuticular hydrocarbon phenotype.

Materials and Methods

Wood. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were tested. Stocks of these species were obtained from the Forest Products Laboratory, University of California (FPL) from collections in Northern California. Three hundred and twenty two sample blocks of each species were cut tangentially into 2 x 2 x 0.5 cm pieces. All blocks for each species were cut from the same log. The blocks were stored on an open surface in a conditioning room at 12% m.c., 20°C, and 66% R.H. 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 x 15 x 10 mm (diameter) each containing an agar medium. Agar was prepared using 20 g of malt extract, 15 g agar and 1000 ml of distilled water and then autoclaved for 20 minutes. Seventy five agar plates were prepared in a sterile room at FPL. Approximately 15 ml of the above prepared agar was poured into each plate and allowed to set for twenty-four hours. Two separate groups were inoculated, one with *Gloeophylum trabeum* (Fr.) Murr. and the other with *P. placenta* (Fr.) M. Lars and Lomb. The inoculated plates were allowed to incubate for 10 to 14 days 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 for 20 minutes and then soaked in similarly autoclaved distilled water. Pine and fir blocks were exposed separately to either of two 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 to 8 weeks in a dark room at 27° C.

Wood decayed by *G. trabeum* required approximately four weeks to reach 10% to 15% weight loss while, *P. placenta* required approximately eight weeks. One block was randomly selected from all the dishes and removed periodically over each of the following weeks to determine weight losses caused by decay. When weight loss on a test block reached between 10% and 15%, all blocks were removed from the decay chambers. The hyphae were removed from the test block using a small toothbrush, and the blocks were returned to the conditioning room for 48 hours in order to equilibrate to a uniform temperature, moisture content and R.H. before weighing.

Feeding Interaction Tests. Round, 3 x 4 cm polystyrene containers filled with a mixture of sand, vermiculite and water (1:1:1 v/v) served as feeding chambers (Haverty 1979). Forty grams of the above mixture was placed in each sample container. A decayed wood block soaked in sterile distilled water for 2 minutes, and 200 termite workers, were added to complete the experimental unit. The experimental units were kept in a dark chamber for 4 weeks. Non-decayed blocks were submitted to the same procedures but without exposure to fungi, and used as controls. Six replications of each test were conducted for a total of 144 experimental units (Table 1).

Termites. 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 (IFG) near Placerville, California. IFG is located between Placerville and Camino, CA, at an elevation of about 775m (*ca.* 2,500 ft). The 50-year old plantation of mixed *Pinus* species encompasses approximately 4 hectares. Three distinct colonies, at least 200m apart, were collected and tested. Termite workers were also

weighed in groups of 200 to determine an approximate individual weight per termite.

Three colonies with the same cuticular hydrocarbon phenotype were tested. These colonies were labeled according to the area in which they were collected as colony #1, colony #2 and colony #3. The test containers were set up to allow continuous observation without significant disturbance to the termites during the 28 day 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 weeks 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 hours and returned to the 12% conditioning room for another 48 hours. They were subsequently weighed and the amount of wood loss determined.

Wood Removal Rate. The removal rate was determined in order to compensate for the effect of mortality over the time of the test. The removal rate is calculated from the average number of termites that were alive during the test period. The following formula was used:

(mg wood removed / (initial # termites/final # of termite)) x 0.5

Data Analysis. For each response variable (percent survival, total percent wood removed by termites, total mg wood removed by termites and mg wood removed per termite) an analysis of covariance (ANCOVA) (SAS Institute 1985) was conducted to assess the potential influence of the covariates, (a) decayed and non-decayed wood weight before feeding, (b) percent weight loss of wood, and (c) weight of wood before decay. Because

there were two significant covariates for percent wood removed by termites, an additional ANCOVA using these two covariates was conducted with both weight of wood before feeding but after decay and initial wood weight before feeding or decay as covariates to adjust for weight differences before decay and before feeding on the blocks. The dominant covariate was found to be initial weight of wood before feeding or decay and the ANCOVA for this covariate was used to assess the main effects and interactions for percent wood removed. The initial decayed wood weight before feeding was used to assess the main effects and interactions for the feeding rate. Except in wood removal rate for fungi treatment there were no statistical significant differences in the main effects. However, statistical significance in the treatment interactions was found.

Results

Colony Mortality. Foraging tunnels could be seen along the edges and bottom of the containers, and termites could be seen moving along these paths. 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/on the wood and out of view. By day 14 and thereafter, colony #2 termites were not visible upon daily inspection. Both colony #1 and colony #3 termites could be seen in at least one or more experimental containers on each day's inspection.

After the termites fed for 28 days, they were removed and the number of survivors counted. Colonies #1 and #3 were found to have a high mean percent survival of 96.1 and 89.5, respectfully (Table 2), 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

100% mortality and evidence of the dead termites was not apparent. Termite survivorship did not appear to depend on treatment; colony #1 and colony #3 had significantly higher numbers of survivors than colony #2 irrespective of fungi or wood species being tested 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 significant interaction between colony and fungus ($F = 5.53$; $df = 2, 62$; $P < 0.0062$), and because of this, the statistical significance of the main effects (colony, wood species, and fungal species) are not discussed (Table 2). When analyzing the mean percent survival amongst the interactions, the survival of colonies #1 and #3 were 94.7% and 92.8%, respectively (Table 2), when fed non-decayed blocks. Survival was 96.2% and 96.0% 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 the lowest survival (79.8%). This is likely the reason for the overall lower survival (88.6%) for the main effect of *G. trabeum* (Table 2). However, this was not significantly different from survival of termites on blocks decayed by *P. placenta*.

Weight (mg) Wood Removed. There was a significant interaction between colony and fungus ($F = 5.77$; $df = 2, 62$; $P < 0.0050$), therefore the statistical significance of the main effects will not be discussed. The least amount of wood in the interactions was removed from non-decayed blocks by either colony #1 (236.7 mg) or colony #3 (238.3 mg) (Table 2). When colonies

were fed on wood decayed by *P. placenta*, both removed the same average amount of wood during the test (306.7 mg). The amount of wood removed by colony #1 on *G. trabeum*-decayed wood (358.3 mg) was significantly more ($F = 5.77$; $df = 2$; $P < 0.0050$) than that for colony #3 (310.8 mg) confined to the same fungal treatment. These results are probably due to survival differences between the two colonies.

Percent Wood Removed. The main effects were not statistically significant while there was a statistically significant interaction ($F = 3.83$; $df = 2, 61$; $P < 0.0271$) between colony and fungi . Colony #1 and colony #3 both 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%, while colony #3 removed 26.9%. There was no significant difference in 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.

Wood Removal Rate. There was no statistically significant interaction between colonies and fungi on wood removal rate of *R. hesperus*. However, there was a statistically significant difference in wood removal rate between fungal treatments ($F = 62.80$; $df = 2, 62$; $P < 0.0001$) (Table 2). There was a significant difference in wood removal rate among the two fungal and their non-decayed wood treatments. This study showed that *G. trabeum* produced a higher feeding rate than *P. placenta*. Termites fed on *G. trabeum*-decayed wood had a rate of 1.77 mg/termite, while those fed on *P. placenta*-decayed wood had a rate of 1.55 mg/termite. Non-decayed wood blocks had a rate of 1.25 mg /termite.

Discussion

Toxic factors (Becker 1969), disease (Becker 1969), parasites (Becker 1965; Büchli 1952, 1960; Lund 1966), and colony characteristics such as size (Waller 1988; Lund 1966) or time of collection (Lund 1966; Becker 1969) can all be associated with high termite mortality in cultures and laboratory testing. Accidental inoculation of pathogenic fungi, such as *Aspergillus flavus* or *Trichoderma viride*, which has been found to grow rapidly on pinewood (Becker 1965), may explain the high mortality of colony #2. Lund (1966) found that in tests of *Lenzites trabea* Pers. ex Fr. and *Poria monticola* Murr., among others, dead termites appeared to be initiating points for fungal hyphal mats. Büchli (1952, 1960) found that fungal mycelia, (i.e. *Antennopsis* sp.) may enter living termites and cause their death, and possibly the eventual extinction of a colony. Also, bacteria such as *Serratia marcescens* var *kilensis* are pathogens of a number of different insects (Steinhaus 1963), especially the genus *Reticulitermes* (Lund 1966).

Termites that have been recently collected from the field, compared to colonies that have been in rearing chambers for some time, seem to be less tolerant of microorganisms that are pathogenic (Lund 1966; Becker 1969). Both colony #1 and #3 had been reared in the lab over a six month period while colony #2 was collected only thirty days prior to the initiation of these experiments.

The difference between colonies feeding on *G. trabeum*-decayed wood is likely due to the lower percent survival of colony #3 on *G. trabeum*-decayed wood (Table 2). Initial wood weight before decay appears to also have an effect on the amount of wood removed by termites during feeding. Generally, the larger the wood block size the more wood termites removed. In the laboratory, wood samples were cut by two individuals. The non-

decayed blocks had less variation in weight while blocks used for decay interactions had a greater initial weight range (Table 3). Although the wood blocks appeared similar in size, there were differences that may have influenced the results. However, the data show a proportional increase or decrease in feeding with the varying wood sizes.

Other researchers have found that the percentage of wood removed by termites increased with specimen size (Becker 1966; Howick and Creffield 1975; Akhtar and Jabeen 1981; Waller 1988; Becker and Lenz 1970). Akhtar and Jabeen (1981) found that mean weight losses were only significant for wood specimens 90 mm or greater in length. Samples in the present study were smaller than 90 mm, however.

Wood Removal Rate. Differences in feeding rate may be due to wood anatomy, amounts of nitrogen found in wood, or the role of symbionts. Cowling and Merrill (1966) concluded that there is a higher percentage of nitrogen nearer the cambium compared to the heartwood and sapwood interface. Nitrogenous compounds in wood are, however, quantitatively minimal. The nitrogen content can be increased by the presence of fungi (Becker 1971). Even a slight amount of deterioration by fungi increases the nutritional value of wood for insects (Becker 1948; Light and Weesner 1947). Results from the present study clearly demonstrate that more wood per termite was removed when wood had been decayed by either of two fungi than wood compared to non-decayed wood (Table 2). Possibly, the presence of fungi in the wood leads to an increase in available nitrogen (Moore 1969), enabling more rapid growth and/or feeding rate of termites.

Statistically significant interactions between decay fungi and colonies of the same species were found in this study. Thus the results obtained on one species may not be comparable for other species, unless sufficient

replication among colonies of the same species is examined. This may account, in part, for the variation in results obtained by other workers (Smythe et al. 1971; Waller 1988)

Table 1. Experimental design to test the effect of fungal decay on consumption rates of three separate colonies of *Reticulitermes* sp. (hydrocarbon phenotype "A").

Fungus and Degree of Decay	Colony	Wood Species: Ponderosa Pine	Wood Species: Douglas-fir
Gloeophyllum trabeum			
Non-decayed Controls			
	Colony #1	six replications	six replications
	Colony #2	six replications	six replications
	Colony #3	six replications	six replications
Decayed (10% to 15% weight loss)			
	Colony #1	six replications	six replications
	Colony #2	six replications	six replications
	Colony #3	six replications	six replications
Postia placenta			
Non-decayed Controls			
	Colony #1	six replications	six replications
	Colony #2	six replications	six replications
	Colony #3	six replications	six replications
Decayed (10% to 15% weight loss)			
	Colony #1	six replications	six replications
	Colony #2	six replications	six replications
	Colony #3	six replications	six replications

Table 2. Mean (standard error) percent survival, mg wood removed, percent wood removed, and wood removal rate (mg/termite) of experimental groups of 200 workers of one of two colonies of *Reticulitermes hesperus* fed one of two species of wood non-decayed or decayed by one of two brown-rot fungi. Duration of test was 28 days.[a, b]

	% Survival[c,d]	mg wood removed[c,d]	% wood removed[c,d]	Wood Removal Rate[c]
Colony (*n*=36)				
colony #1	96.1 (1.67)a	300.6 (4.74)a	26.4 (0.46)a	1.52 (0.028)a
colony #3	89.5 (1.67)a	285.3 (4.74)a	24.6 (0.46)a	1.53 (0.028)a
Wood Species (*n*=36)				
Ponderosa Pine	94.5 (1.67)a	290.0 (4.74)a	27.0 (0.85)a	1.58 (0.051)a
Douglas-fir	91.2 (1.67)a	295.8 (4.74)a	24.1 (0.85)a	1.46 (0.051)a
Fungal Treatment (*n*=24)				
Gloeophylum trabeum	88.6 (2.05)a	334.6 (5.81)a	29.2 (0.55)a	1.77 (0.034)a
Postia placenta	96.1 (2.05)a	306.7 (5.81)a	27.8 (0.55)a	1.55 (0.034)b
Control	93.7 (2.05)a	237.5 (5.81)a	19.4 (0.57)a	1.25 (0.035)c
Interactions[d] (*n*=12)				
colony #1 x *Gloeophylum trabeum*	97.5 (2.90)a	358.3 (8.22)a	31.5 (0.78)a	1.77 (0.050)a
colony #1 x *Postia placenta*	96.2 (2.90)a	306.7 (8.22)b	28.3 (0.77)b	1.54 (0.048)b
colony #1 x control	94.7 (2.90)a	236.7 (8.22)c	19.5 (0.78)c	1.24 (0.049)c
colony #3 x *Gloeophylum trabeum*	79.8 (2.90)b	310.8 (8.22)b	26.9 (0.83)b	1.76 (0.047)a
colony #3 x *Postia placenta*	96.0 (2.90)a	306.7 (8.22)b	27.5 (0.79)b	1.56 (0.047)b
colony #3 x control	92.8 (2.90)a	238.3 (8.22)c	19.4 (0.79)c	1.26 (0.048)c

[a] Each combination of factors (colony x wood species x fungal treatment) was replicated 6 times.

[b] 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 test (SAS Institute 1985).

[c] Analysis of covariance indicated a statistically significant influence ($p<0.05$) of wood weight before feeding for % wood removed and initial wood weight for wood removal rate. No significant covariate was found for % survival or mg wood removed. The reported means for % wood removed and wood removal rate are reported at the overall average of the covariate.

[d] 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/among main effect means was not tested.

Table 3. Range of beginning wood weight (mg) for decayed and control blocks.

	Decayed Blocks		Non-decayed Controls		% Difference Decayed vs. Non-decayed
Wood Species	Weight Range	mg Difference	Weight Range	mg Difference	
Ponderosa pine	810-1140	330	1340-1410	70	79%
Douglas-fir	1370-2140	770	1150-1220	70	91%
% Difference Between Wood		57%		0%	

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