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BEHAVIOR AND SURVIVAL OF *Reticulitermes hesperus* BANKS (ISOPTERA: RHINOTERMITIDAE) ON SELECTED SAWDUSTS AND WOOD EXTRACTS

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Abstract—Survival of *Reticulitermes hesperus* workers was assessed in *Pseudotsuga menziesii*, *Lysiloma seemanii*, and *Tabebuia ochracea* sawdusts; and on heartwood solvent extracts of *P. menziesii*, *L. seemanii*, *T. ochracea*, *Pinus ponderosa*, *Tabebuia guayacan*, and a *Centrolobium* species. Survival in *P. menziesii* sawdust was 100% at 5 days and 81–87% at 15 days. Survival in *L. seemanii* and *T. ochracea* sawdusts was significantly less over both 5 and 15 days than in the starvation control, indicating toxicity. Survival on filter papers treated with solvent extracts of *T. ochracea* and *P. ponderosa* was significantly less than that on control papers, but only *P. ponderosa* differed significantly from the starvation control. In behavioral assays with groups and with individual *R. hesperus* workers, extracts of *P. menziesii* and *P. ponderosa* were preferred. In the individual behavioral assays, extracts of *T. guayacan* and *T. ochracea* were repellent. Results of toxicity assays were not predictable from preference assays.

Key Words—*Reticulitermes hesperus*, Isoptera, Rhinotermitidae, termite feeding behavior, termite bioassay, tropical hardwoods, wood extractives.

INTRODUCTION

Subterranean termites in the genus *Reticulitermes* (Isoptera: Rhinotermitidae) are important structural pests throughout North America. Along the Pacific coast, *Reticulitermes hesperus* Banks is the most destructive species (Weesner, 1965; Ebeling, 1975). Currently, use of preservative-treated wood and soil treatment with insecticides are the principal methods used to prevent or control subterranean termite damage.

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Naturally occurring toxicants and semiochemicals (e.g., attractants, arrestants, repellents, feeding deterrents, and feeding stimulants) may offer safer alternatives to the current reliance upon insecticidal treatments. Extractives from termite-resistant woods have been under investigation for many years (Wolcott, 1924) and offer some promise as protective treatments for nonresistant woods (Carter and Beal, 1982). However, Smythe and Carter (1970) demonstrated that different termite species may respond differently to sawdust from the same tree species, requiring that all target termite species be investigated. Despite the economic importance of *R. hesperus*, the feeding responses of this species to different woods have not previously been studied. In addition, there has been little evaluation of behavioral (as opposed to toxic) effects associated with termite-resistant woods. As with feeding responses, chemical stimuli may elicit quite different behavioral responses in different termite species (Becker et al., 1972).

In the present study, investigations were conducted on the survival and behavior of *R. hesperus* workers on wood of a North American conifer readily fed upon by termites, and wood of five tree species thought likely to possess some resistance to termite feeding. Bioassays were designed to examine the relative importance of behavioral and toxicological factors in termite feeding and survival on these species. The behavioral responses of both groups and individual *R. hesperus* workers were determined.

Woods of six tree species were evaluated. Two of these, *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus ponderosa* Dougl. ex Laws., are softwoods (Family Pinaceae) of North American origin. The other four species are Central American hardwoods: *Centrolobium* sp. (Leguminosae), *Lysiloma seemanii* Britt. & Rose (Leguminosae, subfamily Mimosaceae), *Tabebuia guayacan* (Seem.) Hemsl. (Bignoniaceae), and *Tabebuia ochracea* (Cham.) Standl.

P. menziesii and *P. ponderosa* are, respectively, the first and second most important timber-producing tree species in North America (Harlow et al., 1979). *P. menziesii* is used extensively for house construction in California, and the three termite colonies used in our experiments were collected from Douglas-fir lumber. In studies with other termite species (Carter, 1976; Carter and Smythe, 1974; Smythe and Carter, 1970), *P. menziesii* heartwood and sapwood have been found to promote termite feeding and survival. These same studies have shown *P. ponderosa* heartwood to be detrimental to termite feeding and survival.

One of the four tropical hardwood species, *T. guayacan*, resists subterranean termite attack in field tests with heartwood stakes (Bultman and Southwell, 1976) and has been found to reduce survival of the termites *Coptotermes formosanus* Shiraki and *Reticulitermes flavipes* (Kollar) (Beal et al., 1974), as have congeners of the other hardwood species (Beal et al., 1974; Wolcott, 1950). Selection of these four particular tropical hardwoods from the great number of possibly termite-resistant species was due in part to convenience. The heartwoods of *T. guayacan* and *Centrolobium* sp. were already under chemical investigation (Jurd and Wong, 1984), and solvent extracts were available for biological assays. The other two tree species, *L. seemanii* and *T. ochracea*, are abundant in Guanacaste Province, Costa Rica, and were collected there in conjunction with other studies (Frankie et al., 1983). These species were selected before their collection by correlating an extensive study of Costa Rican tree phenology (Frankie et al., 1974) with the available literature on termite resistance, especially Beal et al. (1974), Carter (1976), and Wolcott (1950). Their abundance in Guanacaste Province suggests resistance to the structural damage caused by termites feeding on the heartwood of living trees, a common occurrence in the tropics (Sen-Sarma, 1986). Although not harvested commercially, these woods are locally reputed to be termite and decay resistant (GWF, unpublished observation).

In termite-infested buildings, differential feeding by termites on apparently identical timbers is frequently observed by researchers and pest-control personnel (Kofoid and Bowe, 1934). To examine whether *R. hesperus* workers responded differently to adjacent structural timbers exhibiting different amounts of feeding, we included sawdust from field-collected *P. menziesii* timbers in the survival assays.

METHODS AND MATERIALS

Source of Insects. Western subterranean termites, *R. hesperus*, were collected from three sites in Alameda County, California. One colony (Berkeley) was removed from a Douglas-fir, *P. menziesii*, form board embedded in the soil beside a residential driveway in the city of Berkeley, the second (Gilman) from infested Douglas-fir wall framing in a residence in Berkeley, and the third (Oakland) from infested Douglas-fir floor joists in a residence in the city of Oakland. Termites were removed from the wood and kept in separate groups in plastic trays at room temperature (21–25°C) in a humidity chamber (94 ± 5% relative humidity) (Grace, 1986). Only workers (pseudergates, or undifferentiated individuals older than the third instar as determined by size), were used in assays due to their predominance in foraging activities.

Preparation of Sawdusts and Wood Extracts. Solvent extracts of the heartwood of *P. menziesii*, *P. ponderosa*, *T. guayacan*, and *Centrolobium* sp. were provided by L. Jurd and G.D. Manners (Western Regional Research Center, USDA, ARS, Albany, California). These woods were purchased from local merchants in California, and the *Centrolobium* species could not be identified to species by the United States Forest Products Laboratory in Madison, Wisconsin (L. Jurd, personal communication). Dried concentrates from five-day continuous acetone extraction in a Soxhlet apparatus were diluted 1 g/10 ml acetone. Due to crystaline insolubility, *P. menziesii* extract was diluted in equal parts $CH_3OH:CHCl_3$.

L. seemanii and *T. ochracea* heartwoods, collected in Costa Rica, were ground in a Wiley mill (40-mesh screen), and 200 g of each sawdust was extracted by soaking in methanol at room temperature (21–25°C) for seven days. The resulting filtrates were concentrated by rotary evaporation and desiccation under vacuum, yielding ca. 10 g *L. seemanii* and 17 g *T. ochracea* dry extracts, which were diluted 1 g/10 ml methanol.

Survival in Douglar-Fir Sawdust. Samples of the timbers from which the *P. menziesii* solvent extracts were prepared were not available, and a separate experiment was designed with two field-collected *P. menziesii* samples. These samples were from two adjacent floor joists in a severely infested house where the Oakland colony was collected. One of these timbers had been extensively tunneled by termites, while the other exhibited only minor tunneling. Excluding the tunneled areas, such sample (heartwood plus sapwood) was reduced to sawdust in a Wiley mill (40-mesh screen).

The assay consisted of an open, 40-mm × 27-mm bottom diam. × 37-mm top diam., ca. 30-ml (1 US fluid oz., Anchor Hocking No. 5175) plastic cup containing 2 g of sawdust, 2 ml steam-distilled water, and 40 *R. hesperus* workers from the Oakland colony. These cups were placed in a humidity chamber, and termite mortality recorded by gently removing and replacing the contents of each cup at 5 and 45 days. This assay was replicated six times with each of the two *P. menziesii* samples.

Survival in Hardwood Sawdusts. Of the six woods used in this study, only samples of the unextracted heartwood of *L. seemanii* and *T. ochracea* were available, since the others were provided in the form of solvent extracts. These two species were reduced to sawdust and assayed as described above for *P. menziesii* sawdust, except that mortality of Oakland workers was recorded at 5, 15, and 45 days. Each substrate was tested with three groups of 40 termites. Alpha-cellulose (Alphacel, Nutritional Biochemicals Corp., Cleveland, Ohio) was included as a feeding control. A starvation control with 2 g white sand in lieu of sawdust was performed under the same experimental conditions, although not simultaneously with the other substrates.

Survival on Wood Extracts. Survival on filter papers treated with solvent extracts of the six woods was assayed in a manner comparable to that used with sawdusts. A 25-mm-diam. Whatman No. 1 filter paper disk was saturated with 100 μl of wood extract (diluted 1 g/10 ml solvent). Each feeding substrate thus consisted of ca. 18% wood extractives by weight. Treated disks were air-dried ca. 20 min, and placed in an open 30-ml plastic cup with 40 Oakland workers. The cups were placed in a humidity chamber and termite mortality recorded at 5, 15, and 45 days. Each wood extract was tested with three groups of termites.

Starvation (no filter paper) and feeding (filter papers treated with methanol only) controls were included in the experiment.

Group Behavioral Responses. Preference (either attraction or arrestment) or repellence of groups of 10 *R. hesperus* workers (Berkeley and Gilman colonies) in response to wood extracts was measured in an assay similar to that used by Amburgey and Smythe (1977) to assess termite responses to solvent extracts of fungus-decayed wood. A 9-cm-diam. Whatman No. 1 filter paper disk treated with 1 ml wood extract (sufficient to saturate the disk), equivalent to ca. 15% extractives by weight, and air-dried ca. 20 min was cut in half and each half taped to one half of a solvent-treated paper disk. Each reconstituted two-choice disk was placed in an open glass Petri dish, uniformly illuminated by overhead fluorescent lighting (13.5–19.5 foot-candles) at room temperature (21–24°C). Five *R. hesperus* workers were gently deposited onto each half of the disk. The number of termites (in the group of 10) on the extract-treated half of the disk was recorded every 30 sec for 20 min.

The behavioral response of the group was calculated as the number of times more than five insects were recorded on the extract-treated half-disk, divided by the number of times more than five insects were recorded on either half-disk. This index of preference thus indicated the proportion of time spent on the extract-treated half-disk by the majority of each group of 10 termite workers. Each assay was replicated eight times, and the mean proportional response computed for each wood extract. Control assays using half-disks treated only with methanol were also performed.

Individual Behavioral Responses. Behavior of individual workers (Gilman and Oakland colonies) was measured similarly to group behavior. An 18-mm-diam. Whatman No. 1 filter paper disk was saturated with 40 μl wood extract (ca. 15% extractives by weight), air-dried ca. 20 min, and paired with a solvent-treated disk in an open 5-cm-diam. glass Petri dish under uniform overhead lighting. A single *R. hesperus* worker was placed on the glass between the two disks, and its position on either (or neither) disk recorded every 30 sec for 20 min.

The behavioral response of each individual was calculated as the number of times it was recorded on the extract-treated disk divided by the number of times it was recorded on either disk. Again, this index of preference indicated the proportion of time spent on the extract-treated disk by the worker. A mean proportional response was computed from 50 individual assays with each wood extract. As in the group assays, control assays with two disks treated only with solvent (methanol) were also performed.

Statistical Analyses. Termite survivorship was analyzed with standard *t* test and analysis of variance (ANOVA) techniques, and means were compared with the Ryan-Einot-Gabriel-Welsch (REGW) multiple F Test ($\alpha \leq 0.05$) (SAS Institute, 1982). In the behavioral assays, the mean proportional responses of groups and of individual termites to wood extracts were tested against the mean response of 0.50 expected under the null hypothesis of no effect (two-tail *t* test, $\alpha \leq 0.05$) (Dixon and Massey, 1983).

RESULTS AND DISCUSSION

Survival in Douglas-Fir Sawdust. Termite survivorship over 45 days was uniformly high and not significantly different (*t* test, $P = 0.06$) in sawdust from *P. menziesii* samples exhibiting either minor (81 ± 6% surviving) or extensive (87 ± 4% surviving) prior tunneling by the same *R. hesperus* colony. Survivorship at five days was 100% for workers in both treatments. These data do not support the hypothesis that the pattern of selective termite infestation observed in the field can be attributed to differential survival in the two timbers. Smythe and Carter (1970), however, demonstrated that differences do exist within tree species of different geographic origin that influence feeding by *R. flavipes*.

The overall high survivorship (range = 73–90%) of *R. hesperus* in *P. menziesii* sawdust is comparable to the high survivorship previously reported for *R. flavipes* (Carter, 1976; Carter and Smythe, 1974; Smythe and Carter, 1970) and *Incisitermes minor* (Hagen) (Kofoid and Bowe, 1934; Rust and Reierson, 1977) on blocks and sawdusts of this tree species. In contrast, Smythe and Carter (1970) reported poor survival (0–8%) in groups of *Reticulitermes virginicus* Banks on *P. menziesii* heartwood blocks.

Survival in Hardwood Sawdusts. Very few of the workers fed sawdust from either of the two Costa Rican hardwoods *L. seemanii* or *T. ochracea* survived 15 days, and none survived 45 days (Table 1). Mortality in *T. ochracea* sawdust at five days was significantly different from and greater than that in

TABLE 1. PERCENT SURVIVAL OF *Reticulitermes hesperus* WORKERS IN HEARTWOOD SAWDUST OF TWO COSTA RICAN TREE SPECIES

	Mean survival (% ± SEM)[a]		
Substrate	5 days	15 days	45 days
Lysiloma seemanii	35 ± 11b	2 ± 2b	0b
Tabebuia ochracea	5 ± 4c	0b	0b
α-Cellulose	100 ± 0a	100 ± 0a	74 ± 3a
Starvation Control	99 ± 1a	97 ± 3a	0b

[a] Mean of three groups of 40 *R. hesperus* workers. Means in the same column followed by different letters are significantly different (ANOVA, REGW multiple *F* test, $\alpha \leq 0.05$).

L. seemanii sawdust, and mortality in both sawdusts differed significantly from that observed in the starvation control. Mortality can thus be attributed to toxicity of the woods rather than feeding deterrence alone, since 15-day survivorship in the sand starvation control was very high (97 ± 3%) and did not differ significantly from the α-cellulose feeding control (100 ± 0%).

Survival on Wood Extracts. Survivorship after five days on filter papers treated with each of the six wood extracts (Table 2) was 96–100% and did not differ significantly from survivorship in either the solvent (99 ± 1%) or starvation (100 ± 0%) controls. At 15 days, only survivorship on papers treated with extracts of *T. ochracea* (55 ± 11%) and *P. ponderosa* (27 ± 19%) heartwoods differed significantly from the solvent control (98 ± 2%), and only *P. ponderosa* differed from the starvation control (78 ± 12%). Thus, toxic materials in *P. ponderosa* were extracted in acetone, and toxicants and/or feeding deterrents in *T. ochracea* were extracted in methanol. Compounds extracted from *P. ponderosa* sawdust with a mixture of acetone, hexane, and water have also been found to reduce the survival of *R. flavipes* (Carter, 1976).

The poor survivorship of *R. hesperus* on *T. ochracea* extracts corresponds with the toxicity of the *T. ochracea* sawdust, although the much greater mortality observed in the sawdust assays (Table 1) suggests incomplete extraction of toxicants from both *T. ochracea* and *L. seemanii*. Mortality was virtually complete in all treatments but the solvent control at 45 days (Table 2), and extraction of feeding deterrents from all six woods is supported by the observation that only the control disks had been extensively fed upon. In two-choice feeding assays with the drywood termite *I. minor*, Rust and Reierson (1977) observed that filter papers treated with methanol extracts of various woods,

TABLE 2. PERCENT SURVIVAL OF *Reticulitermes hesperus* WORKERS ON FILTER PAPERS TREATED WITH WOOD EXTRACTS

Extract	Mean survival (% ± SEM)[a]		
	5 days	15 days	45 days
Centrolobium sp.	100 ± 0a	99 ± 1a	26 ± 26b
Lysiloma seemanii	96 ± 2a	95 ± 1ab	1 ± 1b
Pinus ponderosa	100 ± 0a	27 ± 19c	0b
Pseudotsuga menziesii	97 ± 0a	60 ± 7abc	0b
Tabebuia guayacan	100 ± 0a	72 ± 11abc	0b
Tabebuia ochracea	97 ± 1a	55 ± 11bc	0b
Solvent control	99 ± 1a	98 ± 2a	98 ± 2a
Starvation control	100 ± 0a	78 ± 12ab	0b

[a] Mean of three groups of 40 *R. hesperus* workers. Means in the same column followed by different letters are significantly different (ANOVA, REGW multiple *F* test, $\alpha \leq 0.05$).

including *P. menziesii* and *P. ponderosa*, were not fed upon in favor of untreated or solvent-treated papers.

Group Behavioral Responses. In behavioral assays with groups of ten *R. hesperus* workers (Table 3), only the responses to extracts of *P. menziesii* and *P. ponderosa* differed significantly from the 50% response expected under the null hypothesis of no effect (t test, $\alpha \leq 0.05$). In both cases, these were positive responses, suggesting a behavioral preference for filter papers treated with these extracts. Although not differentiated in this assay, such a preference could result either from attraction to the extract-treated papers (orientation to airborne volatiles) or from arrestment after contact (cessation of locomotion), or from a combination of the two behaviors.

Individual Behavioral Responses. The responses of individual workers (Table 3) to extracts of *P. menziesii* and *P. ponderosa* also differed significantly and positively from the no-effect null hypothesis. In these individual assays, the behavioral responses to extracts of *T. guayacan* and *T. ochracea* were also significant, but in a negative direction. Methanol extracts of *T. ochracea* thus appear to contain repellents, in addition to toxic and/or antifeedant materials. The response of *R. hesperus* workers to *P. ponderosa* extract, on the other hand, suggests the presence of positive allelochemical stimuli in addition to toxicants.

Lapachol is considered to be an antitermitic agent in *T. guayacan* (Bultman

TABLE 3. BEHAVIORAL RESPONSES OF GROUPS AND OF INDIVIDUAL *Reticulitermes hesperus* WORKERS TO FILTER PAPERS TREATED WITH WOOD EXTRACTS

	Mean proportional response (±SEM)[a]	
Extract	Group assays[b]	Individual assays[c]
Centrolobium sp.	0.48 ± 0.08	0.46 ± 0.03
Lysiloma seemanii	0.51 ± 0.06	0.44 ± 0.04
Pinus ponderosa	0.73 ± 0.12[d]	0.73 ± 0.04[d]
Pseudotsuga menziesii	0.78 ± 0.16[d]	0.69 ± 0.03[d]
Tabebuia guayacan	0.52 ± 0.14	0.41 ± 0.04[d]
Tabebuia ochracea	0.58 ± 0.06	0.30 ± 0.04[d]
Solvent control	0.36 ± 0.09	0.48 ± 0.05

[a] Proportional response indicates the proportion of time spent by the majority of the group or by an individual worker on an extract-treated paper rather than on a solvent-treated control paper in a 20-min, two-choice assay. In the solvent control assays, a "treatment" paper was designated at random.

[b] Mean of eight groups of 10 *R. hesperus* workers.

[c] Mean of 50 assays with individual *R. hesperus* workers.

[d] Mean proportional response is significantly different from the expected mean of 0.50 under the null hypothesis (two-tail t test, $\alpha = 0.05$).

and Southwell, 1976; Kukachka, 1970). Becker et al. (1972) found that this compound was repellent to *Microcerotermes crassus* Snyder, and possibly repellent to *Kalotermes flavicollis* (Fabr.), but did not repel the other 12 termite species tested, including three species of *Reticulitermes*. Lapachonone, however, isolated from other *Tabebuia* species, was repellent to 10 termite species, including *R. flavipes*, *Reticulitermes lucifigus* (Rossi), and *Reticulitermes santonensis* Feytaud (Becker et al., 1972).

Several studies have indicated that termites from different colonies may respond differently in bioassays (Carter et al., 1972; Lenz, 1985; Su and LaFage, 1984). Since different *R. hesperus* colonies were used in our behavioral assays with groups and with individual termites, we can make no inferences from these experiments on individual versus group behavior. Problems are apparent, however, with both types of behavioral assays. Rather than averaging individual responses in a single measure of group behavior, or measuring the responses of single termites within the artificial context of an individual assay, an alternative approach of current interest to us is to record the responses of individual termites within the context of a group assay.

CONCLUSIONS

The chemical nature and biological activity of wood extractives have been investigated with respect to termites for over 60 years. Most of this work has utilized tropical hardwoods, with the aim of identifying more resistant building materials (Bultman et al., 1979; Su and Tamashiro, 1986) or isolating toxins or antifeedants that could be applied to susceptible lumber to increase termite resistance (Carter and Beal, 1982).

Only a few researchers (e.g., Carter and Mauldin, 1981; Carter et al., 1983) have investigated behavioral responses to wood extractives in conjunction with feeding assays. Varma et al. (1984) also investigated the attractiveness of extracts of plant materials to *Odontotermes guptai*. It is hoped that the extraction, and subsequent isolation and identification, of behaviorally active compounds from susceptible and resistant woods will contribute to the development of new techniques of behavioral termite control, such as the use of baits (Esenther and Beal, 1979), rather than simply replacing current wood preservatives and insecticides with naturally occurring toxicants.

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