Black-Staining Fungus Effects on the Natural Resistance Properties of Alaskan Yellow Cedar to the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT The effects of a black wood stain, caused by one or more fungi, on the natural resistance of Alaskan yellow cedar (AYC), *Chamacyparis nootkatensis* (D. Don) Spach, to the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, were studied. Feeding and survival of groups of 300 *C. formosanus* feeding on unstained Alaskan yellow cedar heartwood and sapwood and fully and partially black-stained heartwood were compared with a control group feeding on loblolly pine, *Pinus taeda* L., wood. All termite groups feeding on unstained AYC died by the end of 14 wk. At the end of 32 wk, mortality of termite groups feeding on fully and partially black-stained AYC was significantly higher than that of groups feeding on pine. Termite mortality was significantly higher when feeding on partially than on fully black-stained AYC at the end of 32 wk. Wood consumption was significantly different among all treatment groups, with means of 4.07, 8.76, 19.81, and 29.77 mg/d in the unstained, partially, and fully black-stained AYC, and loblolly pine, respectively. This suggests that toxic and feeding deterrence properties of AYC heartwood were significantly reduced by black-staining fungus infection but were not totally lost. Chemical analysis of unstained and black-stained AYC wood showed approximately a 50% reduction in concentration of secondary chemicals in the black-stained wood. Carvacrol was totally absent in the black-stained wood. Concentrations of nootkatone in the black-stained wood were one-fourth of those observed in unstained AYC wood. Ecological implications are discussed.

KEY WORDS *Coptotermes formosanus*, feeding deterrence, *Chamacyparis nootkatensis*, nootkatone, wood chemistry

THE HEARTWOOD OF ALASKAN yellow cedar, *Chamaecyparis nootkatensis* (D. Don) Spach., also known as yellow cypress, possesses characteristics that give it natural resistance against the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) (Grace 1994, Morales-Ramos and Rojas 2001). The Formosan subterranean termite native of China (Kistner 1985) was introduced into the United States after the end of World War II (Beal 1987). Since then, this termite has become one of the most destructive household pests in the southern United States, causing millions of dollars in damage annually (Su and Tamashiro 1987, Su and Scheffrahn 1990, 1998). The Formosan subterranean termite is more destructive than native subterranean termites (*Reticulitermes* spp.) because of the larger colonies and foraging areas (Su and Tamashiro 1987, Su and Scheffrahn 1988).

Alaskan yellow cedar heartwood induced mortality and feeding deterrence in Formosan subterranean termite workers in no-choice feeding tests (Morales-Ramos and Rojas 2001). Alaskan yellow cedar heartwood possesses a complex chemistry, but the predominant compounds include carvacrol, nootkatin, chanootin, nootkatone, chamic acid, and chaminic acid (Carlsson et al. 1952, Erdtman and Topliss 1957, Barton 1976). The sesquiterpene nootkatone possesses toxic, repellent, and feeding deterrent effects on the Formosan subterranean termite (Maistrello et al. 2001, Zhu et al. 2001). In addition, this compound affects microbial symbionts of termites. Formosan subterranean termite workers feeding on blocks of balsa wood (*Ochroma lagopus* Swartz) treated with a 1% alcohol solution of nootkatone showed ≈95% reduction in gut counts of the symbiotic flagellate *Pseudotrichonympha grassii* Koidzumi compared with nontreated controls (Maistrello et al. 2001). These characteristics make Alaskan yellow cedar an excellent candidate to be used in the construction of homes in Formosan subterranean termite-infested areas.

The heartwood of Alaskan yellow cedar is resistant to degradation by fungi (Harris 1971). However, some species of fungi producing black stain are found in the heartwood of live Alaskan yellow cedar trees (Smith 1970). Unfortunately, fungi producing black stain in

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Alaskan yellow cedar heartwood remain unidentified. However, a number of black-colored fungi have been isolated from Alaskan yellow cedar sapwood (Hennon 1990), some of which degrade the tropolone nootkatin and infect the heartwood (Smith and Cserjesi 1970). This stained heartwood of Alaskan yellow cedar should not be confused with the tree-killing black stain root disease of conifers in the Pacific Northwest caused by *Leptographium wageneri* (Kendrick) Wingfield (Harrington and Cobb 1988).

Recent observations of black-staining fungi in Alaska provide one hypothesis about how these fungi become established in the wood of Alaskan yellow cedar (P.E.H., unpublished data). The pattern of stain suggests that these fungi invade sapwood before it is converted to heartwood. Cross-sections of infected trees reveal narrow (e.g., 1.5–2 cm wide radially) bands of black-stained wood with variable circumferential widths that follow growth rings. The radial dimensions are consistent with the sapwood width for these trees (Hennon et al. 2000). These stain patterns can be found near the cambium or buried proximally toward the pith in the heartwood, but their radial dimensions are distinctive. The long, thin vertical development of black stain described by Smith (1970) is also consistent with sapwood colonization.

Attempts to isolate fungi from these black-stained bands have produced several fungi, most commonly *Sporidesmium* sp. and *Phialophora melinii (*Nannf.) Conant. The former fungus is of particular interest because its color in culture is nearly identical to the bluish-black stain observed in heartwood. These species are likely some that are among the fungi isolated, but not identified, by Smith (1970). These staining fungi likely enter trees through wounds and dead branches (Smith 1970). The stained heartwood in Alaskan yellow cedar trees in Alaska also frequently contains small holes bored by a woodwasp (*Sirex juvencus* L.) (Smith and Schiff 2002), indicating that this insect may be transmitting the stain fungus. This association is also currently under study.

If these black-colored fungi do invade sapwood rather than heartwood, it is conceivable that they interfere with the deposition of normal heartwood constituents as sapwood is converted to heartwood.

Because black-staining fungi may degrade nootkatin, it is possible that these fungi can also degrade other chemicals, such as nootkatone. Degradation of secondary chemicals of Alaskan yellow cedar heartwood may compromise its insect resistance properties. Regardless of whether these fungi limit the initial development of compounds or actually degrade them, understanding the effects of black-staining fungi on the insect resistance properties of Alaskan yellow cedar is of great importance for its application. The objectives of this study were to determine if black-staining fungi alter the susceptibility of Alaskan yellow cedar heartwood to feeding by the Formosan subterranean termite and to quantify any changes in wood chemistry associated with fungal infection.

Materials and Methods

Natural Resistance Evaluation. Portions of Formosan subterranean termite nests were collected from three different locations within the New Orleans metropolitan area. Three different nests were collected: one from New Orleans City Park in June 1998, one from a house in the suburb of Gretna in August 2000, and one from a sweet gum tree near New Orleans art museum in February 2001. Each collection site was separated by a distance of at least 2 km from each other. The nests were kept in 30-gal polyethylene shipping containers (Delex UN/1H2/Y180; United States Plastics, Lima, OH) in a room held at 25–30°C and 50–80% RH.

Termites were extracted from the collected field colonies by exposing soaked pieces of corrugated cardboard to the termite-holding containers for 6–24 h. The pieces of cardboard were taken to the laboratory, where termites were extracted and counted using an aspirator connected to a vacuum source. Groups of 250 workers and 50 soldiers of *C. formosanus* were placed in bioassay arenas containing nesting and foraging areas. The arenas were constructed by gluing two, 150-mm diameter petri dishes to one another, lid to bottom, and connecting the two dishes with a central hole as reported by Morales-Ramos and Rojas (2001). The nesting dish (bottom) was filled with 200 ml of a mixture (1:1) of sand and topsoil, 100 ml of distilled water, and 1 g of water-absorbing polymer (cross-linked potassium polyacrylate/polyacrylamide copolymer, T-400; Terawet, San Diego, CA). The foraging dish (top) provided space for presenting the food treatment to the termites.

Food treatments consisted of unstained Alaskan yellow cedar heartwood, unstained Alaskan yellow cedar sapwood, partially black-stained Alaskan yellow cedar heartwood, fully black-stained Alaskan yellow cedar heartwood, and loblolly pine (*Pinus taeda* L.) (LoP) as a control. The criterion to differentiate partially versus fully black-stained wood was based on presence or absence of healthy tissue. Partially black-stained samples contained a mixture of healthy and infected tissue. Fully black-stained samples contained only infected tissue. Black-stained wood samples were taken from five different trees and unstained wood samples from seven different trees from Vancouver Island, Canada. Wood samples were donated by the Coast Forest and Lumber Association, Vancouver, British Columbia, Canada. Wood samples were taken from a commercial shipment of wood received in New Orleans, LA, by Riverside Lumber.

Each treatment was replicated 30 times. A total of 180 blocks (30 by 15 by 7 mm) were cut from each treatment wood. The blocks were dried (vacuum oven, 58°C temperature, −51 Hg cm pressure) for 24 h, stabilized in an environmental chamber (Percival I-36VL; Percival Scientific, Boone, IA) at 27 ± 1°C and 95% RH for 30 min, and weighed in a precision balance (Toledo AB204; Mettler, Greifensee, Switzerland). The dishes containing the termite groups were kept at

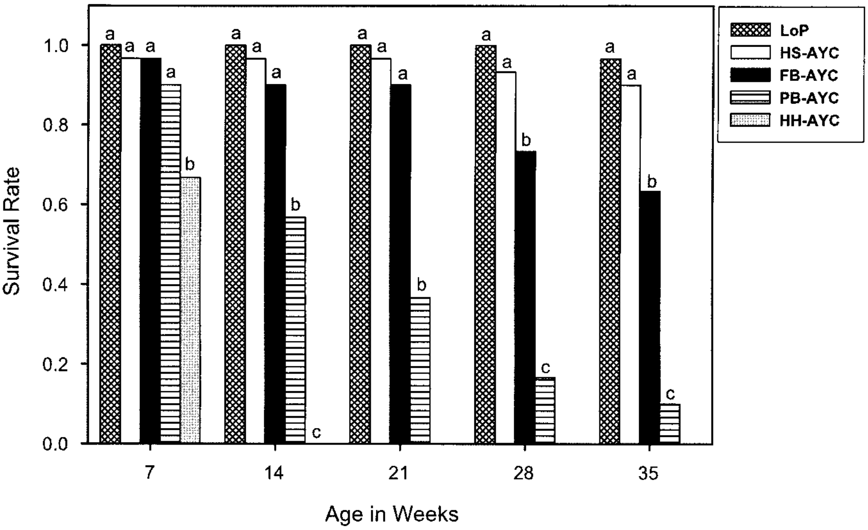

Fig. 1. Survival of termite groups of 250 workers and 50 soldiers feeding nonchoice on five different wood treatments: loblolly pine (LoP), unstained Alaskan yellow cedar sapwood (HS-AYC), fully black-stained (FB-AYC), partially black-stained (PB-AYC), and unstained (HH-AYC) Alaskan yellow cedar heartwood. Bars with the same letter are not significantly different after Z-test at $\alpha = 0.05$.

27 ± 1°C, 94 ± 5% RH, in total darkness for 6 mo. All termite groups received wood blocks originated from at least five different trees and no one treatment was done using samples originated from a single individual.

Mortality of termite groups was monitored weekly. Only groups that had no survivors were considered dead. Survival rates were calculated monthly by dividing starting number of groups by surviving groups for each treatment. Survival was compared among treatments by categorical analysis using Z-test.

Wood consumption was measured every 6 wk by calculating weight loss of wood blocks as they were replaced. The partially consumed wood blocks were dried, stabilized, and weighed as described above. Wood consumption was calculated as the difference in block weight before and after exposure to termite feeding. Wood consumption was compared among treatments using analysis of variance (ANOVA) and general linear model (GLM) analyses by Student's *t*-test (SAS Institute 2000).

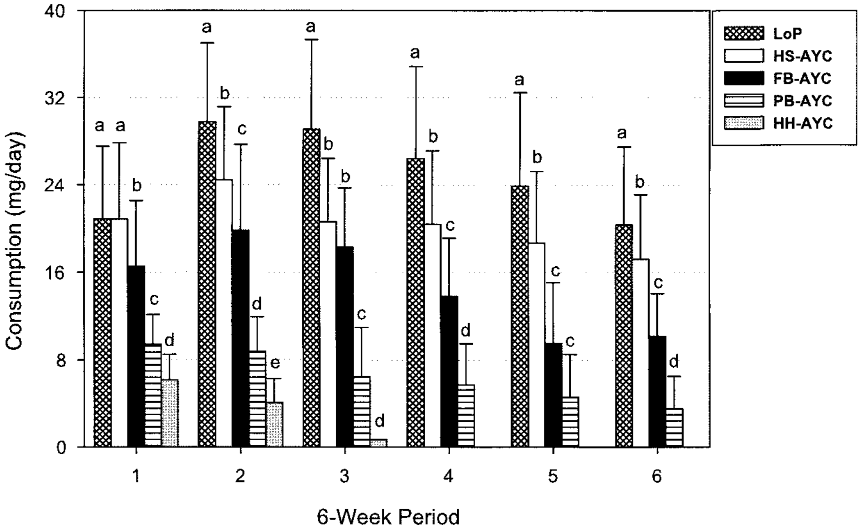

Fig. 2. Consumption rates in milligrams per day of termite groups of 250 workers and 50 soldiers nonchoice on five different wood treatments: loblolly pine (LoP), unstained Alaskan yellow cedar sapwood (HS-AYC), fully black-stained (FB-AYC), partially black-stained (PB-AYC), and unstained (HH-AYC) Alaskan yellow cedar heartwood. Bars with the same letter are not significantly different after Student's *t*-test at $\alpha = 0.05$. Error bars represent SD.

Table 1. Linear regression models of decline of wood consumption rate (mg/d) per termite groups of 250 workers over time within five different food treatments

Treatment[a]	Intercept (*a*)	Slope (*b*)	R^2	*F*	*P*
LoP	34.31 ± 1.075a	−0.40 ± 0.047a	0.96	71.52	0.0035
HS-AYC	26.01 ± 1.107b	−0.27 ± 0.049b	0.91	31.43	0.0112
FB-AYC	24.13 ± 1.919c	−0.47 ± 0.085a	0.91	30.46	0.0117
PB-AYC	10.07 ± 0.337d	−0.20 ± 0.016c	0.98	158.58	0.0002
HH-AYC	7.73 ± 0.655e	−0.46 ± 0.064ab	0.98	50.85	0.0887

Parameter estimates ± SE: df = 1, 3, except PB-AYC df = 1, 4, and HH-AYC df = 1, 1. Parameters with the same letter are not significantly different after *t*-test at $\alpha = 0.05$.

[a] Lop, loblolly pine; HS-AYC, Alaskan yellow cedar unstained sapwood; FB-AYC, fully black-stained Alaskan yellow cedar heartwood; PB-AYC, partially black-stained Alaskan yellow cedar heartwood; HH-AYC, unstained Alaskan yellow cedar heartwood.

Simple linear regression was used to analyze the decline of wood consumption over time within treatments. Means of wood consumption rates in milligrams per day per termite group during 6-wk periods were used as the dependent variable and age in weeks as the independent variable. The corresponding age of termite groups (dish) for each consumption rate was set at the middle of each 6-wk interval (3, 9, 15, 21, 27, and 33 wk of age for first, second, third, fourth, fifth, and sixth 6-wk intervals, respectively). A modification of the Mahalanobis (1930) distance using a jackknife data deletion technique (SAS Institute 2000) was used to identify outlier data points. Data points with Mahalanobis jackknife distances exceeding 4.8 were eliminated from the model. A *t*-test of estimated parameters *a* and *b* (Zar 1999) compared regression equations of different treatment groups.

The regression models were used to estimate per capita consumption rates of termite groups of each treatment using the Morales-Ramos and Rojas (unpublished data) method. Per capita consumption rates were estimated by $CR_w = a_w/N_0$, where CR_w is the per capita consumption rate of wood treatment, *w*, a_w is the intercept of the linear model of wood treatment, *w*, and N_0 is the starting number of termite workers per dish (250). Per capita measurements of wood consumption are considered more reliable and easier to obtain than biomass-based estimates because the weights of individual termite workers change over time in confined groups because of feeding and growth (J.A.M.-R., unpublished data). Workers can also develop into soldiers, affecting the foraging population size (Su and La Fage 1984, 1986).

Assuming that per capita consumption rates remain constant over time, changes in the consumption rate of termite groups over time were considered proportional to the number of foraging termites alive per dish. The linear models obtained with the regression analyses were used to simulate changes in survival of individuals within dishes over time, assuming a constant per capita wood consumption rate. The models were modified using the formula $N_{wt} = N_0 \times a_w/(a_w + b_w \times t)$, where N_{wt} is the number of termite workers per dish of wood treatment *w* at time *t*, N_0 is the starting number of workers per dish, a_w and b_w are the intercept and the slope for wood treatment *w*, respectively, and *t* is the time in weeks.

Chemical Analysis. Blocks of unstained and black-stained Alaskan yellow cedar heartwood were sanded using a high-speed rotary tool (Multipro 5; Dramel, Racine, WI) equipped with a sanding band (60 grit) to obtain wood dust. The wood blocks were sanded inside a plastic box (35 by 23 by 14 cm) with a hole in each end (2 and 9 cm diameter) to allow manipulation of wood blocks toward the sanding tool inside the closed box capturing the wood dust. The plastic box was cleaned between the sanding of each treatment wood to prevent contamination.

The terpenoid compounds of unstained and black-stained Alaskan yellow cedar heartwood were extracted from 500-mg samples of sawdust from each treatment with a total volume of 50 ml of 100% anhydrous ethyl ether. After extraction and evaporation, samples were redissolved with 700 μl of a solution of hexane:ethyl acetate (9:1). Five of these samples from each of the two treatments were analyzed using a Hewlett Packard GC/MS 6890, and an average peak height was calculated among the five samples from each treatment. Peak identification was done using GC/MS database library Wiley 7N software (Hewlett Packard 1998). Standards were used to corroborate peak identification. The content of nootkatone of each wood sample in parts per million (ppm) was estimated by comparison of peek areas with a known concentration of a nootkatone standard (Fluka 74437; Fluka Chemie, Buchs, Switzerland) analyzed in the same instrument.

Table 2. Per capita consumption rates (mg/d) and weakly mortality rates of termite groups feeding on five different wood treatments

Treatment[a]	Per capita consumption rates (μg/d)[b]	Weekly mortality[c]	Estimated longevity[d]
LoP	137.27 ± 4.30	2.92	85.49
HS-AYC	104.04 ± 4.43	2.63	94.95
FB-AYC	96.52 ± 7.68	4.84	51.61
PB-AYC	40.28 ± 1.35	5.08	49.20
HH-AYC	30.92 ± 2.62	14.75	16.95

[a] Lop, loblolly pine; HS-AYC, Alaskan yellow cedar unstained sapwood; FB-AYC, fully black-stained Alaskan yellow cedar heartwood; PB-AYC, partially black-stained Alaskan yellow cedar heartwood; HH-AYC, unstained Alaskan yellow cedar heartwood.

[b] Calculated as a_w No where a_w is the intercept of linear model of wood treatment w, and N_0 is the starting number of workers per dish. Estimates ± SE.

[c] As termite workers dying per termite group per week.

[d] In weeks calculated as a_w/b_w where b_w is the slope of the linear model of wood treatment *w*.

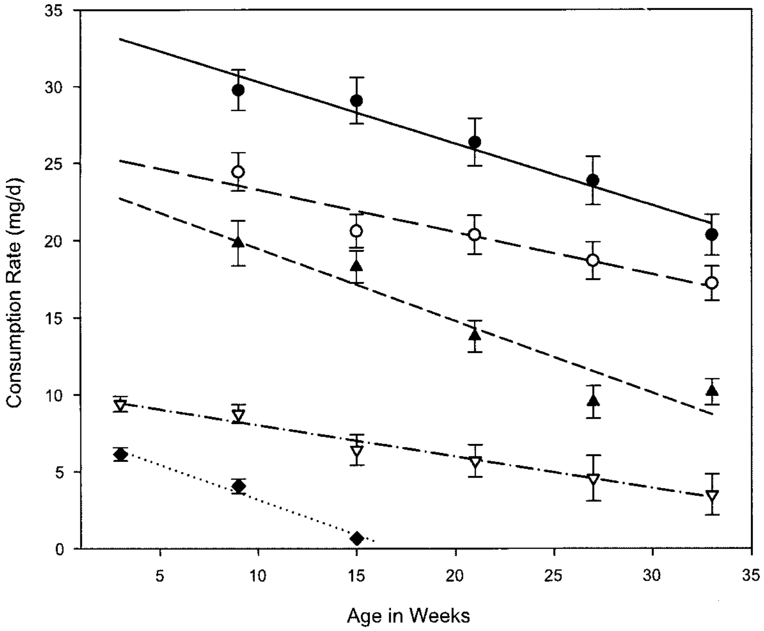

Fig. 3. Regression lines modeling the decline of wood consumption rates in milligrams per day with age in weeks of termite groups of 250 workers and 50 soldiers. Symbols represent observed means, error bars represent SEM, and lines represent regression models. Food treatments consisted of loblolly pine (●), unstained Alaskan yellow cedar sapwood (○), and fully black-stained (▲), partially black-stained (△), and unstained (◆) Alaskan yellow cedar heartwood.

Results

Natural Resistance. At the end of 7 wk, survival was significantly higher in termite groups fed with the fully black-stained Alaskan yellow cedar than in those fed with the unstained Alaskan yellow cedar heartwood ($|Z| = 3.0, \alpha = 0.05$). Survival of groups feeding on fully and partially black-stained cedar was statistically similar to that of groups feeding on the loblolly pine at the end of 7 wk (Fig. 1). By the end of 14 wk, all of the groups feeding unstained yellow cedar heartwood were dead. At the end of 14 wk, survival of groups feeding on fully black-stained cedar was not significantly different than that of groups feeding on loblolly pine, but groups feeding on partially stained cedar showed a significant reduction in survival ($|Z| = 4.1$, $\alpha = 0.05$; Fig. 1). Survival of groups feeding on partially stained cedar was significantly lower than that of groups feeding on fully stained cedar at the end of 21 wk ($|Z| = 4.3$, $\alpha = 0.05$). Mortality started to increase in the groups feeding on fully stained cedar by the end of 6 mo and was significantly higher than that of the loblolly pine treatment ($|Z| = 3.0$, $\alpha = 0.05$) by the end of 28 wk (Fig. 1). Groups feeding on Alaskan yellow cedar sapwood showed survival rates statistically similar to those of groups feeding on loblolly pine throughout the test (Fig. 1).

Termites consumed as much loblolly pine wood as yellow cedar sapwood but consumed significantly less wood from all the other treatments ($|T| > 3.1$; df = 145; $P < 0.002$) during the first 6-wk interval. During the second to the sixth 6-wk intervals, wood consumption in the loblolly pine group was significantly higher than in all other groups ($|T| > 2.0$; df = 132, 103, 95, 89, and 79, respectively; $P < 0.047$; Fig. 2). Unstained Alaskan yellow cedar sapwood was consumed in significantly higher quantities than unstained or black-stained yellow cedar heartwood during all 6-wk intervals ($|T| > 2.9$; df = 145, 132, 103, 95, 89, and 79, respectively; $P < 0.004$; Fig. 2). There was only one exception when, during the third 6-wk interval, termite groups consumed similar amounts of unstained yellow cedar sapwood and fully black-stained heartwood (Fig. 2).

Termites consumed significantly less unstained yellow cedar heartwood than both black-stained treatments ($|T| > 2.38$; df = 145 and 132; $P < 0.019$) during the first two 6-wk periods (Fig. 2). Termites feeding on fully black-stained Alaskan yellow cedar consumed significantly higher amounts of wood than groups feeding on partially black-stained cedar during all but the fifth 6-wk periods ($|T| > 2.29$; df = 145, 132, 103, 95, and 79, respectively; $P < 0.024$; Fig. 2).

Regression analysis showed a significant negative correlation between termite group consumption rates (mg/d) and group age in weeks (Table 1). Consumption rates during the first 6-wk period in the loblolly pine, unstained Alaskan yellow cedar sapwood, and fully stained Alaskan yellow cedar heartwood were identified as outlier observations and eliminated from the models. These observations deviated from a natural trend because of the initial adaptation period of termite groups to the new environment. During the first 6-wk period, termite workers expended considerable amount of time and energy digging tunnels in

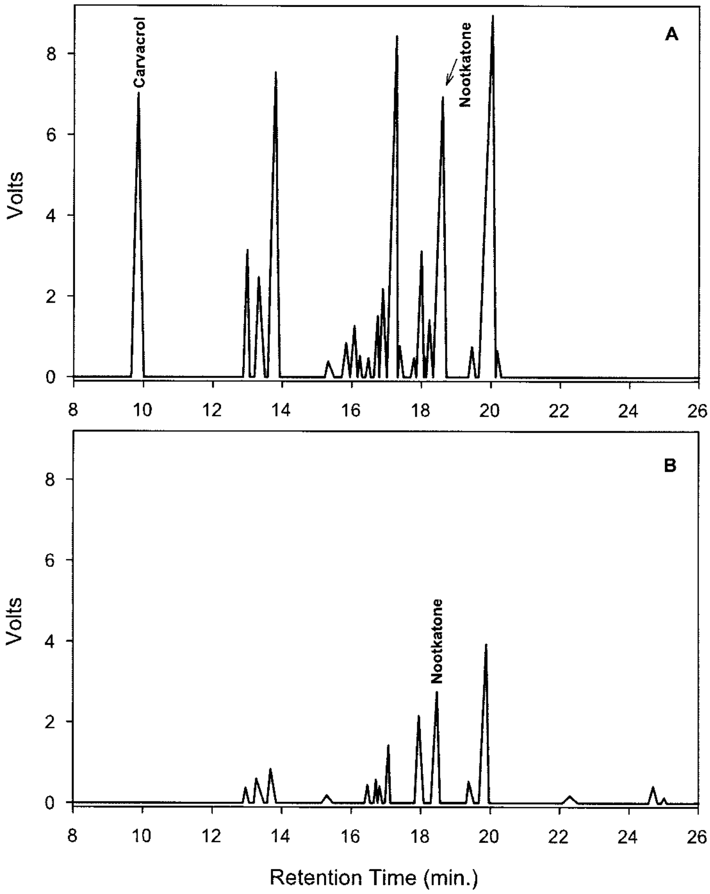

Fig. 4. Gas chromatograms of unstained (A) and fully black-stained (B) Alaskan yellow cedar hearwood.

the soil mix of new dishes, reducing their time available for foraging.

Per capita consumption rates estimated by the regression lines shown in Table 1 showed a food treatment–dependent pattern similar to that observed in termite group consumption rates (Table 2). Intercepts of all models were significantly different ($T > 6.3$, df = 1–4; Table 1), making the estimates of per capita consumption rates significantly different as well (Table 2).

Estimated weekly termite worker mortality was the lowest in the unstained Alaskan yellow cedar sapwood (2.6) and the loblolly pine (2.9) treatment groups (Table 2). The unstained Alaskan yellow cedar heartwood showed the highest estimated weekly worker mortality (14.75), which is consistent with the rapid decline of this treatment group. Estimates of group longevity by the regression models showed a slightly higher longevity for the unstained yellow cedar sapwood (95 wk) than that of loblolly pine (85.5 wk) treatment group (Table 2). Estimate of group longevity of the loblolly pine treatment group resemble observed mean longevity (83 ± 40 wk) of 30 similar termite groups feeding on loblolly pine in a long-term force feeding study (J.A.M.-R., unpublished data).

Chemical Analysis. Gas chromatograph analyses of unstained and black-stained Alaskan yellow cedar heartwood showed evident differences in the number and magnitudes of peaks detected. A large peak (at 9.84 min, retention time) appeared in the unstained Alaskan yellow cedar heartwood samples but not in the black-stained heartwood (Fig. 4). Mass spectrometer analysis identified this peak as the tropolone carvacrol. This was confirmed by using a carvacrol standard (Fluka 22051; Fluka Chemie) analyzed in the same instrument. Unstained Alaskan yellow cedar heartwood contains 723.9 ± 52.3 ppm carvacrol, but black-stained cedar wood contained no measurable quantities of this compound. Most other large peaks were found in both stained and unstained wood, although at markedly lower magnitudes in black-stained samples (Fig. 4). Content of nootkatone was more than four times higher in unstained (753.6 ± 68 ppm) than in black-stained (181.4 ± 15.5 ppm) yellow cedar heartwood.

Discussion

Termites consumed significantly more loblolly pine than any other type of wood during all 6-wk intervals.

Per capita consumption rates were also higher in the loblolly pine than in the rest of the treatments. This indicates that, even when it is infected with black-staining fungi, Alaskan yellow cedar retains significant levels of feeding deterrence to Formosan subterranean termites. However, infection with black-staining fungi in Alaskan yellow cedar significantly reduces the natural resistance of this heartwood to Formosan subterranean termite feeding. Feeding deterrence properties were affected proportionally to the degree of black-staining fungal infection; fully black-stained Alaskan yellow cedar was consumed at a significantly higher rate than partially black-stained Alaskan yellow cedar during all but one of the 6-wk periods (Fig. 2).

The mechanism behind this altered feeding deterrence appears to be, at least partially, allelochemical. Concentrations of nootkatone, for example, were four times higher in unstained than in black-stained Alaskan yellow cedar heartwood. Because of the reported toxic and feeding deterrence properties of nootkatone on Formosan subterranean termite, we conclude that the results presented can be explained mostly by the reduction of nootkatone in the black-stained yellow cedar heartwood. However, the absence of carvacrol and the reduction in concentration of other compounds in the black-stained samples may increase the degree of susceptibility of the infected wood to Formosan subterranean termite attack. Smith and Cserjesi (1970) reported that black-staining fungi reduced concentrations of nootkatin to 3% of those found in unstained wood. Because nootkatin is photosensitive when dissolved in organic solvents (Smith and Cserjesi 1970), it is unlikely that this tropolone compound appeared in our GC analysis.

The Forest Products Laboratory (USDA Forest Service, Madison, WI) is currently conducting a field trial on the deterioration of heartwood pieces with and without black-staining fungi in contact with soils. These trials are being conducted at two locations: one in Mississippi where termites are common and another in Alaska where termites are absent. Perhaps the field test in Mississippi will corroborate our findings of increased termite feeding in black-stained wood.

Although infection of Alaskan yellow cedar with black-staining fungi diminishes its resistance to termites, and perhaps, decay fungi, strength properties are not compromised (Green et al. 2002). Thus, black-stained yellow cedar wood might be recommended for applications where its structural properties are needed but not where exposure to moisture, decay, or termites will limit its durability.

Acknowledgments

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