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Field Evaluations of Subterranean Termite Preference for Sap-Stain Inoculated Wood

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Abstract Few studies have focused on interactions between subterranean termites and the ophiostomatoid fungal associates of pine bark beetles or root feeding weevils. Field stake tests were employed at four locations throughout Mississippi to determine the feeding preference of subterranean termites for blue-stained, unstained, and partially decayed southern pine sapwood stakes. This study also utilized wood decayed by *Gloeophyllum trabeum*, a fungus previously shown to elicit a positive subterranean termite feeding response, as a positive control. Stakes inoculated with *G. trabeum* received significantly more attacks than all other treatments after 16 weeks. Of the stakes attacked by subterranean termites, stakes inoculated with *Ophiostoma minus* were degraded faster than any other treatment. Subterranean termite preference for stakes treated with either of two *Leptographium* spp. and the untreated negative controls did not differ; however, each was fed upon less than all other treatments. The feeding rate on stakes inoculated with *O. ips* and *G. trabeum* being fed upon by subterranean termites was not significantly different. These results represent the first evidence of wood containing non-structurally degrading fungi (*O. ips* and *O. minus*) eliciting a feeding preference from subterranean termites greater than that of decayed wood. The implications of these results are particularly relevant to pine forest ecology, nutrient cycling, subterranean termite control, and the utilization of blue-stained southern pine building products in the southeastern U.S.

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Subterranean termites and decay fungi are the predominate woody decomposers in most forest ecosystems. Although these organisms appear to provide a similar service to ecosystems, intricate interspecific, mutualistic, commensal, and parasitic relationships occur, which increase the efficiency of decomposition and nutrient cycles. Insight into previously unknown interspecific symbiotic relationships may alter our perception of the processes involved in tree death and early stages of wood degradation.

Subterranean termites are well documented as associates of decay fungi (e.g. Hendee 1934; Sands 1969; Becker 1976; Amburgey 1979; Zoberi and Grace 1990). Wood inhabited by some brown-rot decay fungi has been shown to elicit trail following behaviors and feeding preferences from subterranean termites (Esenther et al. 1961; Esenther and Beal 1979; Grace and Wilcox 1988; Rust et al. 1996). Conversely, wood containing various white-rot decay fungi are sometimes avoided (Amburgey and Beal 1977), but *Reticulitermes* spp. are known to feed directly on basidiocarps of various wood decay fungi (Waller et al. 1987).

No positive or negative feeding response with subterranean termites was found in downed woody debris infested with non-decaying stain or mold fungi in four forest habitats in Mississippi (Kirker et al. 2012). However, other studies (Little et al. 2012a, b) showed that wood inhabited by blue-stain fungi (*Ophiostoma* spp.), which are not known to degrade any structural components of wood (Schirp et al. 2003; Valiev et al. 2009), yielded a significant positive feeding response from both Eastern (*R. flavipes* Kollar) and Formosan subterranean termites (*Coptotermes formosanus* Shiraki) in laboratory assays. The mechanism(s) behind subterranean termite feeding preference for wood inhabited by various fungi is still unclear; however, it may involve a biologically active water soluble fungal metabolite(s) or a fungal-modified extractive.

Our previous laboratory findings on subterranean termite feeding preference for southern yellow pine sapwood containing *Ophiostoma* species (Little et al. 2012a, b) inspired new research regarding subterranean termite interactions with *Leptographium* species, a genus closely related to *Ophiostoma*, which is also non-wood degrading. Many *Ophiostoma* species are vectored by above-ground bark beetles that attack southern pines (Table 1). Likewise, many species of *Leptographium* are vectored by below-ground feeding beetles (Table 1) and at least one species of above-ground bark beetle, the black turpentine beetle (*Dendroctonus terebrans* Oliver). Some species of *Leptographium* are prevalent in roots and root collars of pine trees, often for a long time before above-ground non-structurally degrading fungi associated with various pine bark beetles are present. The affiliation of *Leptographium* species with below- and certain above-ground attacking beetles, some of which also carry *Ophiostoma* species, makes it plausible that other ophiostomatoid species may elicit a positive feeding response from subterranean termites similar to that observed in previous studies (Little et al. 2012a, b).

The objectives of this study were to determine if results similar to Little et al. (2012a, b) could be observed with another closely related fungal genus, and to corroborate findings from earlier laboratory studies (Little et al. 2012a, b) in a field

Table 1 Select vectors, their preferred hosts, and portions of host(s) for blue-stain fungi used in this study

Fungus	Select vectors	Preferred host(s)	Preferred portion of host	References
O. minus	*D. frontalis; D. terebrans*	*Pinus taeda L.* and *Pinus echinata L.*	Lower-bole; Mid-bole	Rumbold (1931); Wagerner and Mielke (1961); Payne (1980); Paine et al. (1981); Drooze (1985); Paine et al. (1997)
O. ips	*I. calligraphus*; *I. grandicollis*; *I. avulsus*; *D. terebrans*	*P. taeda*	Lower-bole; Mid-bole; Upper-bole	Paine et al. (1981); Rane and Tattar (1987); Paine et al. (1997); Harrington and Cobb (1988)
L. terebrantis	*D. terebrans; Ips* spp.; *Hylastes* spp.	*Pinus* spp.	Root-collar; Lower-bole; Mid-bole; Upper-bole	Wagerner and Mielke (1961); Goheen (1976); Wood (1982); Rane and Tattar (1987); Harrington and Cobb (1988)
L. procerum	*D. terebrans*; *Ips* spp.; *Hylastes* spp.	*Pinus* spp.	Root-collar; Lower-bole; Mid-bole; Upper-bole	Wagerner and Mielke (1961); Goheen (1976); Wood (1982); Rane and Tattar (1987); Harrington and Cobb (1988)

setting. This study employed AWPA Standard E7 field tests with unstained, stained, and partially decayed southern pine sapwood stakes with a wood decay fungus which has previously been shown to elicit a positive subterranean termite feeding response (Esenther et al. 1961; Esenther and Beal 1979; Grace and Wilcox 1988; Rust et al. 1996).

Materials and Methods

Wooden stakes were prepared from defect-free green southern yellow pine sapwood lumber obtained from a local sawmill. Two hundred forty field stake samples, 1.9× 1.9×45.7 cm (r × t × l), were sawn from green lumber, and placed into autoclave bags in groups of 20 stakes. The stakes were autoclaved for two consecutive 45 min cycles to ensure phytosanitization of the wood. The sealed autoclave bags were then transferred to a biological safety hood.

Previously identified cultures of *Leptographium terebrantis* Barras and Perry and *L. procerum* (W.B. Kendr.) M.J. Wingf. were secured from a laboratory at Auburn University, AL. A culture of *Ophiostoma ips* (Rumb.) Nannf., a sap-stain fungal associate of local *Ips* species, was obtained from a tree infested primarily by *I. calligraphus* (Germar). Mycelia (0.05 g) from pure cultures were extracted for DNA using the Nucleospin Plant II kit protocol for fungi (Macherey-Nagel, Düren, Germany). DNA fragments were amplified by PCR using ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS4R (TCCTCCGCTTATTGATATGC) (Gardes and Bruns 1993). PCR protocols included a 4 min hot start at 94 °C, followed by 39 cycles of 94 °C for 35 s, 55 °C for 55 s, and 72 °C for 1 min, ending with a 72 °C extension for 10 min. Fragment amplifications were verified on a 2 % agarose gel. Fragment DNA was cleaned using the Nucleospin Extract II kit following the protocol for direct purification of PCR products (Macherey-Nagel, Düren, Germany). DNA fragment concentrations were determined by a Nanodrop 1000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA). Fragment DNA samples were prepared for sequencing following the Beckman Coulter dye terminator cycle sequencing protocol using the sample appropriate forward or reverse primer (Beckman Coulter, Fullerton, CA). Both forward and reverse fragments were sequenced for each sample using a Beckman Coulter CEQ 8000 capillary sequencer. All sequence data were checked for quality and the forward and reverse sequences for each sample were aligned using LaserGene MegAlign software. The consensus sequence for each sample was submitted to a National Center for Biotechnology Information (NCBI) GenBank Blast search for match identifications and validated visually using morphological characters. Local cultures of *O. minus* (Hedgc.) Syd. & P. Syd. a sap-stain fungal associate of the southern pine beetle, and *Gloeophyllum trabeum* (Pers.) Murrill, a brown-rot decay fungus known to elicit feeding preference and trail following behavior from subterranean termites (Esenther et al. 1961; Esenther and Beal 1979; Grace and Wilcox 1988; Rust et al. 1996), were obtained from laboratories at Mississippi State University. All fungi used in this study, with the exception of *O. ips*, were grown from cultures previously deposited in the American Type Culture Collection (ATCC). The fungal isolate identified during this study, *O. ips*, will be deposited with ATCC.

All five species of fungi were cultured individually on malt extract agar plates. Ten plugs from one petri dish, which contained hyphae from a single fungus on malt extract agar, were used as starting growth stock in three separate 500 ml flasks containing 200 ml of liquid malt extract media. Mycelia were allowed to grow at 28 °C on an incubated orbiting table for 7 days to achieve peak growth. The content from each of the three flasks was filtered under a biological safety hood using a vacuum funnel and 125 mm filter to separate the mycelia from the growth media. The mycelia were scraped from the filter with a sterile spatula, separated from the agar plugs, and weighed under the biological safety hood. One gram of mycelia was placed into a sterilized laboratory blender with 100 mL of deionized (DI) water. The blender was operated for 12 seconds to fully macerate and evenly distribute the fungal mycelia within the sterile water, creating a fungal slurry. A paint brush was used to apply the fungal slurry to field stakes contained within sealable tubs that were lined with sterilized cheese cloth material, moistened with sterile DI water, and vented with cotton plugs. One hundred milliliter of the inoculation slurry was used to treat each of the two tubs that contained 12 field stakes to achieve a total of 40 field stakes per treatment. Untreated control stakes were subjected to the same methodology; however they were treated with 100 mL of sterile DI water instead of the fungal slurry.

Ten field stake replications for each of the four locations were inoculated with six different fungal treatments; 1) *O. minus*, 2) *O. ips*, 3) *L. terebrantis*, 4) *L. procerum*, 5) *G. trabeum*, and 6) untreated controls. With the exception of the decay fungus *G. trabeum*, which had to be monitored carefully due to rapid strength loss caused by brown-rot decay fungi, the tubs were placed in an incubator at 28 °C until the fungal hyphae had visually stained the entire cross section of the stakes. The fungal matt of *G. trabeum* had to be monitored to allow for some holo-cellulose degradation but where some strength of the stakes remained. The stakes were subsequently tagged and installed in four separate forest locations throughout MS: one site in Harrison Experimental Forest near Saucier, MS, two different sites near McNeill, MS, and one site in the Dorman Lake area, near Starkville, MS.

Field stakes were arranged in a grid pattern, with ten rows of six stakes for each location. There was 6.1 m between each row and 2.4 m between stakes within a row. Each stake was installed in the soil to ½ of its total depth. Each row of six stakes within a location contained one replicate from each treatment, which yielded a total of ten treatment replications per location. The within-row position of each treatment replicate was randomly assigned. Stakes were installed on April 22, 2011 and rated every 4 weeks for subterranean termite degradation, ending December 2, 2011. The study was terminated after eight inspections to prevent wood decay fungi from becoming established in the stakes and, perhaps, thus affecting the results. Stakes were visually rated using American Wood Protection Association (AWPA) Standard E7-09 termite rating scheme of 10 to 0, beginning with 10 (sound), 9.5 (trace, surface nibbles), 9 (slight attack with no more than 3 % of cross-sectional area affected), 8 (moderate attack, 3–10 % of cross-sectional area affected), 7 (moderate/severe attack and penetration, 10–30 % of cross-sectional area affected), 6 (severe attack, 30–50 % of cross-sectional area affected), 4 (very severe attack, 50–75 % of cross-sectional area affected), and ending with 0 (failure) (AWPA 2009).

Statistical Analyses

Initial analyses were performed using Pearson's χ^2 Test in the SAS program PROC FREQ (SAS Institute 2009) to determine percent of stakes attacked by subterranean termites (ratings of 9.5 or lower) on all stakes throughout the 32 week test ($P \leq 0.05$). Additional analyses were then conducted on wood degradation due to subterranean termite feeding using the SAS program PROC GLMMIX (SAS 2009) for increasing subterranean termite degradation of wood stakes over time for each treatment. The degradation analyses were made on a modified AWPA Standard E7-09 index, with scores ranging from 10 to 3 instead of 10 to 0. Although the AWPA E7-09 index was initially utilized, it resulted in a serious skew to the lower values. Changing the 0 (failure) score to 3 removed much of the skew, which better approximated the desired Gaussian distribution for the response variable. Stakes that were not degraded by subterranean termites throughout the entire sampling period were omitted from the wood degradation analyses; however, some stakes of all treatments received attacks at each location. Mean stake ratings for each treatment were calculated so that each location was utilized as one replicate. The data were analyzed with location and row within a location as random effects. Treatment significance was determined at $\alpha \leq 0.05$.

Results

Beginning at 20 weeks after installation, stakes treated with the positive control fungus *G. trabeum* had significantly more subterranean termite attacks than all other treatments ($\chi^2 = 14.96$; df=5; $P = 0.01$) (Fig. 1). This trend continued throughout the remainder of the 32 week test. The mean infestation rate of the stakes of the remaining five treatments was 31.8 %. Subterranean termite attacks on the five

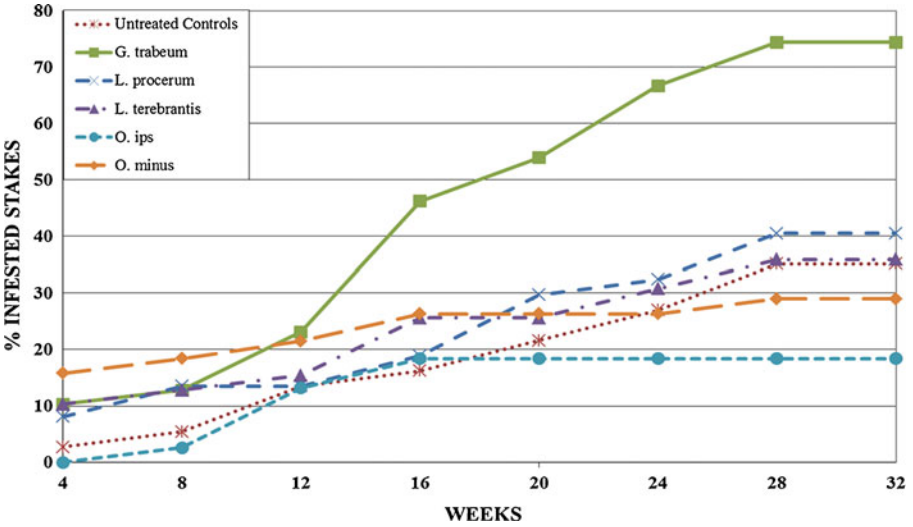

Fig. 1 Percent of stakes with subterranean termite damage over the entire test for each fungal inoculation treatment

remaining treatments did not significantly differ from each other at any point of inspection ($\chi^2 \leq 8.61$; df=4; $P \geq 0.07$).

Diagnostic testing was performed for quadratic and linear responses of wood feeding over time and their interactions with the treatments. This testing showed a significant interaction between treatment and time. Individual regressions were fit for each treatment and the quadratic term was not significant for any treatment. The data were then tested to determine which of the linear regressions were significantly different from others. The original six regressions were reduced to three significantly different regressions: *O. minus* (F=64.17; df=1, 22; P<0.0001), *O. ips* and *G. trabeum* (F=101.96; df=1, 62; P<0.0001), and *L. procerum, L. terebrantis*, and the untreated controls (F=38.16; df=1, 94; P<0.0001) (Fig. 2).

Stakes inoculated with *O. minus* had consistently greater degradation [lower ratings] due to subterranean termites than any other treatment. Subterranean termite feeding damage on stakes treated with either of the two *Leptographium* spp. and the untreated controls did not differ; however, each experienced less feeding damage than all other treatments throughout the study. Although the feeding damage of stakes inoculated with *O. ips* or *G. trabeum* did not significantly differ from each other, they had greater degradation than stakes treated with either of the two *Leptographium* spp. or the untreated control stakes.

Discussion

Stakes inoculated with the positive control treatment *G. trabeum*, a fungus known to elicit a significant feeding attraction from subterranean termites, received more attacks than all other treatments. However, stakes inoculated with *O. minus* were degraded consistently faster than all other treatments. The rate of degradation due to subterranean termites on stakes inoculated with the treatment *O. ips* was not

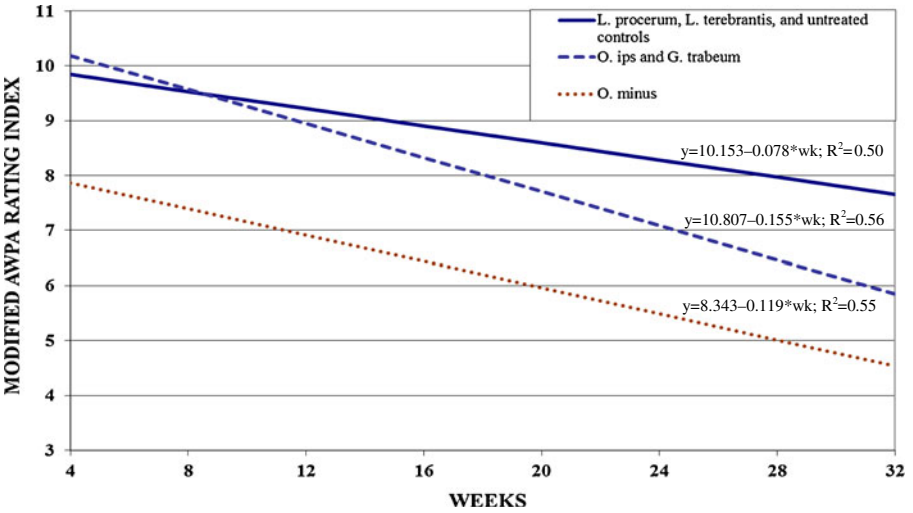

Fig. 2 Linear regressions of modified AWPA rating means fit to linear models for fungal inoculation treatments

significantly different than that observed on the positive control treatment *G. trabeum*. Stakes inoculated with *O. ips* and *G. trabeum* were both degraded faster by subterranean termites than stakes inoculated with either of the two *Leptographium* spp. and the untreated controls. The results from this study are indicative of the production of a compound(s) at the wood/fungal interface by non-decay fungi (*Ophiostoma* spp.).

A compound that mimics the trail following behavior of Eastern and Formosan subterranean termites, (Z,Z,E)-3, 6, 8-dodecatrien-1-ol, has been isolated and identified from wood decayed by *G. trabeum* (Smythe et al. 1967; Matsumura et al. 1968, 1969, 1976), which was used as the positive control treatment in this study. Subterranean termite responses to wood inhabited by some decay fungi vary between fungal strains, wood species inhabited, and decay rate (Amburgey and Smythe 1977; Lenz et al. 1980, 1991). However, only positive responses/orientations have been reported in the literature for wood inhabited by *G. trabeum*. Fungal extracts from wood decayed by other species of brown-rot fungi are reported to elicit trail-following activity from Formosan subterranean termites (Matsuo and Nishimoto 1974); however, these responses were not due to the compound (Z,Z,E)-3, 6, 8-dodecatrien-1-ol (Ohmura et al. 1995). It is unknown whether ophiostomatoid fungi produce (Z,Z,E)-3, 6, 8-dodecatrien-1-ol or additional compound(s) that mimic a subterranean termite trail following pheromone. However, the high rate of subterranean termite feeding on stakes inoculated with *O. minus* in this study and laboratory feeding preferences observed by Little et al. (2012a, b) indicate that a compound(s) may be produced by stain fungi.

Many sap-stain fungi produce masses of spores at the tops of long stalks, which are adapted for dispersal by different species of bark beetles or their phoretic arthropod symbionts. Once a beetle and its symbiotic fungus have penetrated the inner bark of a host tree, oleoresin is produced and compartmentalization within the tree occurs. Sap-stain fungi metabolize simple sugars, lipids, proteins, and other non-structural compounds in wood (Abraham et al. 1993, 1998; Breuil and Huang 1994; Brush et al. 1994; Breuil et al. 1995; Gao and Breuil 1995, 1998; Abraham and Breuil 1996). During infection, sap-stain fungi degrade defensive barriers within the tree (Whitney 1971; Ballard et al. 1983; Tisdale et al. 2003), lowering its defensive capabilities against other organisms.

Subterranean termite bait enhancements derived from decayed wood have been largely unsuccessful. A bait matrix using decay fungus-infected sawdust, bagasse dust, potato dextrose agar, and mirex was developed for control of Formosan subterranean termites in China (Gao 1985); however, it was developed before the mechanism(s) of attraction was fully understood. Cornelius et al. (2002) demonstrated that extent of wood decay was inversely related to Formosan subterranean termite feeding preference, while Eastern subterranean termites showed no difference in response over time to decayed wood. Although Formosan subterranean termite preference for decayed wood wanes over time (Cornelius et al. 2002), it is unknown whether the degradation rate of blue-stained wood effects subterranean termite preference. A better understanding of the mechanism(s) of subterranean termite preference for wood-inhabiting fungi is needed to optimize the efficacy of any bait matrix produced from fungal metabolites.

The results presented herein affirm findings reported by Little et al. (2012a, b) from similar studies conducted on wood wafers in a laboratory setting. Furthermore,

results for this study represent the first instance of subterranean termite feeding preference for an ophiostomatoid fungus in a field setting. Further research is needed for the following: 1) determine if a water-soluble compound(s) is produced by ophiostomatoid fungi, 2) investigate the ecological interactions between ophiostomatoid fungi, their vectors, and subterranean termites in roots or stems of living or recently dead pines, 3) and investigate the prevalence of this fungally-mediated behavior in subterranean termites native to other regions of the world.

Conclusions

Subterranean termite preference for wood inoculated with ophiostomatoid fungal associates of bark beetles and root feeding weevils common in the southeastern U.S. was investigated in four forested settings in Mississippi. These results for subterranean termite feeding on wood infected by ophiostomatoid fungi are similar to those reported by Little et al. (2012a, b). However, results for this study using *Ophiostoma* spp. were obtained outside of a laboratory setting. After locating a stake, subterranean termites fed more aggressively on wood inoculated with the blue-stain fungus *O. minus* over all other treatments, including wood inoculated with the decay fungus *G. trabeum*. This study corroborated findings from previous laboratory assays by Little et al. (2012a, b). Additionally, this study represents the first evidence of wood containing a non-structurally degrading ophiostomatoid fungus eliciting a feeding response from subterranean termites greater than observed for decaying wood. The implications of these results are particularly relevant to pine forest ecology, nutrient cycling, subterranean termite control, and the utilization of blue-stained southern pine building products in the southeastern U.S.

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