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Wood Consumption by Formosan Subterranean Termites (Isoptera: Rhinotermitidae) as Affected by Wood Moisture Content and Temperature

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ABSTRACT Understanding foraging behaviors and food preferences of termite colonies is critical to optimizing control strategies. The relationship between the moisture content (MC) of wood blocks and the feeding preference of Coptotermes formosanus Shiraki (Isoptera: Rhinotermitidae) at three ambient temperatures (19, 28, and 35°C) was investigated with multiple-choice as well as no-choice feeding bioassays. In multiple-choice tests, when four wood blocks with initial MC as dry (0–3%), low MC (22–24%), medium MC (70–90%), and high MC (125–150%) were exposed to workers and soldiers, the highest consumption was found in the high MC wood blocks at all three temperatures, although high MC wood consumption at 19°C was significantly lower than that at 28 or 35°C. The preference for high MC wood blocks was detectable within the first few hours and continued for the duration of the test. In no-choice tests, the highest wood consumption also was obtained on the high MC wood blocks at all three temperatures. However, in no-choice tests, significant mortality was observed with termites exposed to dry or low MC wood blocks. Termite mortality was found to be higher with higher ambient temperature. Sustained feeding was not observed on wood blocks with ≤24% MC. When wood moisture is low, no free water exists in the cell cavities, which perhaps influenced feeding choices. Temperature played a vital and complementary role for wood consumption at all moisture levels.

KEY WORDS Coptotermes formosanus, wood moisture, temperature, wood preference

Moisture is one of the most important environmental requirements for the survival of subterranean termites (Collins 1969). Unlike many other insects, subterranean termites have a very thin, soft cuticle that readily desiccates (Moore 1969, Sponsler and Appel 1990). As a survival strategy, subterranean termites always associate with moist and humid environments. Moisture can be obtained from many sources, including metabolic breakdown of sugars (food source) and wet food materials (Pearce 1997). Wood being the principle food of subterranean termites, its moisture is one of the important factors that affect their mode of feeding and ultimately their survival. Delaplane and La Fage (1989) suggested that high moisture content makes wood fiber soft and easy to masticate. They also reported that Coptotermes formosanus Shiraki (Isoptera: Rhinotermitidae) preferred wet wood blocks over dry blocks. Behr et al. (1972) showed a positive correlation between wood moisture level and the feeding by Reticulitermes flavipes (Kollar).

In addition to moisture on the food source, relative humidity of the surrounding atmosphere is of utmost importance to subterranean termites. Generally, high moisture on the food source contributes to increased atmospheric humidity. However, high relative humidity alone may not be sufficient for long-term survival if the food moisture content is not adequate. Although wood and nest material moisture level of ≥16% makes the relative humidity of termite galleries near saturation (Sponsler and Appel 1990), R. flavipes cannot survive on wood having ≤16% moisture (McManamy et al. 2008).

Temperature is another important factor for feeding and survival of subterranean termites. The highest feeding rate by C. formosanus was reported at 30°C (Nakayama et al. 2004). By using an acoustic emission technique, Imamura and Fuji (1995) reported the highest wood-attacking activity by these termites at 36°C. However, despite feeding rate being the highest at these temperatures, termite survival is the critical factor for total consumption. The highest survival of C. formosanus as reported by Fei and Henderson (2002) was obtained at 30°C. Given the importance of these factors, a fluctuation in either moisture or temperature will impact the overall termite consumption and survival. Previous studies were undertaken either at one constant temperature with different moisture levels or one constant moisture level with different temperature conditions (Smythe and Williams 1972, Delaplane and La Fage 1989, Fei and Henderson 2002, Nakayama 2001).
humidity for 3 d. Finally, oven-dried wood blocks in a container having saturated relative humidity content (22–24%) was obtained by keeping the wood blocks soaked for 5 h. Low moisture content (70–90%), the blocks were soaked for 5 d. For medium moisture content (125–150%), wood blocks were soaked in deionized water to make the desired initial moisture content at laboratory conditions and after oven-drying the dry blocks had moisture content from 0 to 3%. This is because the oven-dried wood blocks had to expose for several seconds during the weighing process and that probably increased the moisture content up to 3% in some blocks. The dry blocks were then soaked in deionized water to make the desired initial moisture content of the wood by weight. For high moisture content (0–3% moisture content) were used as a control. The moistened wood blocks were weighed to determine the moisture content before placing on the treatment dish, and any blocks that had higher or lower moisture content than a given range for a particular category were discarded from the tests.

No-Choice Bioassay. The experiment consisted of 12 combinatorial treatments of four wood moisture levels and three temperature levels. The three temperature levels, namely, 19, 28, and 35°C were maintained in three incubators. Required number of wood blocks of four different moisture levels were prepared as described above. A single block having designated moisture content was placed in each petri dish (100 by 15 mm, Fisherbrand, Thermo Fisher Scientific, Waltham, MA) and 115 termites (103 workers and 12 soldiers) were released (Fig. 1A). Before this, termites required for the tests were counted and put in separate petri dishes containing a moistened filter paper. In total, six replications were conducted with termites taken from two different colonies. The petri dishes were then placed in humidity chambers (described below) to provide high relative humidity throughout the experiment and put in three incubators set to the three different temperatures. No water was added to the units during the bioassay period. On day 6, the units were taken down, termite mortality was recorded, and the wood blocks were cleaned and oven-dried to calculate the total wood consumption.

Choice Bioassay. Choice tests used larger petri dishes (150 by 15 mm, Fisherbrand, Thermo Fisher Scientific) than the dishes used for no-choice tests. Each dish consisted of four wood blocks having four different moisture levels, and 250 termites (200 workers and 25 soldiers) were released on the central point of the dish (Fig. 1B). The choice tests also consisted of six replications with termites taken from two colonies. Total wood consumption and termite mortality was recorded at the end of the experiment as described in the no-choice tests.

Preparation of Humidity Chamber. A Rubbermaid clear box (capacity, 11.3 liters; Latchables, Rubbermaid Home Products, Fairlawn, OH) was filled with 1-cm-thick layer of sterilized sand. Distilled water was added to the level that the sand was oversaturated and a thin film of free water was maintained. Three plastic plates were placed on top of the sand on which the treatment petri dishes were placed. Several holes were made into the lids of the petri dishes using a soldering

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**Fig. 1.** (A) No-choice feeding test apparatus. (B) Choice feeding test apparatus.
iron and placed one above another in a way that the airspace inside each dish was connected with the saturated airspace of the humidity chamber. The humidity chamber was covered with aluminum foil to help maintain the saturated relative humidity inside the chamber for the 6-d test period. Before this, the relative humidity inside the chamber was measured using Testo 625 humidity meter (Testo Inc., Sparta, NJ) and was found to be in saturated condition. Preliminary tests were carried out to determine the relative humidity condition inside the chamber for 6 d in the similar set up. The relative humidity measured daily for 6 d indicated that there was a constant saturated humidity inside the chamber.

Statistical Analysis. Statistical analysis was performed using SAS9.1 software (SAS Institute, Cary, NC). Colony effects were determined using two sample t-tests. Analysis of variance (ANOVA) was performed to determine the effects of temperature, moisture and interaction effects using Proc Mixed model. Tukey-Kramer’s honestly significant difference (HSD) procedure was used for post-ANOVA comparisons. All significant levels were determined at α = 0.05.

Results

Temperature and wood moisture levels had significant and complementary roles in wood consumption by C. formosanus. In the no-choice test, there was a significant colony effect (T = −2.23, df = 70, P = 0.028). In both the colonies, wood consumption by C. formosanus significantly differed based on wood moisture (F = 124.04; df = 3, 59; P < 0.0001), temperature (F = 28.77; df = 2, 59; P < 0.0001), and wood moisture by temperature (F = 9.68; df = 6, 59; P < 0.0001). In general, consumption of high moisture content (125–150%) wood was significantly higher than low moisture content and dry wood at all three temperatures in both the colonies (Fig. 2). In colony 2, consumption of medium moisture content wood was also significantly higher at all three temperatures compared with low moisture and dry wood; however, in colony 1, it was significantly higher at 28°C only. High moisture content wood consumption at 35 or 28°C was significantly higher than at 19°C. Similarly, consumption of dry and low moisture content wood was substantially low at all three temperatures (Fig. 2).

In the choice test, colony had no significant effect (T = −1.56, df = 70, P = 0.122), and the data from both the colonies were pooled for analysis. As in the no-choice test, wood consumption by C. formosanus differed significantly based on initial wood moisture (F = 64.08; df = 3, 59; P = 0.0001), temperature (F = 23.73; df = 2, 59; P = 0.0001), and wood moisture × temperature (F = 7.65; df = 6, 59; P = 0.0001) (Fig. 3). Consumption of high moisture content wood was significantly higher than low moisture content and dry wood at 28 and 35°C. At 19°C, although the consumption of high and medium moisture wood was higher than dry and low moisture wood, the difference was not statistically significant (Fig. 3).

There was no termite mortality during the test period in the choice test, but termite mortality was observed in the no-choice test. In the no-choice test, there was no significant difference on mortality based on colony (T = 1.05; df = 70; P = 0.297), but significant differences in mortality was observed based on wood moisture (F = 57.98; df = 2, 59; P = 0.0001), temperature (F = 68.10; df = 2, 59; P = 0.0001), and wood moisture × temperature (F = 20.01; df = 2, 59; P = 0.0001). Significantly higher mortality was observed on dry or low moisture content wood blocks than on medium or high moisture content wood blocks at 28 or 35°C (Fig. 4). Mortality at 35°C was almost 100%, which was significantly higher than at 28°C. At 19°C, however, termite mortality was very low irrespective of the wood moisture content (Fig. 4).

Discussion

Preference for high moisture content wood by termites may be due to the wood fiber softness and ease to masticate (Delaplane and La Fage 1989). However, this does not imply that C. formosanus always prefer soft wood species over hard wood species because there are quite a few hard wood species that are equally preferred by this termite (Morales-Ramos and Rojas 2001). For a given wood species (whether hard or soft wood), in addition to making the wood fibers soft, high moisture content is an added advantage for desiccation-prone termites because it is a source of free water. In the choice tests, although termites contributed to enhance the process of equilibrium among the wood blocks having different levels of moisture (Delaplane and La Fage 1989, Gallagher and Jones 2010), they were found to feed most heavily on the first attacked food. Termites preferred the highest
initial moisture content wood blocks early when the wood moisture levels were more discrete, and then they continued to feed on those initially preferred blocks. This is consistent with the findings by Delaplane and La Fage (1989) who reported that *C. formosanus* preferred wood blocks having the highest initial moisture content offered (97%). With Japanese red pine, however, Nakayama et al. (2005) reported that medium moisture content (79–103%) wood was preferred over high moisture content (133–191%) wood by *C. formosanus*. Wood species and possible other factors may have played a role in determining wood block preference in their experiment.

Of the temperatures tested, 28°C can be regarded as the optimum temperature for feeding because at the higher temperature (35°C), although the feeding was not significantly different than that at 28°C on high moisture content wood, a substantially high mortality was obtained when the wood moisture levels decreased. However, at the lower temperature (19°C), no substantial feeding occurred at any wood moisture level. Therefore, based on total overall feeding and termite survival, we conclude that 28°C temperature and high moisture wood is the best combination for feeding for *C. formosanus* among all the treatment combinations of this study. Fei and Henderson (2002) reported that *C. formosanus* survival was higher at 30°C than at 25 or 33°C. *Paraneotermes simplicicornis* (Banks) also had the highest wood consumption at 28°C when they were exposed to various temperatures ranging from 16 to 36°C (Haverty and Nutting 1974). In the temperate-inhabiting western subterranean termite, *Reticulitermes hesperus* Banks, however, the optimum temperature for feeding was reported to be 21°C (Smith and Rust 1993). Smith and Rust (1993) further reported that temperatures >26°C produced very high mortality in *R. hesperus* in days. *Heterotermes aureus* (Snyder) was reported to have the highest consumption at 36°C (Haverty and Nutting 1974).

It is obvious from the present results that a high relative humidity environment alone is not adequate for sustained feeding by Formosan subterranean termites. For sustained feeding, the termites either need to be in contact with a moist substrate (soil) or the moisture content of wood needs to be well above the fiber saturation point that is defined as the moisture content of wood at which the cell walls are saturated with bound water and the cell cavities contain no free water (Babiak and Kudela 1995). Most wood species have a fiber saturation point from 25 to 30%, in which moisture becomes largely inaccessible to the degrading organisms (Morrell 2002). This indicates that the wooden structures that are not in connection with outside water sources may not be at high risk of in-
festation from *C. formosanus* even if the atmospheric relative humidity is at saturation. Requirements of wood moisture above the fiber saturation point also was reported for the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), which could not survive on wood with moisture content ≤ 24% even if the relative humidity was at saturation (McManamy et al. 2008).

Very low mortality at 19°C in the no-choice test, irrespective of the wood moisture level, could be attributed to the low activities and reduced physiological mechanisms of the termites, which probably allowed them to live longer. However, a substantially high mortality at 28 or 35°C on the termites exposed to only low moisture or dry wood blocks but not on those exposed to medium or high moisture wood blocks indicates that *C. formosanus* cannot survive on low moisture wood even if the ambient temperature is favorable for consumption. These results suggest that *C. formosanus* searches for high-moisture-content wood and ultimately congregates on it. Smythe and Carter (1970) suggested that *C. formosanus* could be forced to consume more wood of less preferred species in no-choice tests than in multiple-choice tests; however, our results suggest that they could not be forced to feed on the low moisture content wood (at least for southern yellow pine wood) and therefore have a critical requirement for wood moisture above a certain threshold level.

Monitoring and baiting systems can possibly be improved by exploiting termite behavior as affected by temperature and wood moisture. To make the monitoring device more effective, provisions should be in place that attract termites and keep them for prolonged periods. Although numerous factors, such as wood species and hardness, presence of secondary metabolites, and presence or absence of fungi, play a role in wood consumption by termites (Smythe et al. 1971, Carter and Smythe 1974, Nagnan and Clement 1990), our concern here is with the moisture content of wood. For this, initial moisture content of the monitoring or baiting stake should be higher. Possibly a continuous drip of water could be provisioned in dry places that attract termites and keep them for prolonged periods. This manuscript is approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript 2010-234-5252.

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