Effects of Sand Moisture Level on Food Consumption and Distribution of Formosan Subterranean Termites (Isoptera: Rhinotermitidae) with Different Soldier Proportions[1]

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Abstract Formosan subterranean termites, *Coptotermes formosanus* Shiraki, were tested under laboratory conditions to determine preferences among different sand moisture levels in a choice test. Foraging behavior, rate of filter paper consumption and distribution patterns of the termites were studied among 3 soldier ratios: low (4% soldier), normal (16% soldier) and high (32% soldier) and 7 sand moisture gradients (4, 8, 12, 16, 20, 24 and 28% wt/wt) in a circular 3-dimensional arena. The results showed that sand moisture had a significant effect on termite distribution and filter paper consumption, whereas soldier proportions had no effect. Treatment means comparisons indicated that there were no significant differences in termite distribution or consumption among moisture levels ranging from 4 - 24%; however, significant differences were obtained when termite distribution or consumption on these moisture levels were compared with that of the saturated sand (28% moisture). Termites also were not present in the center release chamber (which had dry sand and no food) at any observation point. Within the range of 4 - 24%, we found a very uneven distribution pattern where 70 - 80% of the total released termites aggregated in 1 of the 6 moisture chambers. Filter paper consumption generally corresponded with the aggregation sites. Importantly, among the 27 replicates no particular moisture chamber was consistently chosen for aggregation indicating that Formosan subterranean termites probably can adapt to a range of substrate moisture levels in nature provided other conditions are suitable.

Key Words *Coptotermes formosanus*, sand moisture, aggregation, foraging

Field studies have indicated that subterranean termites display seasonal variation in activity (Haverty et al. 1974, Haagsma and Rust 1995, Forschler 1996), which is perhaps influenced by extrinsic factors such as moisture and temperature (Haverty et al. 1974). Moisture is one of the most important environmental requirements for the survival of subterranean termites. Because of their soft cuticle with poor water-retaining properties (Moore 1969), subterranean termites lose moisture through the integument more readily than from respiration (Sponsler and Appel 1990) rendering them very susceptible to desiccation. Subterranean termites obtain moisture either from the abiotic environment or from the food source. The water content of the food source is, in turn, directly dependent on the water content of the substrate or soil where the food source is located (Williams 1934). The moisture

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content of the nest material provides a glimpse of their habitat moisture requirements. Sponsler and Appel (1990) examined the nest material of several species of subterranean termites and reported a moisture content ranging from 23 - 60% by weight. The variation in the moisture content of the nest material may be due to the different types of substrates used by the different species of the termites and their ecological requirements.

Green et al. (2005) studied the substrate moisture preference for 3 species of *Reticulitermes* and reported that *Reticulitermes flavipes* (Kollar) and *Reticulitermes tibialis* Banks had a slightly narrower substrate moisture preference range than *Reticulitermes virginicus* (Banks). Unlike *Reticulitermes* spp., *Coptotermes formosanus* Shiraki is not native to the US and is an extremely aggressive species (Tamashiro et al. 1980) that poses a greater threat to wooden structures. Henderson (2001) reported a dramatic increase in the number of parishes in Louisiana infested by *C. formosanus* by the end of 1990s, reaching 29 parishes from only 5 or 6 infested parishes reported by La Fage (1987). One of the main factors for its successful establishment in a new area is its ability to forage and adapt to the new environment. Unlike its native counterparts, *C. formosanus* is known to build above-ground nests in trees and buildings (King and Spink 1969) thereby reducing their dependency on below-ground nests (Forschler and Henderson 1995, Henderson and Fei 2002). The adaptation of *C. formosanus* to the environment separated from ground soil leads us to hypothesize that they readily forage in substrates having a relatively wide moisture range. Although there have been some studies involving the moisture effects on *C. formosanus* (Forschler and Henderson 1995, Fei and Henderson 1999, Su and Puche 2003), no studies have been conducted to determine their substrate moisture level preference in multiple choice situations.

Soldier proportion in *C. formosanus* varies seasonally, which is regulated by both environmental as well as colony factors (Haverty 1979, Waller and La Fage 1988, Delaplane et al. 1991, Henderson 1998, Mao et al. 2005). Wells and Henderson (1993) suggested that the abnormally low number of soldiers in the foraging population of *C. formosanus* showed less movement into new areas as compared with high number of soldiers while foraging. We were interested to see if high or low soldier proportion has any role in the selection and aggregation among various soil moisture levels. This study, therefore, was aimed at determining the substrate moisture level preference for distribution and consumption by *C. formosanus* with different soldier proportions in a 3-dimensional discrete moisture gradient arena.

Materials and Methods

Termites. Workers and soldiers from 3 colonies of Formosan subterranean termites were collected from Brechtel Park, New Orleans, LA, on 29 May, 14 June and 26 July 2007 using milk crate traps. This trap consists of a plastic milk crate (external dimension: L = 33.2, W = 33.2 and H = 28.1 cm; Rehrig Pacific Company, Los Angeles, CA) that houses a wooden lattice structure composed of 44 pieces of softwood lumber of 2 different dimensions viz., 3.5 × 3.5 × 29.5 cm (for horizontal arrangement) and 3.5 × 3.5 × 27 cm (for vertical arrangement). A potential Formosan subterranean termite infested area is identified in the field by inspecting in or around live and dead trees, logs, tree stumps or any type of wooden structure. Once an area has been identified as infested with the termites, the crates are buried within a few meters of the infested spot and covered with 3 - 5 cm of soil. After 3 - 6 wks, the crates are examined for termite infestation by pulling 1 or 2 wood pieces out of the crates. If sufficiently infested, the crates are retrieved and replaced with new ones.

For the present experiments, termites were maintained in the laboratory for 1 - 3 months before they were used in the bioassays. Healthy and uniform-looking (by size) termites were collected using moist brown paper towels as described in Gautam and Henderson (2008).

Bioassay. The bioassay arena was constructed with 7 peripheral plastic containers (8.5 cm diam × 3.4 cm) and 1 central container (12.4 cm diam × 3.6 cm) (Pioneer Plastics©, North Dixon, KY). The central container (release chamber) was connected to all the peripheral containers (moisture chambers) with clear vinyl tubes (9.5 mm outside diam, 6.5 mm inside diam, Watts Clear Vinyl Tubing, North Andover, MA) and all the peripheral containers were connected side by side in a way that termites could have easy access from one chamber to another through the tubes (Fig. 1).

Forty grams of dry sterilized sand (fine beach sand) were put in each peripheral container. Distilled water was then added to create the required moisture content, viz., 4%, 8%, 12%, 16%, 20%, 24% and 28% wt/wt where 28% was the saturation level. The sand moisture level in the peripheral chambers was increased sequentially from one direction (left to right in some replications and right to left in others) to maintain a moisture gradient in the arena. The sand and water was evenly mixed with a steel rod and leveled. The central chamber contained 80 g of dry sand. Dry filter paper discs (42.5 mm diam, Whatman®) were weighed and placed in each of the peripheral chambers as a food source. No filter paper was put in the central release chamber. After 2 h, the moisture content of each filter paper was measured and found to be >100% by weight, i.e., even at 4% sand moisture chamber the moisture content of the filter paper was very high. The relative humidity (RH) was also near saturation (> 98%) in all the moisture chambers regardless of whether the sand moisture level was 4 or

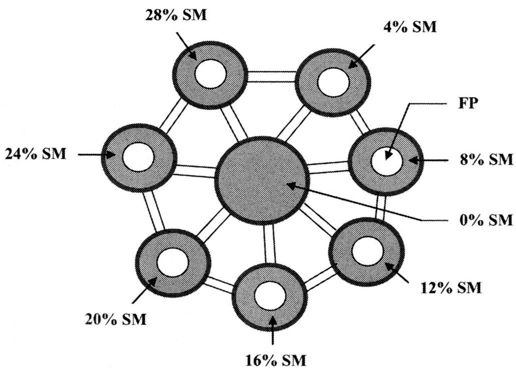

Fig. 1. Moisture gradient bioassay arena with the central release chamber containing dry sand (0% moisture) with no filter paper and the peripheral chambers containing sand having moisture levels from 4 - 28% with a filter paper disc as a food source. Chambers are connected in a way that termites can go to all the chambers from the central chamber and they would have access to both higher and lower moisture chambers from any of the peripheral chambers (FP: filter paper, SM: sand moisture).

28%, possibly because the airspace inside the closed container was very small and became saturated with just a little amount of moisture from the substrate.

Three hundred termites with 3 different soldier proportions, viz., 4% (low), 16% (normal) and 32% (high) were released in the central release chamber. Three colonies of termites were used for the experiment with 3 replications for each soldier proportion from each colony. Altogether, 27 experimental arenas were prepared. The experimental arenas were then placed in a dark corner of the laboratory at 24 ± 1°C. Preliminary tests were conducted to determine the water loss after 5 d in the plastic containers that were set up identical to bioassays but without termites. The weight of the containers taken before and after 5 d indicated that there was no substantial change in moisture level for any treatment chamber.

Daily inspections were made to record foraging patterns, particularly the aggregation pattern of the termites and movement from one moisture level to another. On day 6, the experiment was terminated. The chambers were carefully, but quickly, detached from each other and the openings of the chambers (or tubings) were sealed with Parafilm® immediately. The filter papers were removed, cleaned of any debris with soft forceps and a small brush and air-dried before taking weights. The loss of weight before and after the experiment was the estimation of the filter paper consumption. Location counts of the termites in each chamber were conducted by dumping the sand from each container into a large plastic tray and counting termites.

Statistical analysis. Data were analyzed using SAS software (SAS 9.1, 2002 - 2003). To stabilize the variance, data were transformed using appropriate transformation methods. Location count data were square-root transformed, and the consumption data were log transformed before they were subjected to analysis of variance using proc mixed models. Means were compared using Tukey's honestly significant difference (HSD) at $\alpha = 0.05$. Untransformed means were used for reporting. A simple linear regression analysis was conducted to determine the relationship between distribution and consumption.

Results

Distribution (aggregation). Colony had no significant effect on termite distribution in different moisture chambers ($F = 0.07$; df = 2, 206; $P = 0.9337$). Similarly, soldier proportion also had no significant effect on termite distribution ($F = 0.11$; df = 2, 206; $P = 0.9001$). Because there were no colony and soldier proportion effects, the data for all 3 colonies and 3 soldier proportion were pooled to determine the effects of sand moisture levels. Sand moisture level had a significant effect on termite distribution ($F = 6.39$; df = 7, 192; $P < 0.0001$). Tukey's HSD revealed that there were no significant differences in distribution among moisture levels from 4 - 24% but significant differences were present when these moisture levels were compared with either 0 or 28% moisture levels (Fig. 3). The distribution pattern as shown in Fig. 3 was obtained only after calculating and using the average of all 27 replications, which differed from each individual replication (or experimental arena).

Immediately after release, termites began to explore the surroundings of the dry release chamber. They quickly found their way out through the peripheral tubes leading to the moisture chambers. After a few minutes, the release chambers were completely evacuated, and termites were gathered in one or more of the peripheral moisture chambers. In the initial few hours, termites were observed moving from one moisture level to another except for the one with saturated sand moisture level (28%),

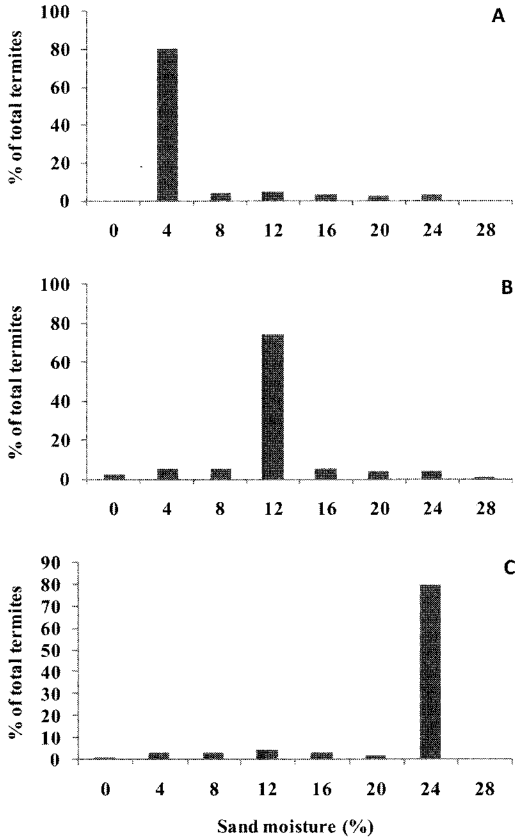

Fig. 2. Distribution pattern of Formosan subterranean termites at various moisture chambers for 3 individual replications (A, B, C).

where they would immediately retreat to the 24% or 4% moisture level, depending on the direction from which they arrived. Similarly, termites would not go back to the dry sand chamber. From day 2, there was clear evidence that termites aggregated to 1 of the 6 moisture chambers ranging from 4 - 24% in each replicate. Examination of each experimental arena revealed a distribution pattern where about 70 - 80% of the released termites aggregated in 1 of the 6 moisture chambers and the remainder of the termites were distributed in the remaining 5 of the 6 moisture chambers. A sample of individual experimental arenas showing the distribution pattern of the termites is shown in Fig. 2(A, B, C). All 27 experimental arenas exhibited this distribution pattern. Table 1 shows the number of experimental arenas (replications) that termites aggregated in a particular moisture chamber. Once the termites were found to be aggregated in a chamber with a specific moisture level, the majority of the termites remained in the same chamber for the entire experimental period, i.e., for 6 d (Table 2). Although termites wandered from one chamber to another, the movement did not change the overall distribution pattern.

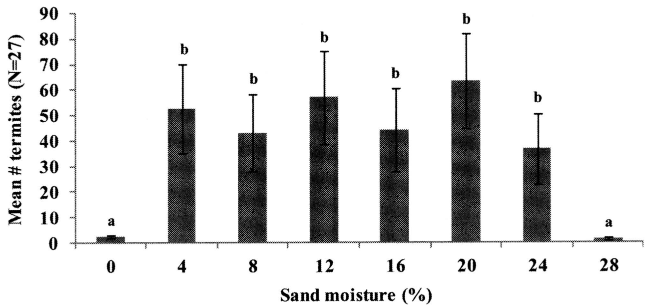

Fig. 3. Mean ± SEM distribution of Formosan subterranean termites in various moisture chambers recovered at the end of termination 6-d bioassay. Means with the same letter are not significantly different ($P > 0.05$) using Tukey's hsd.

Consumption. Colony had no significant effect on filter paper consumption (F = 1.13; df = 2, 180; P = 0.3262). Similarly, soldier proportions also had no significant effect on filter paper consumption (F = 0.25; df = 2, 180; P = 0.7828). Owing to no significant effects of colony or soldier proportions on consumption, the data were pooled to determine the effects of sand moisture levels. Sand moisture had a significant effect on filter paper consumption (F = 18.24; df = 6, 166; P < 0.0001). Filter paper consumption by the termites in the respective chambers corresponded to their distribution (r = 0.829; Fig. 4). Tukey's means comparison showed that filter paper consumption at 28% moisture level was significantly lower (in fact, it was almost nonexistent) as compared with 4 - 24% moisture levels. However, no significant difference in filter paper consumption among 4 - 24% was observed (Fig. 5). Like the distribution pattern, the consumption pattern of individual replication also was very uneven; however,

Table 1. Number of experimental arenas showing the aggregation of termites in different sand moisture levels out of total 27 experimental arenas.

Sand moisture level (% by wt.)	# experimental arenas termites aggregated (Out of total 27)
0	0
4	5
8	4
12	5
16	4
20	6
24	3
28	0

Table 2. Termite aggregations from day 2 to day 6 in various sand moisture chambers.

	Termite aggregation in different sand moisture %				
Treatments	2nd day	3rd day	4th day	5th day	6th day
4% soldier Colony1 R1	12%, 16%	12%, 16%	12%	12%	12%
R2	4%	4%	4%	4%	4%
R3	24%	24%	24%	24%	24%
Colony 2 R1	20%	20%	20%	20%	20%
R2	8%	8%	8%	8%	8%
R3	20%	20%	20%	20%	20%
Colony 3 R1	4%	4%	4%	4%	4%
R2	20%	20%	20%	20%	20%
R3	12%	12%	12%	12%	12%
16% soldier Colony 1 R1	8%	8%	8%	8%	8%
R2	4%	4%	4%	4%	4%
R3	8%	8%	8%	8%	8%
Colony 2 R1	16%	16%	16%	16%	16%
R2	24%	24%	24%	24%	24%
R3	20%	20%	20%	20%	20%
Colony 3 R1	12%, 16%	12%	12%	12%	12%
R2	8%	8%	8%	8%	8%
R3	8%	8%	8%	8%	8%
32% soldier Colony 1 R1	16%	16%	16%	16%	16%
R2	20%	20%	20%	20%	20%
R3	16%	16%	16%	16%	16%
Colony 2 R1	4%, 12%	4%, 12%	12%	12%	12%
R2	4%	4%	4%	4%	4%, 8%
R3	16%	16%	16%	16%	16%
Colony 3 C1	4%	4%	4%	4%	4%
C2	20%	20%	20%	20%	20%
C3	20%	4%	4%	4%	4%

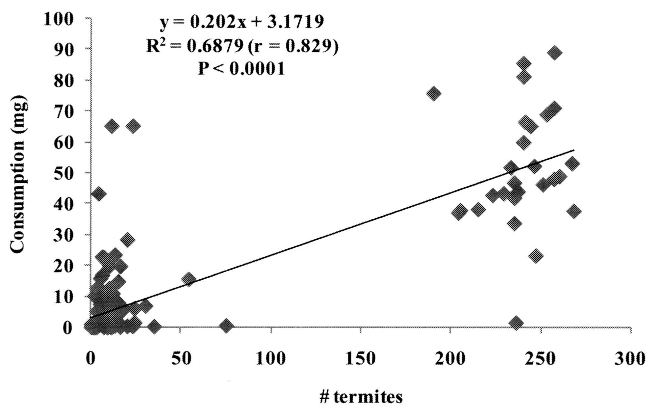

Fig. 4. Relationship between numbers of termites retrieved in various moisture chambers and the filter paper consumption in corresponding chambers.

by using the average of all 27 replications we obtained the consumption graphs as shown in Fig. 5.

Discussion

Acceptable range of substrate moisture for foraging. The distribution pattern of *C. formosanus* to different moisture chambers in multiple choice arenas suggests that a range of substrate moisture levels are acceptable for *C. formosanus* provided other conditions are suitable. Populations of subterranean termites often encounter

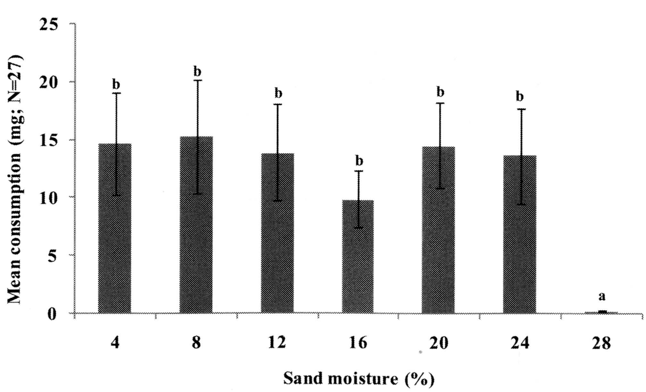

Fig. 5. Mean ± SEM consumption of filter paper in various moisture chambers by Formosan subterranean termites over the 6-d bioassay. Means with the same letter are not significantly different (*P* > 0.05) using Tukey's hsd.

different levels of moisture in nature (Forschler and Henderson 1995). This may range from absolutely dry to full saturation or even inundation. The fact that Formosan subterranean termites are found to infest water-bound trees and are abundant in areas near levees (Forschler and Henderson 1995, Henderson 2008) suggests that they may be able to forage near areas having a high moisture level. It is also possible that their presence near waterways reflects their mode of dispersal via ships. On the other hand, unlike *Reticulitermes* spp., *C. formosanus* constructs above-ground nests (King and Spink 1969, Forschler and Henderson 1995), sometimes in complete isolation from the ground nest indicating their ability to forage in relatively dry substrates. The current study confirmed that *C. formosanus* randomly foraged in the treatment chambers that had a range of sand moisture levels from 4 - 24%. Although *C. formosanus* exhibits a range of acceptable moisture levels preferences, they immediately evacuated the dry sand chamber, indicating that they quickly avoid the unfavorable conditions. Our preliminary test with a filter paper in the center dry sand chamber had shown that termites would not stay in the dry sand chamber irrespective of filter paper presence. In this chamber, the filter paper was also dry, and the relative humidity of the chamber was very low (~55%). A couple of termites that were present in the dry sand chamber were found dead by the next day. We believe that subterranean termite nest and gallery systems are designed to maintain a required moisture level and high RH.

Our results suggest that *C. formosanus* activities would be drastically reduced if substrates are saturated. This is consistent with the findings of field studies by Forschler and Henderson (1995) who reported a sharp decline in subterranean termite populations in the field due to heavy rainfall. Similarly, Snyder (1962) reported the elimination of *Reticulitermes* from an area coupled with frequent inundations. In the present experiment, we observed that *C. formosanus* avoided the saturated substrate. However, when suddenly inundated with water subterranean termites were found to enter a state of quiescence until more favorable conditions prevailed (Forschler and Henderson 1995).

The moisture-retaining capacity of any soil primarily depends on the soil type. The sand substrate that we used in the present study has a low water retention property, with a saturation point at 28% by wt. Addition of clay or vermiculite in the sand would increase the moisture absorption capacity making the saturation point higher. A mixture of equal volume of sand and vermiculite (saturation point: 55% by wt.) was used by Green et al. (2005) to test the substrate moisture preference for 3 species of *Reticulitermes*. They reported that most *R. flavipes* and *R. tibialis* showed the substrate moisture preference range of 35 - 55% and *R. virginicus* 25 - 55% in multiple choice arenas having moisture gradient from 5 - 55%. Although it may not be appropriate to directly compare their study with our present study because of different substrates used, all indications are that Formosan subterranean termites can forage in a relatively drier substrate as compared with *Reticulitermes* spp.

Our present results showing no significant difference in filter paper consumption by *C. formosanus* among 6 moisture chambers (from 4 - 24%) is consistent with the field findings on *R. flavipes* by Potter et al. (2001) who showed that there was no significant difference in damage rate (bait consumption) between Sentricon® (Dow AgroSciences, INpolis, IN) stations placed in soil having different moisture levels. Henderson et al. (1998) documented that ground monitors placed near areas considered conducive for subterranean termite activity, i.e., near water and food sources were attacked in greater numbers. Interestingly, according to the present findings, any soil surface that is not completely dry or saturated might be an area conducive for *C. formosanus* from a moisture point of view. This, perhaps, makes it even more complex to predict the probable area of *C. formosanus* infestation but may help in avoiding the risks of overlooking possible infestation sites based on some preconceived notion.

Aggregation pattern. Aggregation is defined as a higher temporal and spatial density of individuals than in the surrounding area (Southwood 1966, Camazine et al. 2001). It is one of the most basic social phenomena, especially in social insects like termites (Deneubourg et al. 2002). Mutual interactions mediated by information transfer among individuals result in the origin and stability of social aggregates. This can induce group behaviors that are not merely the sum of individual behaviors (Parrish et al. 1997). Group behaviors, like trophallaxis, allogrooming and contact stimulation furnish the organizational glue to keep termite colonies cohesive and functional (Nalepa and Bandi 2000). In the present experiment, we reported that *C. formosanus* aggregated in various moisture chambers. Aggregation to a particular chamber may have been evoked by the trail pheromone produced by the pioneer foragers. However, it is surprising that sand moisture levels ranging from 4 - 24% seemed to be equally acceptable sites for aggregation. We noticed that termites started to aggregate in one chamber after a few hours of the release and by the second day aggregations were observed in all the experimental arenas. By visual estimation, about 70 - 80% of the total released termites were found to be aggregated in one chamber from day 2 to day 5. This held true when we counted the termites on day 6 after terminating the test. Moreover, the aggregation was consistently on the first chosen chamber throughout the experimental period (6 days) in all the experimental arenas indicating that *C. formosanus* feed heavily on the first attacked food before they move to the next one. Previous studies have also reported that *C. formosanus* remained longer and consumed heavily on the first attacked food whereas *Reticulitermes* spp. were not found so (Delaplane and La Fage 1987, 1989, Polizzi and Forschler 1999). The results from the present experiment suggest that there is an equal probability of finding groups of *C. formosanus* in a soil irrespective of the soil moisture levels except dry or saturated conditions. This type of random aggregation pattern exhibited by *C. formosanus* in a wide range of substrate moisture levels should be taken into consideration when placing monitors and baits in termite baiting systems.

Role of soldiers in aggregation. The primary role of soldiers in a termite colony is defense (Deligne et al. 1981, Mill 1982, Noirot 1990). In some species, in addition to alarm and defense, soldiers also are found to play a leading role in food search. For example, *Nasutitermes costalis* (Holmgren) soldiers are reported to be responsible for discovering new food sources and communicating their find to workers (Traniello 1981). On the other hand, worker-initiated foraging has been reported in species like *R. santonensis* Feytaud and *R. flavipes* where soldiers arrive after the food source has been found (Robson et al. 1995, Reinhard et al. 1997). These termite species have rather low numbers of soldiers (1 - 5%) in their population. The role of soldiers in food search in foraging population of *C. formosanus* is not well established. Wells and Henderson (1993) reported that *C. formosanus* with low numbers of soldiers (2.4%) showed less tendency to move to new locations as compared with groups having a higher soldier numbers (18.3%). They speculated that soldiers may be responsible for movement into new areas. In the present study, although we did not determine if soldiers had a leading role in initiation of the movements, we demonstrated that termite aggregation preferences for different sand moisture levels were not affected by soldier proportion.

Acknowledgments

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