Effect of Soil Type and Moisture Availability on the Foraging Behavior of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT This study examined the influence of soil type and moisture availability on termite foraging behavior. Physical properties of the soil affected both tunneling behavior and shelter tube construction. Termites tunneled through sand faster than top soil and clay. In containers with top soil and clay, termites built shelter tubes on the sides of the containers. In containers with sand, termites built shelter tubes directly into the air and covered the sides of the container with a layer of sand. The interaction of soil type and moisture availability affected termite movement, feeding, and survival. In assays with moist soils, termites were more likely to aggregate in top soil over potting soil and peat moss. However, termites were more likely to move into containers with dry peat moss and potting soil than containers with dry sand and clay. Termites were also significantly more likely to move into containers with dry potting soil than dry top soil. In the assay with dry soils, termite mortality was high even though termites were able to travel freely between moist sand and dry soil, possibly due to desiccation caused by contact with dry soil. Evaporation from potting soil and peat moss resulted in significant mortality, whereas termites were able to retain enough moisture in top soil, sand, and clay to survive for 25 d. The interaction of soil type and moisture availability influences the distribution of foraging termites in microhabitats.

KEY WORDS *Coptotermes formosanus*, tunneling, desiccation, wood consumption

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), forages primarily within an extensive underground gallery system (King and Spink 1969). Therefore, the condition of the substrate greatly influences termite foraging behavior. In urban environments, subterranean termites may encounter various soil types within the foraging ranges of particular colonies. Formosan subterranean termites do not create tunnel space by compacting soil (Li and Su 2008). Formosan subterranean termites excavate tunnels by picking up individual particles from one site and depositing the particles at another site (Li 2006). Detailed studies of tunneling behavior have demonstrated that *C. formosanus* is able to pick up three to four sand particles (range, 0.300–0.355 mm in diameter) at a time (Li and Su 2009). Therefore, particle size has a direct effect on the rate of tunnel excavation. Other studies have demonstrated that subterranean termites tunnel significantly faster through substrates with larger particle size (Houseman and Gold 2003, Cornelius 2005).

Formosan subterranean termites are unable to penetrate sand barriers with a particle size ranging from 1.7 to 2.4 mm. They are unable to pick up and move the individual particles and are unable to move between spaces of particles of 2.4 mm (Tamashiro et al. 1991). If particles are larger than 2.4 mm, *C. formosanus* can move between the spaces of particles (Su and Scheffrahn 1992). In laboratory studies, sand particles ranging in size from 1.2 to 1.7 mm diameter were not penetrated by the western subterranean termite, *Reticulitermes hesperus* Banks (Ebeling and Pence 1957). Particle size had a significant effect on the tunneling patterns of *Coptotermes gestroi* (Wasmann). There was a significant reduction in the number of secondary tunnels constructed in arenas filled with soil with a particle size of 0.002–4.0 mm compared with arenas filled with sand. Workers of *C. gestroi* were able to pick up and move sand particles, with a size of ≈2.0 mm, but were unable to pick up and move some of the larger particles in the soil and had to move between the spaces formed by those particles which reduced the total area explored by termites in soil-filled arenas (Arab and Costa-Leonardo 2005).

Soil compaction also has an effect on termite tunneling behavior. Greaves and Florence (1966) found that *C. acinaciformis* constructed more tunnels in low-density than high-density soil. Also, *Reticulitermes flavipes* (Kollar) tunneled more quickly through low-density soil than through moderate or high-density soil (Tucker et al. 2004).

Because subterranean termites are very susceptible to desiccation, soil moisture is a critical factor affecting

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termite foraging behavior. Subterranean termites preferentially tunnel in soils with a higher moisture gradient over soils with a lower moisture gradient (Evans 2003, Su and Puche 2003, Arab and Costa-Leonardo 2005, Green et al. 2005). Water retention is affected by particle size. Although water retention is higher in clay soils than in sandy soils due to the smaller particle size, termites are able to obtain water from sandy soils with lower water content (Lys and Leuthold 1994). Therefore, water retention and water availability of different soil types are both factors that may affect termite foraging behavior.

Termite foraging behavior also is affected by air and soil temperatures (Smith and Rust 1993, 1994; Haagsma and Rust 1995; Evans and Gleeson 2001). Soil type also has been shown to influence behavior of founding alate pairs. Alate pairs were more likely to dig holes in sand + soil mixtures than in pure sand and more likely to choose to nest in substrates as the proportion of soil to sand increases (Lima et al. 2006).

Subterranean termites construct shelter tubes to reach food sources located above ground. Subterranean termites may preferentially select certain soil types to use in gallery construction. Fungus-growing termites *Pseudacanthotermes spiniger* (Sjēstedt) preferentially select clays for use in mound and gallery construction (Jouquet et al. 2007). Mound-building termites transport calcium carbonate particles from subsoil horizons to aboveground termite galleries where the carbonate detritus becomes part of the gallery construction (Liu et al. 2007). This study examined the influence of soil type on the rate of tunneling, shelter tube construction, the selection of feeding sites by termites, and the ability of termites to colonize wood blocks located on dry soil. This study also examined how the interaction of evaporation and soil type affected termite feeding and survival.

Materials and Methods

Termite Collections and Maintenance. Termites were collected from field colonies in City Park, New Orleans, LA, by using cylindrical irrigation valve boxes (NDS, Inc., Lindsay, CA) that are buried in the ground and filled with blocks of wood (spruce, *Picea* sp.). Collections from different traps in the same section of City Park were considered to be separate colonies based on a mark–release–recapture technique using the dye markers Nile Blue A and neutral red (Sigma-Aldrich, Milwaukee, WI) to determine which traps were part of a single, interconnected tunneling system. Any termites from stations containing dyed termites were considered to be part of the same colony as the station from which the dyed termites were released. Termites were kept in the lab in 5.6-liter covered plastic boxes containing moist sand and blocks of spruce *Picea* sp. until they were used in experiments.

Soil Types. For this study, five soil types were used: a uniformly fine sand (Ottawa sand, Frey Scientific, Mansfield, OH), a uniformly fine clay (Montmorillonite clay, Ecological Laboratories, Freeport, NY), potting soil (Organic Choice Potting Mix, Miracle-Gro, Mississauga, Canada), sphagnum peat moss (Miracle-Gro), and top soil (GardenPlus, Hope Agri Products, Powerly, TX). Sphagnum peat moss is decomposed peat moss mined from bogs. Potting soil consists of a mixture of 50–55% composted bark, Canadian sphagnum peat moss, pasteurized poultry litter, and an organic wetting agent.

Table 1. Particle size and dry bulk density of soil types

Soil type[a]	Particle size (mm)	Dry bulk density (g/cm^3)
Clay	<0.002	0.76
Fine sand	0.125–0.149 mm	1.52
Top soil	≤0.25 (78%), >0.25 and <0.85 (12%), ≥0.85 (10%)	0.98
Potting soil	≤0.25 (46%), >0.25 and <0.85 (20%), ≥0.85 (34%)	0.24
Peat moss	≤0.25 (44%), >0.25 and <0.85 (29%), ≥0.85 (27%)	0.19

[a] Potting soil, peat moss, and top soil also contained bark fragments that were >10 mm.

Soil particle size for the fine sand and clay was homogenous. Soil particle sizes for top soil, potting soil, and peat moss were heterogeneous and the percentage of particles in different size categories was measured using sieve analysis. Dry bulk density was used as a measure of soil compaction for all soil types (Table 1).

Termite Assays. For all assays, there were 200 termites per replicate (190 workers: 10 soldiers) unless stated otherwise. Containers were kept in a dark environmental chamber at 28°C and 97% RH for the duration of the experiment. For all assays using moist soil, a soil moisture meter (Spectrum Technologies, Plainfield, IL) was used to establish moisture levels of 80% saturation for each soil type. For assays measuring wood consumption, blocks (4.2 by 3.8 by 1 cm) of spruce were oven-dried at 90°C for 24 h, weighed, and numbered before the experiment. At the end of each assay, blocks were cleaned, oven-dried, and reweighed. Wood consumption was determined by calculating the weight loss of each block.

For all tunneling and choice tests, cylindrical plastic screwtop containers (9 cm in height, 7 cm in diameter) (Consolidated Plastics, Twinsburg, OH) were connected using PVC tubing (6.35 mm i.d. by 11.11 mm o.d. by 2.38-mm wall) (Nalgene, Fisher, Suwanee, GA). Each end of a piece of tubing was then inserted into a 1.5-cm-diameter hole located at the base of a container and sealed in place with hot glue from a glue gun. Termites were placed in one of the containers and were able to move freely into the tubing. At the end of the experiment, tubes were removed, and a rubber stopper was inserted into the hole of each container. Numbers of termites in each container and in the tubes were counted.

Tunneling Assays. To assess the effect of different soil types on tunneling behavior, no-choice and multiple-choice assays were conducted.

No-Choice Tunneling Assay. The soil types tested were sand, clay, top soil, potting soil and peat moss. Each soil type was moistened with distilled water.

Forty 10-cm-long pieces of tubing were filled with one of the five soil types, with eight tubes of each soil type. Each end of a piece of tubing was then inserted into a container. Termites needed to tunnel through the substrate to reach the other container. There were 40 replicates, 10 replicates per colony from four different colonies, two replicates of each soil type per colony. The number of minutes taken for termites to reach the distal container was recorded, which included time taken to initiate tunnel construction and to tunnel completely through the 10-cm-long tubes.

Four-Way Multiple-Choice Tunneling Assay. The soil types tested were sand, top soil, potting soil and peat moss. Each replicate consisted of one container (6.5 cm in height, 5 cm in diameter) with four 1.5-cm-diameter holes located at the base of the container and 10-cm-long pieces of tubing filled with one of the four soil types inserted into each hole. Each replicate contained four soil types. The position of the four soil types was alternated between replicates to prevent any positional bias. Each soil type was moistened with distilled water. The open end of each piece of tubing was then inserted into a container. A 5.5-cm-diameter filter paper disk (Whatman International, Maidstone, England) was placed in the center of each of the four distal containers connected to substrate-filled tubing. Termites were placed in the center container. Termites were collected from four different field colonies with three replicates per colony. After 8 h, the number of distal containers that had been reached by termites by tunneling completely through the substrate-filled tubes was recorded. After 24 h, the number of termites in each substrate-filled tube and in each distal container attached to that tube was recorded.

Shelter Tube Construction Assay. An assay was conducted to examine the effect of different soil types on shelter tube construction. This assay was conducted using plastic containers (22 by 21 by 17 cm) (Rubbermaid, Winchester, VA). In each container, substrate was added to reach a height of 3 cm so that each container had the same volume of material. Each substrate was thoroughly moistened with distilled water and eight blocks of spruce (8 by 3.5 by 1 cm) were placed on top of the substrate. Released in each container were 4 g of termites consisting of ≈1,200 termites with soldier proportions consistent with their respective field collection, which ranged from 15 to 5%. There were two replicates of each soil type, one from each termite colony. Shelter tube construction was monitored for 30 d. Substrate deposited by termites on the sides of the container was traced onto tracing paper with a blue Sharpie marker. The tracing paper was placed on a white paper and photographed. The digital images were analyzed using SigmaScan to determine the surface area covered by particles deposited by termites on the sides of the container (SigmaScan Pro 5.0, SigmaScan 1999).

Effect of Soil Type on Selection of Feeding Sites. To assess the effect of different soil types on the selection of feeding sites, the following paired choice tests were conducted: peat moss versus potting soil; peat moss versus top soil; potting soil versus top soil; and clay versus sand. Three containers were connected using two 10-cm-length pieces of tubing. In the center container, there was 50 g of sand (Frey Scientific, Mansfield, OH), moistened with 10 ml of distilled water. Each end container was filled with a different soil type to a height of 1 cm so that each container had the same volume of material. In the two end containers, a wood block was placed on top of the soil. Termites were placed in the center container. Termites were collected from four different field colonies with three replicates per colony for each assay. After 14 d, the number of termites in each of the distal containers was counted and wood consumption was determined.

Effect of Soil Type on Termite Survival and Infestation of Wood Blocks in Dry Soils. To determine how physical properties of the different soil types affected termite infestation of wood blocks located on dry soil, an experiment was set up exposing termites to the following dry soils: peat moss, potting soil, top soil, clay, and sand. For this experiment, two containers were connected using a 5-cm-length piece of tubing. In one container, there was 50 g of sand (Frey Scientific), moistened with 10 ml of distilled water and no wood block. The other container was filled with a different soil type to a height of 1 cm and a wood block was placed on top of the soil. Termites were placed in the container with moist sand. There were 50 replicates. Termites were collected from five colonies, two replicates per colony for each of the five soil types. After 14 d, the number of termites located in each container and in the tube was counted and wood consumption was determined.

To compare survival and wood consumption for each soil type under dry and moist conditions, a second experiment was conducted using the same experimental design with moist soil of each of the five soil types. There were 25 replicates. Termites were collected from five colonies, one replicate per colony for each of the five soil types. After 14 d, the number of termites located in each container and in the tube was counted and wood consumption was determined.

Effect of Evaporation and Soil Type on Termite Survival and Wood Consumption. An experiment was conducted to determine how soil type affected termite survival under conditions where moist soils were exposed to ambient laboratory conditions where moisture would gradually evaporate over time. For this experiment, a single container was used. Each container was filled with moist soil to a height of 1 cm, and a wood block was placed on top of the soil. There were 10 replicates of each of the five soil types, five treated and five control replicates. Termites were collected from five colonies, two replicates of each colony for each soil type, one treated and one control. Containers were exposed to ambient laboratory conditions. In control replicates, distilled water was added as needed throughout the experiment. In treated replicates, no water was added. After 25 d, termite survival and wood consumption were determined for each replicate.

Statistical Analysis. In the no-choice tunneling test, the number of minutes taken by termites to reach the distal container by tunneling through tubes filled with different soils was compared using a one-way analysis of variance (ANOVA), and means were separated using a Fisher least significant difference (LSD) test. Colony differences were compared using a one-way Kruskal–Wallis (Systat Software, Inc. 2007). In the four-way multiple-choice tunneling assay, the number of tubes filled with different soil types that were completely penetrated by termites after 8 h and 24 h was compared using a one-way Kruskal–Wallis test, with number of tubes as the dependent variable, and means were separated using a Fisher LSD test (Systat Software, Inc. 2007). The number of termites in those tubes and the distal containers attached to those tubes after 24 h was compared using a one-way Kruskal–Wallis test, with number of termites as the dependent variable, and means were separated using a Fisher LSD test. Colony differences were also compared using a one-way Kruskal–Wallis test (Systat Software, Inc. 2007). In the shelter tube construction assay, the surface area of the container covered by particles deposited by termites on the sides of the container in the different soil types was compared using a one-way ANOVA, and means were separated using a Fisher LSD test (Systat Software, Inc. 2007).

In paired choice tests to examine effect of soil type on selection of feeding sites, the number of termites and the weight loss of wood blocks were compared using paired choice *t*-tests, except the Wilcoxon signed rank test was used in cases where the test for normality failed. Colony differences in the location of termites and wood consumption were examined using a one-way Kruskal-Wallis test (Systat Software, Inc. 2007).

In experiments to examine termite infestation of wood blocks in different soil types, termite proportional survival was transformed by the arcsine of the square root and compared using a one-way ANOVA. For comparisons of number of termites located in each container and in the tube and for wood consumption of blocks, data were compared using a one-way ANOVA, except that the one-way Kruskal-Wallis test was used in cases where the test for normality failed. In all cases, means were separated using Fisher LSD test (Systat Software, Inc. 2007). Comparison of termite survival and wood consumption in the experiments with dry soil and moist soil were conducted using a Mann–Whitney *U* rank sum test.

For the experiment examining the interaction of evaporation and soil type, termite proportional survival was transformed by the arcsine of the square root. The interaction of evaporation and soil type was compared using a two-way ANOVA with treatment (additional water added or not) and soil type as factors. Means were separated using Fisher LSD test (Systat Software, Inc. 2007). A *t*-test was performed to compare survival and wood consumption of termites in treated and control containers for each soil type.

Results

Tunneling Assays. In the no-choice test, termites tunneled more rapidly through the sand than through the top soil and the clay ($F = 3.2$; df = 4, 32; $P = 0.03$) (Table 2). There were no significant differences among colonies ($H = 2.8$, df = 3, $P = 0.43$). In the four-way multiple-choice test, termites tunneled through significantly more sand-filled tubes within 8 h than tubes filled with the other three soil types ($H = 17.5$, df = 3, $P < 0.001$) (Table 3). There were no significant differences among colonies ($H = 6.8$, df = 3, $P = 0.08$). After 24 h, there were no significant differences in the number of tubes tunneled through by termites ($H = 4.5$, df = 3, $P = 0.22$). After 24 h, there were no significant differences among colonies in either the number of tubes tunneled through ($H = 0.49$, df = 3, $P = 0.9$) or the number of termites in tubes ($H = 0.11$, df = 3, $P = 0.99$).

There were significant differences in the number of termites in soil-filled tubes and in distal containers attached to those tubes for the different soil types ($H = 26.2$, df = 3, $P < 0.001$). There were significantly fewer termites in sand compared with the other three soil types and significantly more termites in top soil compared with the other three soil types.

Shelter Tube Construction Assay. There were significant differences in the surface area of the container covered by particles deposited by termites on the sides of the container ($F = 10.8$; df = 2, 3; $P = 0.04$). The mean surface area of the container covered by sand particles (127. 5 ± 25.0 cm^2) was significantly greater than the mean surface area covered by clay particles (24. 9 ± 7.6 cm^2) and soil particles (32.4 ± 15.0 cm^2). However, in containers with sand, termites used a

Table 2. Mean (± SEM) number of minutes taken for termites to tunnel through 10-cm-length tubes filled with different soil types in a no choice tunneling test

Soil	Mean (± SEM) no. min taken to tunnel through 10-cm-length tubes
Sand	228.9 ± 41.1a
Peat moss	326.3 ± 41.4ab
Potting soil	320.6 ± 53.2ab
Top soil	396.0 ± 33.2b
Clay	404.8 ± 24.8b

Means followed by the same letter are not significantly different ($P > 0.05$; ANOVA: Fisher's LSD test).

Table 3. Mean (± SEM) number of 10-cm-length tubes tunneled through after 8 and 24 h, and mean (± SEM) number of termites in tubes and attached containers after 24 h in a four-way multiple choice test

Soil	Mean (± SEM) no. tubes tunneled through		Mean (± SEM) no. termites in tubes and attached containers after 24 h
	8 h	24 h	
Sand	0.58 ± 0.15a	0.83 ± 0.11a	7.9 ± 3.2a
Peat moss	0.17 ± 0.11b	0.58 ± 0.15a	33.1 ± 11.3b
Potting soil	0.0 ± 0.0b	0.83 ± 0.1a	49.9 ± 8.0b
Top soil	0.0 ± 0.0b	0.92 ± 0.08a	75.5 ± 9.2c

Means followed by the same letter within a column were not significantly different ($P > 0.05$; Kruskal–Wallis: Fisher's LSD test).

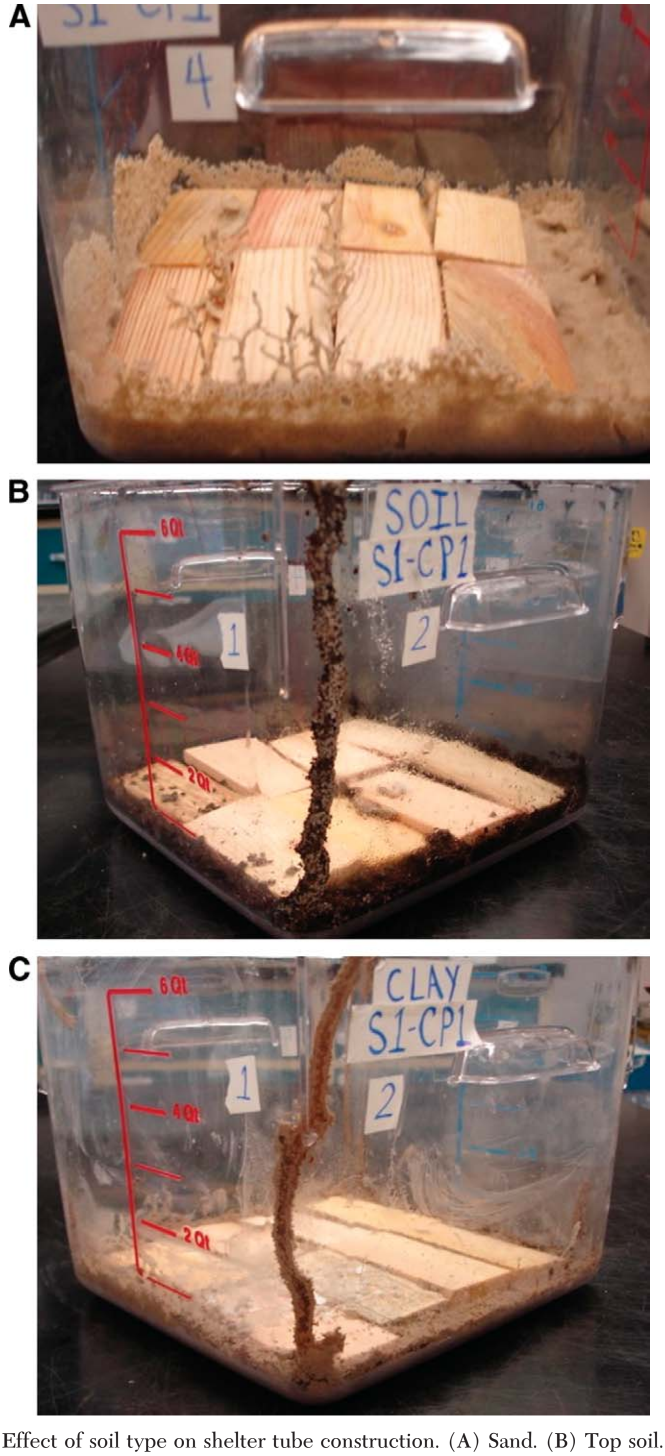

Fig. 1. Effect of soil type on shelter tube construction. (A) Sand. (B) Top soil. (C) Clay.

completely different strategy to move up container walls than in containers with clay or soil. In sand, termites did not build shelter tubes up the sides of the container, they deposited layers of sand particles on the sides of the containers so that the particles were spread out over an area extending upward from the bottom of the container and they built shelter tubes directly into the air from the top of the wood blocks (Fig. 1A). In containers with soil (Fig. 1B) and clay (Fig. 1C), termites constructed shelter tubes up the sides of the containers, but they did not build any shelter tubes directly into the air. Because termites

Table 4. Mean (± SEM) number of termites and mean (± SEM) wood consumption in containers in paired choice tests with different soils after 2 wk

Exp[a,b]	Mean (± SEM) no. termites in each container			Mean (± SEM) wood consumption (mg) of blocks in each container		
	Soil 1	Soil 2	P value[c]	Soil 1	Soil 2	P value[c]
Pm vs. Ps	35.2 ± 15.3	110.8 ± 18.8	0.04	89.2 ± 25.8	260.8 ± 39.5	0.02
Pm vs. Ts	46.7 ± 13.0	101.8 ± 18.1	0.10	42.5 ± 14.1	218.3 ± 32.8	0.001
Ps vs. Ts	34.0 ± 14.3	104.3 ± 20.0	0.04	160.8 ± 26.3	284.2 ± 51.1	0.09
Clay vs. sand	103.8 ± 19.7	43.0 ± 19.7	0.23*	294.2 ± 44.2	244.2 ± 78.9	0.22[c]

[a] Pm, peat moss; Ps, potting soil; Ts, top soil.
[b] Data analyzed using a paired comparison *t*-test in cases where the tests for normality and equal variances passed.
[c] Data analyzed using a Wilcoxon signed rank test because the test for normality failed.

spread the sand particles out on the sides of the container, the total surface area covered was significantly greater than in containers with clay or soil.

Effect of Soil Type on Selection of Feeding Sites. There were significantly greater numbers of termites and wood consumption in containers with potting soil compared with peat moss, and there was significantly more wood consumption in containers with top soil compared with peat moss in paired choice tests (Table 4). Although there were significantly more termites in containers with top soil compared with containers with potting soil, there was no significant difference in wood consumption. Differences between number of termites and wood consumption of blocks in containers with sand and clay were not significant. There were no significant colony differences in either the location of termites or wood consumption in any of the choice tests.

Effect of Soil Type on Termite Infestation of Wood Blocks in Dry Soils. In experiment 1 with dry soils, there were no significant differences in termite survival by colony ($F = 1.1$; df = 4, 45; $P = 0.37$) or soil type ($F = 0.50$; df = 4, 45; $P = 0.75$) (Table 5). However, average survival was <60% for all soil types, and there were 10 replicates with 0% survival, at least one replicate of each soil type. Desiccated termite bodies were observed on the surface of the dry soil in many replicates. There were no significant differences in wood consumption by colony ($H = 6.4$, df = 4, $P = 0.17$) or soil type ($H = 6.5$, df = 4, $P = 0.17$). There were significant differences in the number of termites in containers with dry soil and wood in replicates with different soil types ($F = 3.80$; df = 4, 45; $P = 0.01$), but there were no differences among colonies ($F = 0.76$; df = 4, 45; $P = 0.56$). There were significantly more termites in containers with potting soil and peat moss than in containers with sand and clay and significantly more termites in containers with dry potting soil than dry top soil (Table 5). There were also significant differences in the number of termites in the tubing by soil type ($F = 3.8$; df = 4, 45; $P = 0.01$). There were significantly more termites in the tubing in replicates with dry potting soil and peat moss than dry clay, sand or top soil.

There were also significant colony differences in the number of termites in tubing ($F = 3.4$; df = 4, 45; $P = 0.02$) and in the containers with moist sand only ($F = 4.6$: df = 4, 45; $P = 0.004$) (Table 6). Colony five had significantly greater numbers of termites located in the moist sand after 14 d than colonies 1, 3, and 4. Colony 5 also did not have any replicates with 0% survivors. Colony 1 had significantly more termites located in the tubing than colonies 2, 3, and 4.

In experiment 2 with moist soils, there were no significant differences in survival of termites in the

Table 5. Mean (± SEM) number of termites and mean (± SEM) wood consumption in containers and mean percent (± SEM) survival in a no choice test with different dry or moist soils after 14 d

Soil type	Mean (± SEM) no. termites in container with soil and wood	Mean (± SEM) no. termites in tubing	Mean percent (± SEM) survival of termites	No. replicates with 0% survival	Mean (± SEM) wood consumption (mg)
Exp 1: Dry soil					
Clay	8.9 ± 8.4a	7.2 ± 4.1a	45.3 ± 10.1a	2	96.0 ± 36.4a
Sand	18.2 ± 9.2a	5.9 ± 2.8a	42.4 ± 12.0a	3	126.0 ± 46.5a
Top soil	33.3 ± 13.8ab	5.0 ± 1.8a	50.0 ± 12.6a	3	131.0 ± 33.4a
Peat moss	67.7 ± 20.0bc	19.1 ± 4.9b	58.2 ± 11.1a	1	181.0 ± 48.3a
Potting soil	77.0 ± 20.4c	17.2 ± 4.8b	59.3 ± 10.8a	1	190.0 ± 39.2a
Exp 2: Moist soil					
Clay sand	171.6 ± 6.8a	1.8 ± 1.3c	88.5 ± 3.6a	0	280.0 ± 73.3a
Sand	93.8 ± 25.8b	7.2 ± 2.0bc	80.1 ± 2.3a	0	210.0 ± 34.9a
Top soil	175.6 ± 7.7a	4.0 ± 0.8bc	91.3 ± 3.3a	0	282.0 ± 73.8a
Peat moss	88.2 ± 27.3b	20.0 ± 2.6ab	84.1 ± 2.9a	0	224.0 ± 50.8a
Potting soil	80.2 ± 26.1b	24.0 ± 12.0a	89.7 ± 2.6a	0	282.0 ± 73.8a

Means followed by the same letter, within an exp, were not significantly different ($P > 0.05$; ANOVA: Fisher's LSD test). Proportional survival was transformed by the arcsine of the square root. Wood consumption was compared using a Kruskal–Wallis test for the dry soil experiment because the test for normality failed.

Table 6. Mean (± SEM) number of termites from the five colonies in containers with moist sand only and tubing, mean percentage (± SEM) of survival, and mean (± SEM) wood consumption in containers with either dry soil or moist sand after 14 d

Colony	Mean (± SEM) no. termites in container with moist sand only	Mean (± SEM) no. termites in tubing	Mean percent (± SEM) survival of termites	No. replicates with 0% survival	Mean (± SEM) wood consumption (mg)
Exp 1: dry soil					
1	14.4 ± 6.3a	20.8 ± 5.3b	46.5 ± 11.6a	2	195.0 ± 45.7a
2	59.7 ± 18.5bc	10.1 ± 4.3a	52.5 ± 9.9a	2	154.0 ± 32.3a
3	29.1 ± 14.8ab	3.9 ± 1.6a	43.0 ± 13.7a	3	174.0 ± 58.2a
4	50.1 ± 21.2ab	6.8 ± 3.8a	42.9 ± 12.4a	3	64.0 ± 24.1a
5	97.7 ± 13.2c	12.8 ± 3.6ab	70.3 ± 6.3a	0	137.0 ± 30.8a

Means followed by the same letter, within an experiment, were not significantly different ($P > 0.05$; Fisher's LSD test). Proportional survival was transformed by the arcsine of the square root and compared using a one-way ANOVA. Differences in wood consumption were compared using a Kruskal–Wallis test because the test for normality failed.

different soil types ($F = 1.99$; df = 4, 20; $P = 0.13$). Average survival was ≥80% for all soil types. There were no significant differences in wood consumption in the different soil types ($F = 0.32$; df = 4, 20; $P = 0.86$). There were significant differences in the number of termites in containers with moist soil and wood in replicates with different soil types ($F = 5.3$; df = 4, 20; $P = 0.005$). There were significantly more termites in containers with moist clay and top soil than in containers with sand, peat moss, or potting soil. There were also significant differences in the number of termites in the tubing by soil type ($F = 3.2$; df = 4, 20; $P = 0.04$). There were significantly more termites in the tubing in replicates with moist potting soil and peat moss than moist clay and significantly more termites in moist potting soil than sand or top soil (Table 5).

Survival in the experiment with moist soils (173.7 ± 2.9) was significantly greater than survival in the experiment with dry soils (102.1 ± 9.9) ($P < 0.001$; Mann–Whitney U rank sum test). Wood consumption in the experiment with moist soils (245.6 ± 24.9) was significantly greater than wood consumption in the experiment with dry soils (144.8 ± 18.4) ($P < 0.002$; Mann–Whitney U rank sum test).

Effect of Evaporation and Soil Type on Termite Survival and Wood Consumption. The effect of the interaction of evaporation and soil type on termite survival was highly significant ($F = 14.0$; df = 4, 40; $P < 0.0001$). Percentage of survival of termites was significantly greater in control containers with added moisture (85.9 ± 1.2) than in treated containers without added moisture (51.1 ± 8.8) ($F = 46.5$; df = 1, 40; $P < 0.0001$). Survival of termites was significantly greater in control containers for peat moss and potting soil, but there was no difference in survival between treated and control containers for clay, sand, or top soil (Table 7). The effect of the interaction of evaporation and soil type on wood consumption was not significant ($F = 1.0$; df = 4, 40; $P = 0.40$). Wood consumption was significantly greater in control containers with added moisture (302.0 ± 28.5) than in treated containers with no added moisture (208.8 ± 30.2) ($F = 8.6$; df = 1, 40; $P = 0.006$). Wood consumption was significantly greater in control containers than in treated containers for potting soil and peat moss but not top soil, clay, and sand (Table 7). There were no significant difference in the survival ($F = 1.0$; df = 4, 45; $P = 0.98$) or wood consumption ($F = 2.1$; df = 4, 45; $P = 0.96$) of termites from different colonies.

Discussion

Tunneling behavior was significantly influenced by soil type. The time taken for termites to initiate and construct tunnels in different substrates was directly correlated to particle size in both no-choice and choice tests. In the choice test, termites were most likely to tunnel through sand within 8 h and most likely to aggregate in top soil after 24 h.

Shelter tube construction was affected by the physical properties of the soil. In replicates with clay and top soil, termites built shelter tubes up the sides of the containers. In replicates with sand, termites built shelter tubes into the air with no contact with the container walls. Also, termites placed a large number of sand particles on the walls of the container, but they

Table 7. Mean (± SEM) percentage of survival of termites and mean (± SEM) wood consumption in containers after 25 d in a no choice test where moisture was allowed to evaporate from treated containers and moisture was added as needed to control containers

Soil type	Mean % (± SEM) survival of termites			Mean (± SEM) wood consumption (mg)		
	Treated	Control	P value	Treated	Control	P value
Clay	87.3 ± 2.9	82.7 ± 3.2	0.31	284.0 ± 41.3	276.0 ± 76.8	0.93
Sand	63.2 ± 19.1	86.9 ± 1.9	0.32	356.0 ± 65.5	442.0 ± 61.9	0.37
Top soil	88.6 ± 1.8	88.0 ± 2.2	0.88	274.0 ± 51.5	336.0 ± 66.1	0.48
Peat moss	16.4 ± 16.4	89.5 ± 2.5	0.008	58.0 ± 14.6	226.0 ± 35.9	0.001
Potting soil	0.0 ± 0.0	82.4 ± 3.4	0.001	72.0 ± 14.3	230.0 ± 29.5	0.002

Proportional survival was transformed by the arcsine of the square root. Survival and wood consumption were compared in treated (no additional water added) and control (additional water added) containers for each soil type using a t-test.

did not construct shelter tubes. Although clay soils can retain more water than sandy soils, the clay soils hold the water molecules more tightly so that it is less available to termites (Lys and Leuthold 1994). Shelter tubes not only allow termites to travel up the sides of plastic containers, they provide protection from desiccation. Termites were able to climb up container walls by placing sand particles on the walls. However, they were exposed to the air due to the lack of shelter tube construction. Because the containers were kept in an incubator with 97% RH, sand particles placed on the sides of the containers may have maintained their moisture. It is possible that the ability of termites to obtain moisture from sand particles more easily than soil or clay allowed them to use sand particles to travel up the sides of the containers without the construction of the protective cover of a shelter tube.

There were no colony differences detected in assays examining tunneling behavior, location of termites or wood consumption in moist soils. However, there were significant differences in the behavior of termites from different colonies in the assay using dry soil. Colony five had significantly more termites located in containers with moist sand at the end of the experiment than three of the other colonies. These results suggest that termites from this colony were less likely to colonize wood located on dry soil. Because termites from colony 5 were more likely to remain in the moist sand, they did not suffer 100% mortality in any of the replicates. However, the average survival of colony 5 (70%) was not significantly greater than the average survival of the other colonies (43–53%). Because termites were more likely to remain in the moist sand, there was less evidence of mortality due to desiccation. However, termites from Colony 5 were less likely to colonize the wood blocks and only consumed >200 mg of wood in two of the eight replicates.

Subterranean termites are extremely susceptible to desiccation. To colonize a food source, subterranean termites need moisture. Survival of subterranean termites under conditions of saturated relative humidity and wood moisture content ≤24% was not adequate to sustain a subterranean termite infestation with no soil contact. At least 30% wood moisture was necessary for *R. flavipes* survival for >6 mo. These results indicate that water obtained from the wood by termite feeding did not compensate for water loss, regardless of relative humidity in the air-space (McManamy et al. 2008).

To colonize food sources located in dry soils, termites need to move water molecules from moist soil to the food source (Grube and Rudolph 1999a,b). Contact with the dry soil may have caused rapid desiccation. Sorptive dust causes desiccation by interfering with epicuticular lipids and causing lethal water loss (Ebeling 1971). Although montmorrillonite clay has been used as a sorptive dust to kill termites, it did not cause significantly greater mortality than the other soil types in this study (Ebling 1971). There was at least one replicate from each soil type where termites suffered 100% mortality. Moreover, clusters of desiccated termite bodies were observed on the surface of the dry soil in many of the replicates from all of the soil types tested. These results suggest that components in dry soil of all of the types tested may disrupt epicuticular lipids causing lethal water loss. The cost of colonizing a food source located on dry soil was high even when termites had access to moisture within 5 cm.

Moisture availability affected termite preferences for different soil types. In moist soils, termites were more likely to aggregate in soils with the smallest particle size and the least organic matter. Termites were more likely to aggregate in either top soil or clay than in potting soil or peat moss. In addition, in the paired choice tests, termites were significantly more likely to aggregate in potting soil over peat moss. In contrast, termites were significantly more likely to move into containers with dry soils containing large amounts of organic matter. Termites were more likely to move into containers with dry peat moss and potting soil than in containers with dry sand or clay and significantly more likely to move into containers with dry potting soil than dry top soil.

The susceptibility of termites to desiccation due to evaporation of moisture from soils may have played a role in termite preferences for different soil types. In the assay where water was allowed to evaporate for 25 d, termites could not retain sufficient moisture for survival in either the potting soil or the peat moss and survival was only 63% in the sand due to desiccation of most of the termites in two of the replicates. It is possible that termites were more likely to aggregate in moist top soil and clay because they are able to retain moisture in their galleries for the longest period of time in these substrates.

The ability of termites to move water into dry soils also was affected by soil type. Water molecules hold more tightly to the fine particles of clay than to coarser particles of sand. Therefore, termites were only able to successfully colonize wood blocks located on dry clay in one of the 10 replicates. Generally, soil with more organic matter can retain more water. Sphagnum peat moss and potting soil are used in gardening because they have high water retention capacity, and because the water molecules are readily available to plants. The greater availability of the water molecules to termites seems to be a critical factor in determining the ability of termites to move into containers with dry soil.

The interaction of soil type and moisture availability influences the distribution of foraging termites in microhabitats. Moisture is critical to the survival of subterranean termites. Termites need to be able to transport moisture to construct galleries in dry soils and they need to be able to retain moisture in their galleries when it is evaporating from soils. The need to maintain a constant supply of moisture affects termite behavioral responses to different soil types.

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References Cited

Arab, A., and A. M. Costa-Leonardo. 2005. Effect of biotic and abiotic factors on the tunneling behavior of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). Behav. Processes 70: 32–40.

Cornelius, M. L. 2005. Effect of particle size of different sands on the tunneling behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Sociobiology 45: 173–184.

Ebeling, W. 1971. Sorptive dust for pest control. Annu. Rev. Entomol. 16: 123–157.

Ebeling, W., and R. J. Pence. 1957. Relation of particle size to the penetration of subterranean termites through barriers of sand or cinders. J. Econ. Entomol. 50: 690–692.

Evans, T. A. 2003. The influence of soil heterogeneity on exploratory tunneling by the subterranean termite *Coptotermes frenchi* (Isoptera: Rhinotermitidae). Bull. Entomol. Res. 93: 413–423.

Evans, T. A., and P. V. Gleeson. 2001. Seasonal and daily activity patterns of subterranean, wood-eating termite foragers. Aust. J. Zool. 49: 311–321.

Greaves, T., and R. G. Florence. 1966. Incidence of termites in blackbutt regrowth. Aust. For. 30: 153–161.

Green, J. M., M. E. Scharf, and G. W. Bennett. 2005. Impacts of soil moisture level on consumption and movement of three sympatric subterranean termites (Isoptera: Rhinotermitidae) in a laboratory assay. J. Econ. Entomol. 98: 933–937.

Grube, S., and D. Rudolph. 1999a. The labial gland reservoirs (water sacs) in *Reticulitermes santonensis* (Isoptera: Rhinotermitidae): studies of the functional aspects during microclimatic moisture regulation and individual water balance. Sociobiology 33: 307–323.

Grube, S., and D. Rudolph. 1999b. Water supply during building activities in the subterranean termite *Reticulitermes santonensis* de Feytaud (Isoptera, Rhinotermitidae). Insectes Soc. 46: 192–193.

Haagsma, K. A., and M. K. Rust. 1995. Colony size estimates, foraging trends, and physiological characteristics of the western subterranean termite (Isoptera: Rhinotermitidae). Environ. Entomol. 24: 1520–1528.

Houseman, R. M., and R. E. Gold. 2003. Factors that influence tunneling in the Eastern subterranean termite, *Reticulitermes flavipes* (Kollar) J. Agric. Urban Entomol. 20: 69–81.

Jouquet, P., N. Bottinelli, J.-C. Lata, P. Mora, and S. Caquineau. 2007. Role of the fungus-growing termite *Pseudacanthotermes spiniger* (Isoptera: Macrotermitinae) in the dynamic of clay and soil organic matter. An experimental analysis. Geoderma 139: 127–133.

King, E.G.J., and W. S. Spink. 1969. Foraging galleries of the Formosan subterranean termite, *Coptotermes formosanus,* in Louisiana. Ann. Entomol. Soc. Am. 62: 536–542.

Li, H.-F. 2006. Soil displacement during tunnel excavation by the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) M.S. thesis, University of Florida, Gainesville.

Li, H.-F., and N.-Y. Su. 2008. Sand displacement during tunnel excavation by the Formosan subterranean termite (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. 101: 456–462.

Li, H.-F., and N.-Y. Su. 2009. Buccal manipulation of sand particles during tunnel excavation of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 102: 333–338.

Lima, M. M., T. T. Goncalves, O. DeSouza, and R. Reis, Jr. 2006. Nesting site selection by *Coptotermes gestroi* (Insecta: Isoptera). Sociobiology 48: 681–688.

Liu, X., H. C. Monger, and W. G. Whitford. 2007. Calcium carbonate in termite galleries—biomineralisation or upward transport. Biogeochemistry 82: 241–250.

Lys, J.-A., and R. Leuthold. 1994. Forces affecting water imbibition in *Macrotermes* workers (Termitidae: Isoptera). Insectes Soc. 41: 79–84.

McManamy, K., P. G. Koehler, D. D. Branscome, and R. M. Pereira. 2008. Wood moisture content affects the survival of Eastern subterranean termites (Isoptera: Rhinotennitidae), under saturated relative humidity conditions. Sociobiology 52: 145–156.

SigmaScan. 1999. SigmaScan Pro 5.0 user's guide. SPSS Inc., Chicago, IL.

Smith, J. L., and M. K. Rust. 1993. Effect of relative humidity and temperature on the survival of *Reticulitermes hesperus* (Isoptera: Rhinotermitidae). Sociobiology 21: 225–236.

Smith, J. L., and M. K. Rust. 1994. Temperature preferences of the western subterranean termite, *Reticulitermes hesperus* Banks. J. Arid Environ. 28: 313–323.

Su, N.-Y., and H. Puche. 2003. Tunneling activity of subterranean termites (Isoptera: Rhinotermitidae) in sand with moisture gradients. J. Econ. Entomol. 96: 88–93.

Su, N.-Y., and R. H. Scheffrahn. 1992. Penetration of sized-particle barriers by field populations of subterranean termites (Isoptera: Rhinotermitidae) J. Econ. Entomol. 85: 2275–2278.

Systat Software, Inc. 2007. SYSTAT statistical package, version 12.0. Systat Software, Inc., San Jose, CA.

Tamashiro, M., J. R. Yates, and R. H. Ebeling. 1991. Tunneling behavior of the Formosan subterranean termite and basalt barriers. Sociobiology 19: 163–170.

Tucker, C. L., P. G. Koehler, and F. M. Oi. 2004. Influence of soil compaction on tunnel network construction by the eastern subterranean termite (Isoptera: Rhinotermitidae) J. Econ. Entomol. 97: 89–94.

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