Subterranean Termite Behavioral Reaction to Water and Survival of Inundation: Implications for Field Populations

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ABSTRACT Laboratory tests involving termite response to rising water levels demonstrated that subterranean termites (*Reticulitermes* spp.) do not try to escape being submerged. Studies in which termites were completely submerged in water provided LT_{50}s of 19.6 h for eastern subterranean termites, *Reticulitermes flavipes* (Kollar), 13.9 h for *R. virginicus* (Banks), and 11.1 h for, Formosan subterranean termites, *Coptotermes formosanus* Shiraki. These data suggest that subterranean termites, in the field, escape drowning not by seeking higher ground but by entering a state of quiescence when confronted with excessive amounts of water in their subterranean habitat. Under normal rainfall conditions, water should move through the soil profile within several hours. If this does not occur, then high termite mortality could result. In the summer of 1992, we characterized the foraging populations of 5 subterranean termite colonies using the triple mark–recapture technique. These colonies averaged 99,000 (range, 157,000–14,000) foraging termites per colony. In the spring 1993, these same colonies were recharacterized and their populations averaged 21,000 (range, 53,000–1000) foraging termites per colony. This represents a 77% reduction in the average foraging populations for these colonies. In this article we provide empirical evidence that these population reductions were a result of heavy rainfall in west–central Georgia during the winter of 1992–1993.

KEY WORDS *Reticulitermes flavipes, Reticulitermes virginicus, Coptotermes formosanus,* rainfall, drowning, behavior

SUBTERRANEAN TERMITES OF the family Rhinotermitidae are ubiquitous inhabitants of the soil environment in most of the southern Nearctic region. Termites of this family live in colonies which occupy a diffuse network of underground tunnels connecting 1 or more feeding sites, nurseries, and reproductive chambers. These cryptic insects are important in the degradation of cellulose and the physical and chemical alteration of the soil matrix (Kofoid 1946, Weesner 1965, Wood and Sands 1978).

Termites, however, can be a significant threat to wooden structures. Estimates of the damage and control costs in the United States alone have ranged from $100 million to $3.4 billion annually (Su and Scheffrahn 1990). Despite the ecological and economic importance of subterranean termites little is known about interspecific interactions, seasonal movements, feeding habits, population fluctuations, and response to environmental perturbation in the field. In the United States, recent field work has shown that termite colonies can contain over 1 million termites and occupy foraging territories up to 2,000 m² (Grace et al. 1989, Su et al. 1993).

During our field work on termite biology, we recorded a drastic reduction in estimates of termite foraging populations from 5 colonies of *Reticulitermes* between the summer of 1992 and spring of 1993. We hypothesized that these reductions resulted from heavy rainfall that occurred in central Georgia during the winter of 1992–1993. This led to a series of laboratory tests that examined the reaction of subterranean termites to rising water and their survivorship following inundation. In this article, we report data that supports our contention that conditions of prolonged soil saturation can adversely affect subterranean termite populations.

Materials and Methods

Field Site Establishment and Population Estimates. Areas of termite activity were located using the bait stake method with wooden survey stakes (1.5 by 3.5 by 30 cm) purchased at a local lumber yard (Thompson 1985). Stakes were placed ≈27 cm into the soil in inconspicuous locations (that is, along fence rows, hedges, base of trees) in residential areas or on 1-m centers in grids of various sizes in forested habitats. Stakes were examined monthly for signs of termites by removing stakes from the ground by hand. When termites were found feeding on a stake they were dislodged

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by gently tapping the stake over an aluminum baking pan (44 by 29 cm). A termite monitor was then located in lieu of the stake and the dislodged termites placed inside the newly established termite monitor.

Termite monitors consisted of a PVC pipe receptacle, an undisturbed feeding site, and a removable food and aggregation substrate. Termite monitor receptacles are 16-cm lengths of PVC pipe (10 cm diameter) buried at least 17 cm deep. A 4-cm length of a white pine 2 by 4 was buried below the PVC pipe and served as an undisturbed feeding site. Two termite feeding and aggregation substrates (sandwiches) were placed inside the monitor on top of the undisturbed feeding site. Termite sandwiches consist of 10 pieces of weathered *Pinus* spp. wood (4 cm by 12 cm by 2 mm) separated by wooden dowel sticks (2 mm diameter) held together by plastic cable ties (18 cm length) (GB Electric, Milwaukee, WI). Termite monitors were capped using a plastic Knock-Out Plug (10 cm diameter), and a thin layer (1–3 cm) of soil was placed over the monitor.

When several active monitors were established in the same area termites from one monitor were removed, marked with fluorescent spray paint, immediately released, and recaptured 1 wk later. This technique allowed us to determine which monitors were being used by the same colony of termites (Forschler 1994). Foraging areas for each termite colony were defined as the area encompassed by the active termite monitors from which the same color paint-marked termites were recovered. Once determinations of colony foraging areas was made, foraging populations were estimated using the fat soluble dye, Nile Blue A, and the mark–release–recapture technique of Su et al. 1993. Each week for 5 wk, termites were collected from all monitors for each colony and returned to the laboratory. Termites were marked by placing no more than 2 g of termites in a petri dish (100 by 15 mm) with a No.1 Whatman filter paper (9 cm diameter) that had been stained with a 0.05% (wt:wt) solution of Nile Blue A in distilled water. These petri dishes were maintained in complete darkness in an environmental chamber at 24°C. Termites that were visibly marked at the end of 1 wk were counted and returned to the monitor from which they were collected. Termites collected after the 1st and subsequent releases were examined for the presence of marked individuals. Collected termites were placed on an aluminum baking pan and the number of marked termites recorded following visual examination. The numbers of marked and unmarked termites collected and the number of marked termites released, by week, were used in a weighted mean model for estimation of termite foraging populations and associated standard errors (Begon 1979, Su et al. 1993). Five *Reticulitermes* colonies were characterized in 1992, 4 in Lamar County and 1 in Gwinnett County, Georgia. In 1993, these same colonies were included in a group of 33 colonies characterized in Gwinnett, Lamar, Spalding, Sumter, and Union counties.

Rainfall Data. Rainfall data were recorded by the Georgia Automated Environmental Monitoring Network (GAEMN) at the Georgia Experiment Station for the period from 20 November through 13 January 1990–1993. Four of the 5 termite colonies characterized in 1992 and again in 1993 were within a 30-km radius of this GAEMN station.

Termites. Eastern subterranean termites, *Reticulitermes flavipes* (Kollar), and *R. virginicus* (Banks) were collected from infested logs found at the University of Georgia Westbrook Farm near Griffin, GA. Termites were extracted from logs brought into the laboratory using the technique described by La Fage et al. (1983). Groups of, Formosan subterranean termites, *Coptotermes formosanus* Shiraki were collected from cardboard rolls placed into the bole of infested trees in New Orleans, LA. Alates associated with each *Reticulitermes* colony were used to identify species and soldiers were used for identification of *C. formosanus* (Weesner 1965).

Reticulitermes groups were maintained in clear plastic boxes (26 by 19 by 9 cm) containing several moistened No.1 Whatman filter papers and 1-cm^3 blocks of white pine wood. *Coptotermes* were maintained as described above except each plastic box also contained a small portion of carton nest material taken from the field site. Termites were maintained in an environmental chamber in total darkness at 24°C for no longer than 1 mo before inclusion in a bioassay. Only undifferentiated workers, of at least 3rd instar, were used in all tests. Four different colonies of each termite species were used in each bioassay.

Termite Behavior in Response to Rising Water. In the 1st tests, *R. flavipes* termites were exposed to rising water levels to examine their behavioral response. Fifteen groups of 100 termites were placed in 500-ml plastic weigh dishes (Fisherbrand, Fisher, Pittsburgh, PA) that had 3 sets of wood blocks anchored, using silicone sealant, to the bottom of the weigh dish. The 1st block of wood measured 5 by 3 by 0.2 cm and constituted the 1st level. The 2nd level consisted of 2 blocks (2 by 2 by 1 cm) side by side on top of which were two 1-cm^3 blocks. This arrangement created 3 levels above the bottom of the weigh dish.

Water was introduced into the weigh dish using a 100-ml burette supported by a burette stand. Water was slowly dripped into the weigh dish from the burette at 1 of 4 rates; 1, 2, 5, and 10 ml/min (5, 5, 4, and 1 replicates, respectively). When the 2nd tier of wood blocks was covered with water the number of termites on the highest level (two 1-cm^3 blocks) was counted. In addition, the number of termites floating and underwater was recorded.

In a separate test, 40 groups of 50 *R. flavipes* were placed in a clear plastic container (5 cm di-

Table 1. Comparison of mark–release–recapture estimates of 5 subterranean termite colony foraging populations (mean ± SEM) from west-central Georgia in 1992 and 1993, by colony and year

Colony no.	Species	1992 population estimate	1993 population estimate	% population reduction
1	*R. flavipes*	106,550 ± 9,418	27,667 ± 1,066	74
2	*R. virginicus*	156,997 ± 21,991	20,109 ± 3,278	87
3	*R. flavipes*	104,963 ± 24,119	52,826 ± 5,231	50
4	*R. flavipes*	113,786 ± 9,230	18,117 ± 880	84
5	*R. hageni*	14,556 ± 2,428	970 ± 73	93

ameter) with 20 g of sandy loam soil at 15% soil moisture (wt:wt). Each container had three 1-cm^3 blocks of wood placed one on top of the other so that the top block protruded from the soil surface. Termites were placed in this arena and allowed 72 h to establish a network of tunnels in the soil. Water was then added to the soil-filled arenas as described above, at 1 of 3 rates: 1.0, 0.5, and 0.25 ml/min (20, 10, and 10 replicates, respectively). Behavior of termites, in tunnels adjacent to the sides of the arena, was recorded as the water level rose in the arenas. When water covered the soil surface, the number of termites on the exposed wood block was recorded.

Termite Survivorship Following Submersion. Termites inundated in the soil arenas described above were excavated from the soil after 24, 48, 72, 96, and 110 h. Termites were recovered from the inundated soils using a pair of soft forceps and placed on moistened filter paper disks inside petri dishes (100 by 15 mm). The number of living termites was recorded 24 h after they were removed from the soil.

In another set of experiments, termites were submerged in arenas free of possible air contact. For each of the 3 species tested, 10 termites were placed in clear plastic vials (6 cm height, 1.5 cm in diameter) containing a 13-mm-diameter disk of No.1 Whatman filter paper moistened with deionized water. A 1-mm mesh plastic screen (5 by 5 cm) was then pushed half-way into each vial to form a barrier to flotation. Vials were filled with deionized water and capped with a plastic cap or No.2 rubber stopper. Vials were tapped on the bench top to dislodge air bubbles from the screen or termites.

Termites were left submerged for 1 of 9 time periods: 1, 4, 8, 10, 12, 16, 20, 24, or 28 h. Controls consisted of vials with termites left for the same time period without water. At the appropriate time, vials were opened, the plastic screen removed, and water and termites poured into a Buchner funnel containing a No.1 Whatman filter paper disk (9 cm diameter). Water was allowed to drain through the filter paper after which the filter paper containing termites was placed in a petri dish (100 by 15 mm). The number of live termites was counted 24 h after removal from a vial. There were 10 groups of 10 termites tested for each period for each of 3 termite species. Data were analyzed by probit analysis to obtain lethal time (LT) values, in hours, for each species (SAS Institute 1988).

Results

Termite Foraging Population Estimates. The 5 colonies characterized in the late summer of 1992 averaged 99,000 (range, 157,000–14,000) foraging termites per colony (Table 1). When we recharacterized those same colonies in 1993, the population estimates indicated drastic reductions with an average of 21,000 (range, 52,000–1,000) foraging termites per colony (Table 1). In 1993, we characterized 28 additional colonies and these colonies averaged 51,000 (range, 195,000–3,000) foraging termites per colony.

The 5 colonies monitored in 1992 were characterized during August. They were recharacterized in May 1993. Therefore, we cannot discount the possibility that seasonality affected the foraging population estimates. However, comparison of the termite foraging population estimates made in 1993, by time of year, showed that the mean estimates were similar. Analysis of the colonies characterized in May 1993 showed an average foraging population of 55,000 (range, 195,000–1,000), those characterized in July–September 1993 was 54,000 (range, 121,000–3,000), and those in October–November 1993 was 35,000 (range, 108,000–5,000). In addition, 4 out of 5 colonies characterized in 1992 (80%) had foraging population estimates over 100,000. In contrast, in 1993 only 3 out of 33 (9%) foraging population estimates were over 100,000.

Conditions Conducive to Saturated Soils. Soils of west-central Georgia are typical of the Cecil Series southern Piedmont soils. These soils have a thin layer of material between the B (subsoil) and C (parent material) horizons that displays very low permeability to water and tends to trap water in the A and B horizons (Radcliffe et al. 1990). Cecil soils in the southern Piedmont region are generally near saturation during the winter months so that prolonged periods of rainfall would have the tendency to maintain saturated soil conditions.

Weather data from the winter of 1992 indicated that precipitation amounting to 15.83 cm was recorded between 21 and 26 November (Fig. 1). During this period it rained 6 out of 7 d with the heaviest daily total (8.3 cm) occurring on 25 November. Beginning 4 December rains again fell 6 out of 7 d for a total of 3.4 cm. On 16 and 17

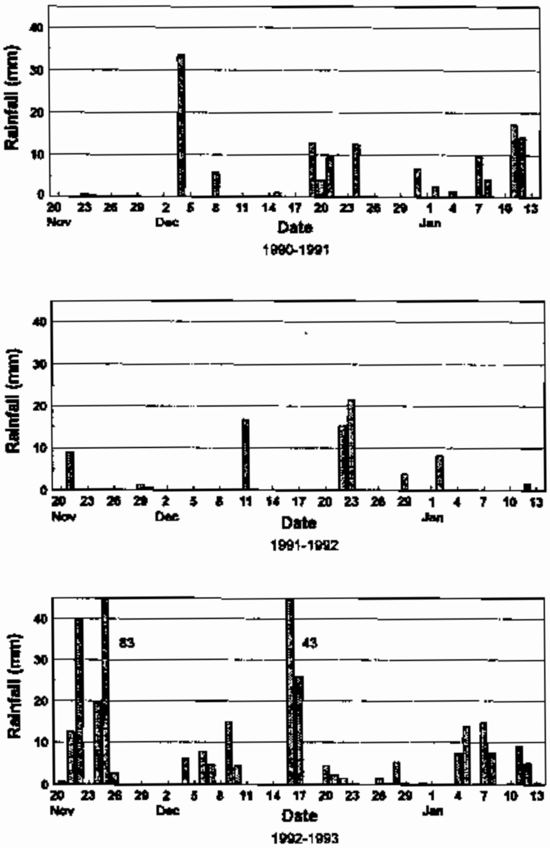

Fig. 1. Daily precipitation (mm), by year, recorded at the Georgia Automated Environmental Network from 20 November through 15 January 1990–1993.

December it rained a total of 7.1 cm. From 20 to 30 December there were only 2 d when no rain was recorded: total rainfall for this period was 1.6 cm. Beginning on 4 January 1993, rainfall totaling 5.8 cm fell over 10 d with only 1 d without rain. This amounted to 4 periods within 55 d, under near-saturated soil conditions, that prolonged periods of rainfall occurred. It rained 58% of the days between 20 November 1992 and 13 January 1993 for a total of 34.4 cm. Precipitation from mid-November 1990 through mid-January 1991 amounted to 13.6 cm with 2 periods (4 of 6 d and 7 of 13 d) with prolonged rainfall or 29% of the days (Fig. 1). During the same period in 1991–1992, 7.8 cm of rain fell including 1 period of extended rainfall (3 of 8 d) for a total of 16% of the days recording precipitation (Fig. 1).

Termite Behavioral Response to Rising Water. Tests conducted in open arenas (weighing dishes) indicate that termites do avoid slowly rising water. Termites would approach the expanding drop of water and antennate the water before making contact with their mouthparts or reversing direction. If water was dripped into the weigh dish at 2 ml/min or slower, <95% of the termites moved away from the advancing water as it filled the bottom of the arena. A small percentage (2–3%) of each group tested simply stopped after antennating the advancing water and were subsequently submerged. If water was added faster than 2 ml/min most termites were overtaken by the advancing water and floated on the surface. Again a small percentage (2%) would stop moving and become submerged.

Tests conducted in soil arenas provided similar behavioral responses. However, water could not be dripped into the arenas slowly enough to elicit avoidance behavior. Those termites in horizontal galleries would antennate the advancing water, stop moving and become submerged. Termites in galleries oriented vertically would antennate the water, turn and move toward the soil surface, stop before reaching the surface, return to the water and often repeat this process several times before stopping in the gallery to be inundated. In no instance did termites in the soil arenas leave the confines of their gallery system to escape the rising water.

Survival of Submerged Termites. Termite survivorship following submersion in water was different for the different species tested. Each termite species tested provided statistically different LT values (hour), as judged by lack of confidence limit (95% CL) overlap. *C. formosanus* demonstrated the least tolerance to submersion with LT_{50} and LT_{90} of 11.1 and 15.8 h, respectively (Table 2). *R. flavipes* proved to be the most tolerant to submersion with a LT_{50} of 19.6 and a LT_{90} of 29.7 h *R. virginicus* was intermediate at 13.9 and 23.0 h (Table 2). The LT_{50} for *R. flavipes* in the submerged soil arenas was 67.0 h (95% CL 44.6–99.6) which was statistically higher than the LT_{50} for that same species in the test tube assays. The reason for this extended survivorship is that, in the soil arenas, termites were frequently surrounded by air pockets within the gallery system. In contrast, termites submerged in test tubes were surrounded by only water. Air pockets in the soil arenas could have provided a reservoir of additional oxygen for those termites. Together these data indicate that

Table 2. Comparison of LT_{50}s (h) and LT_{90}s (h) with 95% CLs and associated slopes ± SEM from termite submersion tests conducted in test tubes, by species

Species	LT_{50}	95% CL	LT_{90}	95% CL	Slope ± SEM
R. flavipes	19.6	(17.9–21.6)	29.7	(26.8–34.1)	0.13 ± 0.1
R. virginicus	13.9	(13.1–14.6)	23.0	(21.8–24.4)	0.14 ± 0.1
C. formosanus	11.1	(10.0–12.2)	15.8	(14.3–18.2)	0.27 ± 0.3

subterranean termites have the ability to survive periods of submersion in water.

Discussion

Mark–recapture estimates of animal abundance have been used for decades to predict gross trends in dynamics of field populations. Our use of the triple mark–recapture technique with termite populations demonstrated, under field conditions, that subterranean termite foraging populations in Georgia were significantly reduced during the winter of 1992–1993. We believe this reduction in foraging population estimates was a result of prolonged periods of rainfall causing saturated soil conditions. The population estimates obtained from 5 colonies in 1992 were lower than those obtained for *Reticulitermes* through similar methodologies by Grace et al. (1989) in Toronto and Su et al. (1993) in Florida but were comparable to those obtained by Howard et al. (1982) who used a destructive sampling technique in Mississippi. The even lower population estimates we obtained in 1993 were not indicative of a seasonality effect with the technique used to estimate termite populations. Therefore, we believe this observed reduction in subterranean termite foraging population estimates was representative of an overall trend across the Piedmont soils in Georgia.

Populations of subterranean termites are, from time to time, confronted with water in their underground galleries and below-ground feeding sites. Although termite galleries may be water-resistant to some degree, under conditions of prolonged precipitation and saturated soils this water-tight integrity would be difficult if not impossible to maintain. The ability of termites to orient in their subterranean gallery system to locations which are not subject to flooding is unknown. However, there would be an evolutionary advantage in termites avoiding movement through water filled galleries. Assuming rainwater moves through the A and B horizons of most soil types within several hours or days it would be advantageous for termites to depress metabolic activity to prolong survivorship and wait before resuming normal activity. It is well known, though we could find no published reference to the fact, that termites cannot be forced out of infested material by slowly submerging the substrate under water. This offers a clue to the unusual behavioral response these insects have evolved to cope with periods of inundation.

Our submersion tests demonstrate that subterranean termites can survive extended periods under water. Our behavioral studies confirm that they will not leave the gallery system to escape rising water. Together these data indicate a decided survival strategy that subterranean termites have evolved to survive periods of heavy rainfall. It is not surprising that *C. formosanus* would provide the lowest lethal time data, indicating less adaptability to surviving inundation. *Coptotermes formosanus* shows a proclivity for building discrete, above ground auxiliary nests and regularly attacks living trees in contrast to *Reticulitermes* species. This reduced dependency on below ground nesting and feeding sites would decrease the necessity for adapting to episodic inundation in the soil matrix and could indicate an alternative strategy for surviving those conditions.

The fact that *R. virginicus* provided results from the test tube assays showing lower survivorship may indicate different resource utilization strategies by termites which are sympatric inhabitants of the same habitats. In Georgia during 1994, we collected 40 termite-infested, fallen logs for collection of laboratory animals. Fifty-three percent of these contained *R. virginicus* despite our best efforts to collect only *R. flavipes*. In contrast, 78% of the 117 active termite monitors we are currently maintaining are *R. flavipes*, 8% *R. virginicus*, and 14% *R. hageni* or another undescribed species from the Coastal Plains and Atlantic Flatwoods soil zones (B.T.F., unpublished data). Because our field site monitors are located by termite attacks on stakes sunk in the ground these empirical data indicate that *R. virginicus* may forage closer to the soil surface exploiting wood resources on the ground more than its sympatric cogenator, *R. flavipes*, which may more likely utilize below-ground wood. This tendency could explain the lower tolerance to submersion by *R. virginicus* in our drowning experiments. These data also are consistent with experiments which have shown that *R. flavipes* is more susceptible to water loss than *R. virginicus* (Collins 1969).

The record of precipitation from 1990–1992 shows no comparable period of prolonged rainfall to that recorded during the winter of 1992–1993. These data indicate that 2 yr previous to 1993 termite populations in this area were not subjected to prolonged periods of saturated soil conditions, as a result, termites were not subjected to that negative effect on their populations. The detrimental effect of saturated soil conditions on subterranean termites was hinted at in a report by A. Giordani-Soika to the 4th Congress of the International Union for the Study of Social Insects held in Pavia, Italy. Giordani-Soika stated "*Reticulitermes* accidently introduced to Venice are very localized or eliminated because of high soil moisture and frequent inundations" (Snyder 1962). Our data further suggest that prolonged periods of rainfall and saturated soil conditions can exert a negative influence on the population dynamics of subterranean termites. This information also may, in part, explain the paradigm that subterranean termites do not find favorable conditions in clay soils (Kofoid 1946).

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