Survival of Termites ( Isoptera ) Exposed to Various Levels of Relative Humidity ( RH ) and Water Availability, and Their RH Preferences

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Survival of termites (Isoptera) exposed to various levels of relative humidity (RH) and water availability, and their RH preferences

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Abstract
Termite (Isoptera) are widely believed to be one of the most desiccation-prone insects. They must combat desiccation by locating and efficiently conserving water resources. Termites have evolved morphological, physiological, and behavioral characteristics that aid in the tolerance of desiccation. In 3 studies using 4 termite species, water loss tolerance and relative humidity (RH) preferences of termites exposed to 5 different RH, as well as the use of different water sources, were examined. Our results showed that Coptotermes formosanus Shiraki (Rhinotermitidae) preferred and survived better at high RH and with readily available water sources. Neotermes jouteli (Banks in Banks and Snyder) (Kalotermitidae) also preferred a high RH, but was more capable of tolerating lower RH and a lack of free water than C. formosanus. Cryptotermes brevis Walker (Kalotermitidae) and Cryptotermes cavifrons Banks (Kalotermitidae) did not exhibit greater survival in a certain RH nor when exposed to various sources of water. These two species also did not exhibit a preference for a certain RH.

Key Words: dampwood termite; desiccation; drywood termite; huddling; subterranean termite

Due to their small size and relatively un sclerotized body, water loss is a common problem facing all termite species, and they must locate and utilize water resources to prevent or tolerate desiccation. Water resources may be found as free water, moist food, or moist soil. Termites live in various habitats and microhabitats with differing levels of ambient humidity and availability of water, and water management among termite species has been the subject of many studies (Collins 1958, 1963, 1966, 1969; Abushama 1974; Rust et al. 1979; Steward 1983; Sponsler & Appel 1990; Rudolph et al. 1990; Grube & Rudolph 1999a, 1999b; Gallagher & Jones 2010; Gautam & Henderson 2014). Some kalotermitid termites exhibit behavior and impacts on survival that indicate that high humidity is toxic to them (Collins 1969; Minnick et al. 1973; Steward 1982, 1983; Rudolph et al. 1990; Woodrow et al. 2000). Strickland (1950), Collins (1958, 1969, 1991), and Khan (1980), found that different termite species can tolerate various (sometimes extreme) humidity and temperature conditions; however, there are undoubtedly conditions that termites prefer over other conditions that they can tolerate.

The first objective of this study was to investigate the survivorship of 4 termite (Isoptera) species that inhabit distinctly different microhabitats, including Coptotermes formosanus Shiraki (Rhinotermitidae), Neotermes jouteli (Banks in Banks and Snyder) (Kalotermitidae), Cryptotermes brevis Walker (Kalotermitidae), and Cryptotermes cavifrons Banks (Kalotermitidae). Cryptotermes formosanus and N. jouteli live in high relative humidity (RH) environments, whereas C. brevis is found in dry timber and C. cavifrons is found in natural wood that can be wet or dry.

The second objective of this study was to investigate the RH preferences of the aforementioned species. Humidity is not the only water source available to termites. There are other water sources that termites might use. These include metabolic water obtained through the breakdown of food, from the fat body, free liquid water, as well as water bound to various substrates (e.g., wood, soil, and nematode cadavers). Different termite species (i.e., drywood, dampwood, subterranean) use or avoid certain environments with different moisture and water sources. Whereas drywood termites depend heavily on metabolically derived water, dampwood and subterranean termites that live in high RH environments obtain water from their surroundings (Lee & Wood 1971, Brammer & Scheffrahn 2007, Scheffrahn & Su 2007). The third objective of this study was to investigate whether these 4 termite species use a variety of water sources for survival.
TERMITES IF FUTURE STUDIES

Materials and Methods

INSECT COLONIES

Individuals from colonies of C. formosanus, N. jouteli, C. cavifrons, and C. brevis were collected in Broward County, Florida. Different colonies of C. formosanus were collected from bucket traps as described by Su and Scheffrahn (1986). Colonies of N. jouteli, C. cavifrons, and C. brevis were collected from different pieces of wood. Coptotermes formosanus and N. jouteli were kept in polystyrene boxes (17.15 × 12.22 × 6.03 cm) with wood (Pinus sp.) maintained at 26.4 °C, and were regularly misted with water to maintain >95% RH. Cryptotermes termites were kept in polystyrene boxes with wood pieces and stored in the incubator (26.4 °C and 41.5% RH). For C. cavifrons, small dishes with water were provided. Populations of each termite species survived well in these conditions and were used for experiments as needed. Termites were kept in the incubator for <6 mo before use.

TERMITE SURVIVORSHIP AT VARIOUS RELATIVE HUMIDITIES

Desiccative humidity chambers consisted of clear polystyrene boxes (17.15 × 12.22 × 6.03 cm) with internal RH conditions stabilized using three saturated salt solutions (i.e., NaCl, Mg(NO$_3$)$_2$, and MgCl$_2$), silica gel, and water (Fig. 1A) as described by Rockland (1960), and Winston and Bates (1960). Open Petri dishes (93 mm diameter, 22 mm height) containing water or 1 of the saturated salt solutions and Winston and Bates (1960). Open Petri dishes (93 mm diameter, 22 mm height) containing water or 1 of the saturated salt solutions were placed at the center of 4 chambers (Fig. 1A, a–d), while silica gel was placed on the bottom of the chamber (Fig. 1A, e) to produce the lowest RH. The container edge was coated with petroleum jelly (Eboone Products Company, Inc., Hartford, Connecticut) to create a seal between the lid and chamber. Temperature and humidity levels were measured daily using a probe (THW3; Amprobe, Everett, Washington) through an access hole (1.59 cm diameter) in the lid. These holes were plugged with rubber stoppers while not in use (Fig. 1B, h). The average RH (± standard error of the mean (SEM)) of the chambers and their associated stabilizing material were as follows (n = 73): 92.0 ± 0.07% (H$_2$O), 72.9 ± 0.08% (NaCl), 55.7 ± 0.09% (Mg(NO$_3$)$_2$), 34.3 ± 0.04% (MgCl$_2$), and 18.2 ± 0.14% (silica gel). The average temperature (± SEM) of the chambers and their associated stabilizing material were as follows (n = 73): 23.5 ± 0.06 °C (H$_2$O), 23.6 ± 0.06 °C (NaCl), 23.5 ± 0.06 °C (Mg(NO$_3$)$_2$), 23.7 ± 0.06 °C (MgCl$_2$), and 23.6 ± 0.06 °C (silica gel). Groups of 10 termite individuals per species were placed in the Petri dish (35 mm diameter, 10 mm height) of each chamber with small holes cut into the lids of the dishes to allow air movement and yet prevent termite escape. Dishes were also provisioned with a small (15 × 15 × 9 mm) piece of wood (Pinus sp.) as a food source. Four dishes, each containing 1 of the 4 termite species, were placed in the humidity chamber surrounding water or salt solutions (Fig. 1A, a–d), or on top of the silica gel in a chamber (Fig. 1A, e).

Temperature and humidity readings were recorded every 24 h post-introduction for 12 d. Daily counts of live termites were recorded for a 12 d period. A follow-up experiment also was conducted to examine recovery of N. jouteli individuals that exhibited visible reduction in body mass. At the conclusion of the 12 d study, the surviving N. jouteli individuals from the various RH were weighed and then placed in a Petri dish and provided with food and water for 1 wk. Surviving termites were counted and weighed again to examine recovery when provided with adequate food and water resources.

Statistical analysis was carried out using JMP statistical software (SAS 2015). An analysis of variance (ANOVA) for a 4 by 5 factorial experimental design was conducted to test for differences. Termite species (4) and RH (5) were the factors, and percentage survival was the response variable. Percentage survival values were arcsine-square root transformed before analysis. Post hoc Tukey honest significant difference tests were used to evaluate all pairwise differences at α = 0.05. Data from 6 replications were analyzed.

TERMITE PREFERENCE FOR VARIOUS RELATIVE HUMIDITIES

Multiple-choice arenas were constructed by connecting a central chamber (89 mL [3 oz] clear plastic jars, 52 mm diameter, 53 mm height) with four radial chambers (Fig. 2A). Drierite (W.A. Hammond DRIERITE Co., Ltd., Xenia, Ohio) was used for the central chamber, whereas water, NaCl, Mg(NO$_3$)$_2$, and MgCl$_2$ were used for the 4 radial chambers to maintain desired RH. The average (n = 21) RH (± SEM) of the chambers and their associated stabilizing material were as follows: 90.7 ± 0.24% (H$_2$O), 71.7 ± 0.20% (NaCl), 52.0 ± 0.12% (Mg(NO$_3$)$_2$), 34.1 ± 0.16% (MgCl$_2$), and 8.4 ± 0.48% (Drierite). The average (n = 21) temperature (± SEM) of the chambers and their associated stabilizing material were as follows: 23.4 ± 0.06 °C (H$_2$O), 23.5 ± 0.06 °C (NaCl), 23.4 ± 0.06 °C (Mg(NO$_3$)$_2$), 23.4 ± 0.06 °C (MgCl$_2$), and 23.4 ± 0.05 °C (Drierite). A temperature and humidity probe was inserted through access holes (1.59 cm diameter) in the lids to take measurements inside the chambers as described previously (Fig. 2A, b). Relative humidity stabilizing solutions or materials were placed in the bottom of the jar chambers (Fig. 2B).

Chambers housed modified plastic vials (25 mm inner diameter, 15 mm height) cut to hold the termites while preventing their escape (Fig. 2C, k). A hole (6 mm diameter) was drilled into the wall of each of the 4 radial chambers (2.5 cm from base) to allow pieces of plastic tubing (5.5 mm diameter, 50.0 mm length) (Fig. 2C, j) to connect radial termite vials to the vial in the central chamber. All termite vials were suspended by plastic tubes above the stabilizing materials. Groups of 25 pseudergates were placed into the introduction chamber for the larger sized species N. jouteli, while 50 termites (pseudergates and workers) were used for the other 3 smaller sized species. Termites could move and acclimate to any chamber for 12 to 16 h. Black satin cloth covered the arenas to provide darkness. Counts of termites within each chamber were then recorded. Termites found in the connecting tubes were included in the counts for the connected chamber. Statistical analysis was conducted using JMP statistical software (SAS 2015). A 4 by 5 factorial analysis was conducted with termite species (4) and RH (5) as the factors and percentage of termites found in a chamber as the response variable. The percentage values were arcsine-square root transformed before the analysis of variance (ANOVA) was used to test whether there was a significant difference among RH preference for the 4 species. Post hoc Tukey honest significant difference tests were used to separate the differences for all pairs at α = 0.05. Data from 6 replications were analyzed.

TERMITE SURVIVORSHIP WITH VARIOUS TYPES OF WATER SOURCES

Experimental chambers were constructed using clear plastic jars (52 mm diameter, 53 mm height) with plastic lids and lid liners. The bottoms of these jars were scratched with sandpaper to provide traction for termite movement. Temperature and humidity levels inside the jars were measured as described previously. Five chambers that provided various sources of water, or the lack thereof, were used for the experiment. These included: chambers with a piece of dry wood (Pinus sp.; 18 × 18 × 8 mm), a piece of dry wood with a humidity source (i.e., a 2 × 6 cm wetted filter paper strips attached to the upper inner side of the chamber), a piece of wet wood, a piece of dry wood with wet sandy soil (5 g sand + 1.5 mL deionized water), and a piece of dry wood with a source of free...
water in a small dish (modified shell vial cap, 15 mm diameter, 3 mm height). Water was added as needed to maintain RH and free water levels. The average (n = 48) RH (± SEM) of the chambers and their associated water sources were as follows: 91.0 ± 0.07% (wet wood), 49.6 ± 0.61% (dry wood), 92.6 ± 0.22% (wet soil), 91.1 ± 0.22% (wood + water), and 94.2 ± 0.18% (wood + RH). The average (n = 48) temperature (± SEM) of the chambers and their associated water sources were as follows: 24.2 ± 0.08 °C (wet wood), 24.1 ± 0.08 °C (dry wood), 24.2 ± 0.07 °C (wet soil), 24.2 ± 0.07 °C (wood + water), and 23.0 ± 0.03 °C (wood + RH).

Three sets of each of the chambers were broken down weekly for 4 wk to record termite survival for each species using destructive sampling. The data were analyzed using JMP statistical software (SAS 2015) and a 4 by 5 factorial experimental design with termite species (4) and water source (5) as the factors, and percentage survival as the response variable. Percentage survival data were arcsine square root transformed before analysis. ANOVA was conducted to test for significant differences and post hoc Tukey honest significant difference tests were used to separate the differences for all pairs at α = 0.05. Data from 3 replications were analyzed.
Results

TERMITE SURVIVORSHIP AT VARIOUS RELATIVE HUMIDITIES

Termites displayed statistically different responses to RH ($F = 90.0; df = 3, 116; P < 0.001$). There was no significant difference in survival at any RH (18.2–92.0%) for *Cr. cavifrons*, *Cr. brevis*, and *N. jouteli*, but there was a significant difference for *C. formosanus*. This species survived at 92.0% RH, but died within a few days when maintained at ≤72.9% RH (Table 1). However, *N. jouteli* individuals in all the humidity chambers (18.2–72.9% RH) except the water chamber (92.0% RH) were visibly smaller at the end of the experiment than at the start. The *Cryptotermes* species did not exhibit this change in size. At 18.2 to 72.9% RH levels, *N. jouteli* groups decreased in mass (4.4–151.2 mg loss per 10 termites). Of the 180 *N. jouteli* individuals that survived at the various RH and were then placed in a dish and provided with food and water, 172 recovered. These 172 individuals exhibited a total weight gain of approximately 327 mg. The remaining 8 individuals were not accounted for, indicating they may have been cannibalized by nestmates as a food and water source. The *N. jouteli* groups of 10 individuals exhibited a decrease in mass of approximately 42.0% of their weight, either due to the loss of body water or body fat.

TERMITE PREFERENCE FOR VARIOUS RELATIVE HUMIDITIES

Termites displayed statistically different responses to RH ($F = 7.06; df = 3, 116; P < 0.001$). The wetwood (nests in wood or soil high in moisture) species of *C. formosanus* and *N. jouteli* preferred the highest RH of 90.7% RH, which was significantly more than *Cr. cavifrons* and *Cr. brevis* and significantly more than the other RH (Table 2). The *Cryptotermes* species did not exhibit a preference for any RH when compared among species and among RH.
Table 1. Percentage of survival (mean ± standard error of the mean [SEM]) of 4 termite species (Coptotermes formosanus, Neotermes jouteli, Cryptotermes brevis, and Cryptotermes cavifrons) exposed to 5 RH and 23 °C for 12 d.

| Species            | RH       | Mean survival (% ± SEM) |
|--------------------|----------|-------------------------|
| C. formosanus       | H2O      | 95.0 ± 2.2Aa             |
|                    | NaCl     | 93.3 ± 4.9Ba             |
|                    | Mg(NO3)2 | 96.7 ± 5.4Ba             |
|                    | MgCl2    | 96.7 ± 2.1Ba             |
|                    | Silica gel | 91.7 ± 4.0Ba            |
|                    | Mean survival | 93.7 ± 1.7B         |
| N. jouteli          | H2O      | 98.3 ± 1.7Aa             |
|                    | NaCl     | 100 ± 0.0Ba              |
|                    | Mg(NO3)2 | 96.7 ± 2.1Ba             |
|                    | MgCl2    | 98.3 ± 1.7Ba             |
|                    | Silica gel | 90.0 ± 6.3Ba            |
|                    | Mean survival | 96.7 ± 2.1Ba         |
| C. cavifrons        | H2O      | 98.3 ± 1.7Aa             |
|                    | NaCl     | 100 ± 0.0Ba              |
|                    | Mg(NO3)2 | 96.7 ± 2.1Ba             |
|                    | MgCl2    | 91.7 ± 4.0Ba             |
|                    | Silica gel | 93.7 ± 1.7B            |
|                    | Mean survival | 90.0 ± 6.3Ba       |
| C. brevis           | H2O      | 91.3 ± 2.8Aa             |
|                    | NaCl     | 73.3 ± 8.9b              |
|                    | Mg(NO3)2 | 71.3 ± 8.7b              |
|                    | MgCl2    | 72.5 ± 8.8b              |
|                    | Silica gel | 70.0 ± 8.6b             |

*Means followed by the same lowercase letters within a row or means followed by the same capital letter within a column are not significantly different at the α = 0.05 level (Tukey honest significant difference test).

Table 2. Relative humidity (RH) (mean ± standard error of the mean [SEM]) preference of 4 termite species (Coptotermes formosanus, Neotermes jouteli, Cryptotermes brevis, and Cryptotermes cavifrons) expressed as the percentage of individuals found at each RH level.

| Species            | RH       | Mean preference (% ± SEM) |
|--------------------|----------|-------------------------|
| C. formosanus       | H2O      | 3.00 ± 2.3Ba             |
|                    | NaCl     | 7.00 ± 4.3Aa             |
|                    | Mg(NO3)2 | 30.7 ± 19.5Aa            |
|                    | MgCl2    | 17.7 ± 10.9Aa            |
|                    | Silica gel | 42.3 ± 15.9Aa           |
|                    | Mean preference | 91.3 ± 2.8Aa       |
| N. jouteli          | H2O      | 89.3 ± 2.5Aa             |
|                    | NaCl     | 4.00 ± 1.5Ab             |
|                    | Mg(NO3)2 | 3.30 ± 1.4Ab             |
|                    | MgCl2    | 2.00 ± 0.9Ab             |
|                    | Silica gel | 1.3 ± 0.8Aa            |
|                    | Mean preference | 91.3 ± 2.8Aa       |
| C. cavifrons        | H2O      | 93.8 ± 1.7Aa             |
|                    | NaCl     | 100 ± 0.0Ba              |
|                    | Mg(NO3)2 | 96.7 ± 2.1Ba             |
|                    | MgCl2    | 91.7 ± 4.0Ba             |
|                    | Silica gel | 93.7 ± 1.7B            |
|                    | Mean preference | 91.3 ± 2.8Aa       |
| C. brevis           | H2O      | 90.5 ± 2.2Aa             |
|                    | NaCl     | 93.3 ± 4.9Ba             |
|                    | Mg(NO3)2 | 96.7 ± 5.4Ba             |
|                    | MgCl2    | 96.7 ± 2.1Ba             |
|                    | Silica gel | 97.7 ± 0.9B            |
|                    | Mean preference | 91.3 ± 2.8Aa       |

*Means followed by the same lowercase letters within a row or means followed by the same capital letter within a column are not significantly different at the α = 0.05 level (Tukey honest significant difference test).

Discussion

Results of this study showed that C. formosanus is less capable of tolerating desiccation than N. jouteli, Cr. cavifrons, or Cr. brevis. This agrees with previous studies of Collins (1958, 1963, 1966, 1969) and Khan (1980) on Kalotermitidae and Rhinotermitidae species. Neotermes jouteli did not express a difference in survival at the various RH, but lost body mass while remaining alive, most likely due to the need to generate metabolic water from reserve body fat, and exhibited a reduction in movement at RH below 72.9%.

The Cryptotermes species did not show a difference in survival when compared at the 5 RH of the first objective and did not exhibit a change in behavior. The physiological mechanisms involved in desiccation tolerance remain to be elucidated, but are probably related to cuticular permeability and percentage of total body water.

The results illustrate the necessity for C. formosanus, and preference of N. jouteli, to inhabit environments with high levels of moisture. Coptotermes formosanus, a subterranean species, not only requires high RH, but also other sources of water for normal activity and survival (Gautam & Henderson 2011). Tunneling activity of Coptotermes gestroi (Wasmann) (Rhinotermitidae), Heterotermes tenuis (Hagen) (Rhinotermitidae), C. formosanus, and Reticulitermes flavipes (Kollar) (Rhinotermitidae) in studies by Arab and Costa-Leonardo (2005) and Su and Puche (2003), showed that these species tunneled more in substrates with higher moisture content. Additionally, the effect of substrate and food moisture levels on survival, consumption, and

TERMITE SURVIVORSHIP WITH VARIOUS TYPES OF WATER SOURCES

Termites displayed statistically different responses to RH for wk 1 (F = 5.71; df = 3, 56; P < 0.001), wk 2 (F = 3.30; df = 3, 56; P < 0.001), wk 3 (F = 3.89; df = 3, 56; P < 0.001), and wk 4 (F = 4.91; df = 3, 56; P < 0.001). Within a week, none of the C. formosanus individuals survived in the chambers provisioned with a piece of dry wood at RH <49.6%. Survival of C. formosanus was significantly lower in the dry wood chamber when compared to the other 3 species at all weeks. They survived significantly better throughout the 4 wk experiment when provided with some form of water at RH >90% (Table 3) when compared to the low humidity of the dry wood chamber. The only exception was the low survivorship of 33.3% when C. formosanus was provided with a piece of dry wood and free water at 91.1% RH for 4 wk. Because of the high survivorship of 96.7% at 4 wk when provided with dry wood at a slightly elevated RH (94.2%), the low 33.3% survival may be attributed to other factors such as handling. In the first 3 weeks, survival was not significantly different for N. jouteli, Cr. Brevis, and Cr. cavifrons when compared between the 5 water source chambers, as well as when compared with each other. After 4 wk, survival of C. formosanus exposed to dry wood was significantly lower when compared to wet wood, wet soil, and wood with a RH source. Cryptotermes brevis also exhibited significantly lower survival with wet wood when compared to C. formosanus, and wood with a RH source when compared to Cr. cavifrons (Table 3).
As was noted by Pence (1956) and Collins (1958), the Cryptotermes species in this study were also less active than the subterranean and dampwood species, and tended to aggregate with little movement unless disturbed. Cryptotermes formosanus and N. jouteli, while more active, also tended to aggregate. This aggregative huddling was likely a behavioral mechanism to prevent desiccation from water loss through evaporation from the body by decreasing overall surface area of the group. This behavior, termed the “group effect” by Grasse and Chauvin (1944), was not explicitly observed in this study, but the fact that there were individuals missing from the Neotermes recovery study suggests they were probably cannibalized. This behavior is an additional means of obtaining water and food resources under water-stressed conditions.

Whereas some termites require access to water sources, too much moisture can be detrimental to other species. While each week of exposure was not statistically compared to the other weeks, there was a decrease in average survival from week 1 to 4 for C. brevis. There was also a decrease in survival for C. brevis when exposed to environments with RH >90%, and indicated that avoiding prolonged contact with free water is important to survival in this species. Our results agree with previous works of Collins (1969), Minnick et al. (1973), Steward (1982, 1983), Rudolph et al. (1990), and Woodrow et al. (2000), in which they found evidence of water toxicity in drywood termite species. If individuals of C. brevis could avoid direct contact with a water source, such as...
on the wood block provided, they were generally better able to tolerate these less-than-favorable environments with extended exposure.

Results of this study highlight the importance of water to the survival of four termite species and the differences in their RH preference, desiccation and RH tolerance, and moisture exposure tolerance. Further studies are needed to examine their morphological and physiological characteristics such as cuticular structure, spiracular openings, and cuticular permeability that may contribute to these differences.

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