

Cuticular Permeability, Percent Body Water Loss, and Relative Humidity Equilibria Comparisons of Four Termite Species

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Abstract

This study compared percentage of total body water (%TBW), water loss rate under desiccative conditions, and cuticular permeability (CP) of four termite species (Order: Blattodea, Infraorder: Isoptera) from different habitats, including one subterranean termite, *Coptotermes formosanus* Shiraki (Blattodea: Rhinotermitidae), one dampwood termite, *Neotermes jouteli* (Banks) (Blattodea: Kalotermitidae), one ‘wetwood’ termite, *Cryptotermes cavifrons* Banks (Blattodea: Kalotermitidae), and one drywood termite, *Cryptotermes brevis* Walker (Blattodea: Kalotermitidae). There was no consistent pattern associated with the habitat relative humidity (RH) levels and the %TBW among the four termite species tested. Because *C. formosanus* forage for food, its lowest %TBW may be due to its ability to access water sources, and its need to be more mobile than kalotermitids that remain in wood. Body water loss rate and CP were lower for xeric species such as *Cr. brevis* than hydric species such as *N. jouteli*. An RH equilibrium represents the capacity of termite water retention mechanisms that may include the physical structure of cuticular layers, behavioral manipulation of natural openings, and physiological means. As with water loss rate and CP data, RH equilibria were lower for xeric species such as *Cr. brevis* than hydric species such as *N. jouteli*. Moreover, RH equilibria for dead individuals of the four termite species were significantly higher than those of live individuals, indicating dead termites lost more water after losing their physiological and behavioral means of retaining water. RH equilibria represent termites’ capability in water retention, and there is a strong linear relationship between RH equilibria and CP values. Hence, RH equilibria may offer simpler alternatives to CP estimates.

Key words: dampwood termite, desiccation, drywood termite, subterranean termite

In order to keep a termite colony healthy, individuals must maintain relative humidity (RH) of the nest and foraging tunnels at desirable levels. One such way involves the direct movement and use of body water from individual termites to modify the microhabitat of the nest (e.g., saliva, feces), a tunnel, or even a food source (Grube et al. 1997; Grube and Rudolph 1999a, 1999b; Nakayama et al. 2004a, 2004b; Gallagher and Jones 2010). Another way is the passive loss of body water, effected by cuticular permeability (CP) which relates the evaporation of water through the cuticle as well as the mouthparts, anus, and spiracles. If this body water is then contained within the nest and galleries, the RH will reach an equilibrium at which the termites will not (or very slowly) lose body water, drastically reducing desiccation pressure. CP is the amount of water lost (μg) per unit surface area (cm^2) per unit time (h) per unit saturation deficit (mmHg), which is often used to describe and compare evaporative water loss from body surface of insects and other arthropods (Wigglesworth 1945, Edney 1977). Previous work on water loss rates, percentage

of total body water (%TBW) and CP in termites was undertaken by Cook and Scott (1932), Collins (1958, 1963, 1966, 1969), Edney (1977), Rust et al. (1979), Sponsler and Appel (1990), Shelton and Appel (2000, 2001), and Shelton and Grace (2003), and in cockroaches by Appel et al. (1983, 1986). These studies indicated that the use of Meeh’s formula, $2/3$ power of body weight multiplied by 12 (Mead-Briggs 1956, Edney 1957, Edney and McFarlane 1974), for determining surface area for use in calculating CP can be problematic and, thus, results may be inconsistent. However, in general, these previous studies indicated that when placed in desiccative conditions, termites associated with more hydric habitats had higher %TBW, higher rate losses, higher CP values, and shorter survival times than did those associated with xeric habitats. Water loss rate was shown to decrease over time, and upon death, termites associated with xeric habitats had lost a lower percentage of body mass (Cook and Scott 1932; Collins 1958, 1963, 1969; Rust et al. 1979; Sponsler and Appel 1990; Shelton and Appel 2000, 2001; Shelton

and Grace 2003). Given this information, habitat/microhabitat RH is clearly an important factor for termite resistance to desiccation. Termites are found in various yet constantly changing habitats with various levels of ambient humidity and available water, but they generally maintain a stable microhabitat RH to avoid desiccation.

This study examined the differences in %TBW, water loss rate under desiccative conditions, and CP of four termite species from different habitats, including one subterranean termite, *Coptotermes formosanus* Shiraki, one dampwood termite, *Neotermes jouteli* (Banks), one 'wetwood' termite, *Cryptotermes cavifrons* Banks, and one drywood termite, *Cryptotermes brevis* Walker. RH equilibria reached in confined spaces were evaluated as an alternative to CP values to represent the water retention capability of termite body surface.

Materials and Methods

Termite Collection

Individuals from colonies of *C. formosanus*, *N. jouteli*, *Cr. cavifrons*, and *Cr. brevis* were collected in Broward County, Florida. Colonies of *C. formosanus* were collected from bucket traps as described by Su and Scheffrahn (1986). Colonies of *N. jouteli*, *Cr. cavifrons*, and *Cr. brevis* were collected from infested pieces of wood. All termites were kept in rectangular polystyrene boxes (17.15 × 12.22 × 6.03 cm) and stored in an incubator at 26.4°C and 41.5% RH. *Coptotermes formosanus* and *N. jouteli* were kept with pieces of wood as food and shelter and were regularly misted with water to maintain >95% RH. Both *Cryptotermes* termite species were kept with pieces of wood as food and shelter, but only *Cr. cavifrons* were provided with small dishes of water that were regularly refilled. Populations of each termite species survived well in these conditions and were used for experiments as needed. Termites were kept in the incubator for no more than 6 mo before use.

Individual Body Weight, %TBW, Water Loss Rates, and CP

Separate groups of live and dead termites were used to evaluate if there was a difference between physical water loss and physiologically mediated water loss from their bodies. Termites prepared for the dead groups were killed with ethyl acetate fumes and immediately used for experimentation. The rate of weight loss (as water vapor) over 12 h was calculated for 10 groups each of 10 live and 10 dead workers/pseudogates for each species, totaling 80 groups. The initial masses of these groups of live or dead termites were measured and recorded. A rectangular polystyrene box (17.15 × 12.22 × 6.03 cm) had a layer of indicating Drierite (W. A. Hammond Drierite Co., Xenia, OH) placed on the bottom was used as a desiccator. Small Petri dishes (3.5 cm diameter × 1 cm high), each containing a group of 10 termites, were set directly on the layer of Drierite, and the desiccator box was placed in an incubator at 26.4°C and 41.5% RH. Humidity levels in the desiccator box were measured using Amprobe THW3 probes (Danaher Corp., Everett, WA) inserted through a hole (1.59 cm diameter) pre-drilled at the center of lid of the box. Eboline petroleum jelly was used to provide a seal for probe and the drill hole. When not in use, the drill hole was plugged with a rubber stopper. RH readings were taken immediately before the groups of termites were removed from the desiccator box and weighed while in their respective Petri dishes. These readings and the weights were taken every 2 h for 12 h to determine the bi-hourly percent water loss. A linear regression analysis was used to determine the relationship between time (independent variable) and cumulative

percent water loss (dependent variable). Regression slopes were considered percent water loss rates. Following the 12-h observation, termites were dried at 60°C for 3 d and cooled in a desiccator before weighing to determine their dry weight. %TBW was calculated by using the initial body mass and final dry weight. CP was calculated similarly to Sponsler and Appel (1990) by using the 12-h water loss data. Surface area was estimated using Meeh's formula, and the saturation deficit calculated as in Edney (1977).

RH Equilibria

Chambers constructed to evaluate RH equilibria (Fig. 1) comprised of wide-mouthed clear plastic jars (5.08 cm diameter × 5.3 cm high). The jar was equipped with a clear plastic lid (Fig. 1A, a) with a hole (1.59 cm diameter) through which an Amprobe THW3 probe (Fig. 1A, b) was inserted to measure RH in the chamber. The probe was fitted with a plastic collar with a flange at the bottom (Fig. 1A, c) that allowed for an upright free-standing and stable probe during the RH reading. The bottoms of the jars were scratched with sandpaper to facilitate termite movement. Separate groups of 25 live or 25 dead termites were placed in their respective jars. The jars were then sealed to eliminate air movement into and out of the chamber by placing a layer of Eboline petroleum jelly where the opening of the jar and the lid intersected. Eboline petroleum jelly also provided a seal for the collar (barrel flange) and the lid of the jar, as well as a seal between the collar and the neck of the probe. Paper or plastic cups with the bottoms cut off were inverted and placed over the chambers (Fig. 1B, d). Two layers of black satin cloth were then draped around the humidity probe, probe collar, and the inverted cup to provide a dark environment in the chambers (Fig. 1B, e). RH readings were taken and recorded every 4 h for 44 h to determine the RH level reached in the jars (as equilibria plateaus). Mean temperature during the experiment was $\sim 26 \pm 1^\circ\text{C}$. These RH equilibria were reached when the chamber vapor pressure equalized with those permeated through cuticular layers and natural openings of 25 termites.

Data Analysis

Statistical analysis was conducted using the JMP statistical software and Sigmaplot (v12.5, Systat Software, Inc., San Jose, CA). Individual bodyweight and %TBW were subjected to the analysis of variance (ANOVA) to test whether there was a significant difference among four species. Percent of TBW values were arcsine-square root transformed before the analysis. For CP estimates, a 2 × 4 factorial analysis was conducted with status (alive or dead) and species as the factors. Tukey's HSD tests were used to separate the differences at $\alpha = 0.05$. Regression slopes that represent water loss rates were compared by using a Z-test, $Z = |S1 - S2| / \sqrt{\text{var}(S1) + \text{var}(S2)}$, where *S1* and *S2* are regression slopes and *var*(*S1*) and *var*(*S2*) are associated variances. All possible pairs of species and status combination were compared and those with $Z > 1.96$ were significantly different at $\alpha = 0.05$. For the RH equilibria study, data at 16 h were used to represent equilibrium levels for all groups, and the relationship between RH equilibria and CP values were analyzed by using linear regression.

Results and Discussion

Individual Body Weight and %TBW

Of the four termite species tested, *N. jouteli* that lives in the most hydric habitat was the largest and contained the highest %TBW (80.2%, Table 1). The subterranean termite, *C. formosanus* was the smallest species that also lives in a hydric environment, but it

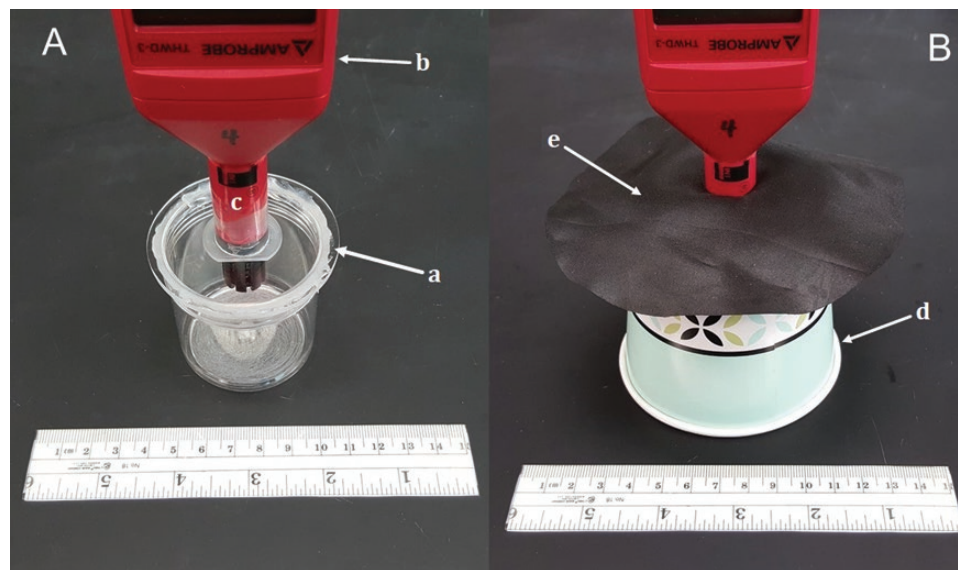


Fig. 1. Experimental units to determine relative humidity-equilibria in a confined space for four termite species. (A) Uncovered evaporation jar. *a*: petroleum jelly seal *b*: humidity probe *c*: probe collar. (B) Covered evaporation jar. *d*: cup covering *e*: cloth covering.

Table 1. Individual body weight (mg \pm SE) and %TBW of workers/pseudogates of four termite species^a

| | Termite species | | | |
|-------------|----------------------|-------------------|----------------------|-------------------|
| | <i>C. formosanus</i> | <i>N. jouteli</i> | <i>Cr. cavifrons</i> | <i>Cr. brevis</i> |
| Body weight | 2.97 \pm 0.10a | 23.7 \pm 0.41b | 3.29 \pm 0.06a | 7.50 \pm 0.21c |
| %TBW | 70.8 \pm 0.63a | 80.2 \pm 0.23b | 73.7 \pm 0.39c | 76.7 \pm 0.45d |

^aMeans followed by the same lowercase letters within a row are not significantly different at $\alpha = 0.05$ (Tukey's HSD post hoc test).

contained the lowest %TBW (70.8%). Body weights and %TBW for two *Cryptotermes* species fell in between, but *Cr. brevis* is significantly larger and contained more %TBW (76.7%) than *Cr. cavifrons* (73.7%). *Cryptotermes brevis* live in an extremely xeric habitat, yet its %TBW water was second to *N. jouteli* that lives in a highly hydric environment. There appeared no consistent pattern associated with the habitat RH levels and the %TBW among the four termite species tested. The fact that the single rhinotermitid, *C. formosanus* contained lower %TBW than the other three kalotermitids despite living in hydric habitat suggested %TBW may be more affected by their nesting structures and behavior than habitat RH. Unlike the one-piece kalotermitids, *C. formosanus* forage out of nest to find food and lower %TBW (and hence the bodyweight) enable them to be more mobile than kalotermitids. Moreover, they probably have access to water sources at foraging sites. Hence, there is little need to store excessive water in the body. Kalotermitids, especially *Cr. brevis*, are confined in wood pieces, and they may have to rely on storage water in case their habitat becomes more xeric over time.

Body Water Loss Rate and CP

When placed in a desiccator box, cumulative %body water loss increased linearly over the 12-h period for both live and dead termites of all four termite species (Table 2). Mean RH ranges and temperatures in the desiccator box during the 12-h period were 0–3.3% at 26°C and 4.5–17.8% at ~26.2°C for live and dead termites, respectively. Body water loss rates (% per hour) derived from regression slopes for live individuals of *C. formosanus* and *N. jouteli* were significantly higher than the two *Cryptotermes* species (Table 3),

suggesting that the former two species that live in hydric environment were less capable of preventing desiccation than the latter. As expected, water loss rate for *Cr. brevis* that live in the most xeric habitat was slowest among the four species. Dead *Cr. brevis* lost water at a faster rate than live individuals, suggesting that the mechanism of preventing desiccation was, at least partially, physiological or behavioral, i.e., closing of spiracles, anal, or mouth openings. Among the four species tested, the water loss rate of dead *Cr. brevis* was the lowest, indicating that the integument structure of this species was the least permeable. Water loss rate of live *Cr. cavifrons* that live in relatively hydric environments was significantly faster than that of *Cr. brevis*, and there was no significant difference in water loss rate between live and dead *Cr. cavifrons*. The result suggested that physiological and behavioral mechanism to prevent desiccation for *Cr. cavifrons*, if present, was less effective than that of *Cr. brevis*. The lack of significant difference in water loss rate between live and dead *C. formosanus* indicated the absence of a physiological or behavioral mechanism in preventing desiccation for this species. The significantly larger water loss rate of live individuals than dead individuals of *N. jouteli* was puzzling, but it could be due to the closing of natural openings of this termite species at the onset of death.

As expected, CP value for live *N. jouteli* that is found in the most hydric habitat was the highest among live termites of the four species (Table 3). The CP value for live *N. jouteli* was comparable to the CP values of several species of adult male cockroaches (Appel et al. 1983). It was also comparable to those found for *C. formosanus* workers by Shelton and Grace (2003). Parallel to water loss rates, CP values for live termites of the two *Cryptotermes* species were the

Table 2. Regression equations of cumulative %TBW lost over time (h) for live termites of four species exposed to 0–3.3% RH and 26°C and dead termites of the same species exposed to 4.5–17.8% RH and ≈26.2°C

| Status | Species | Regression equation ^a | r ² | P-value |
|--------|----------------------|----------------------------------|----------------|---------|
| Live | <i>C. formosanus</i> | Y = 3.68X + 4.72 | 0.97 | <0.001 |
| | <i>N. jouteli</i> | Y = 2.59X + 0.478 | 0.99 | <0.001 |
| | <i>Cr. cavifrons</i> | Y = 0.539X + 0.0697 | 0.98 | <0.001 |
| | <i>Cr. brevis</i> | Y = 0.122X + 0.214 | 0.95 | <0.001 |
| Dead | <i>C. formosanus</i> | Y = 3.55X + 1.88 | 0.99 | <0.001 |
| | <i>N. jouteli</i> | Y = 1.14X + 0.664 | 0.99 | <0.001 |
| | <i>Cr. cavifrons</i> | Y = 0.814X + 0.848 | 0.98 | <0.001 |
| | <i>Cr. brevis</i> | Y = 0.380X + 0.193 | 0.99 | <0.001 |

^aY is cumulative percentage water loss and X is time in hours.

Table 3. Comparisons of water loss rate (% per hour ± SE) and CP value (μgH₂O*cm⁻²*h⁻¹*mmHg⁻¹) among live and dead workers/pseudogates of four termite species^a

| Variable | Status | Termite species | | | |
|-----------------------|--------|----------------------|-------------------|----------------------|-------------------|
| | | <i>C. formosanus</i> | <i>N. jouteli</i> | <i>Cr. cavifrons</i> | <i>Cr. brevis</i> |
| Water loss rate | Live | 3.68 ± 0.20Aa | 2.59 ± 0.12Aa | 0.54 ± 0.03Ab | 0.12 ± 0.02Ac |
| | Dead | 3.55 ± 0.12Aa | 1.14 ± 0.03Bb | 0.81 ± 0.04Ac | 0.38 ± 0.02Bd |
| CP value ^b | Live | 13.0 ± 0.75Aa | 22.7 ± 1.40Ab | 2.66 ± 0.29Ac | 3.80 ± 0.59Ac |
| | Dead | 14.6 ± 0.25Aa | 29.9 ± 0.96Bb | 4.83 ± 0.20Ac | 2.55 ± 0.18Ad |

^aFor each variable, means followed by capital letters within a column and means followed by lower case letters within a row are not significantly different at $\alpha = 0.05$. Z-test was used for water loss rate and Tukey's HSD post hoc test was used for CP value.

^bMean cuticular permeability values for mass loss of an individual after 12 h in desiccative condition.

lowest as they were more xeric tolerant, and our CP estimates were comparable to values found for drywood termites (*Incisitermes* spp.) by Rust et al. (1979). However, the CP value for live *C. formosanus* in this study was not comparable to those of the same species, as well as workers of other subterranean species in previous studies (Shelton and Grace 2003, Hu et al. 2012). The CP value determined for *C. formosanus* workers by Sponsler and Appel (1990) was approximately three times higher than the value found in this study. These discrepancies in CP values for termites from various studies is at least partially due to the problems associated with the difficulties in using Meeh's formula to estimate surface area of small organisms such as termites.

Contrary to our expectation that dead termites may lose more body water, i.e., higher CP values, as they lose their physiological and behavioral mechanism to retain water, no significant difference was detected in CP values between live and dead individuals for *C. formosanus*, *Cr. cavifrons*, and *Cr. brevis* (Table 3). The only exception was *N. jouteli*, where the dead termites lost more water per body surface area than live individuals. In agreement with the water loss rate data, CP value for dead *Cr. brevis* was the lowest among the dead termites of the four species, indicating its integument structure was the most desiccation resistant.

RH Equilibria

RH levels in confined chambers that received 25 live *C. formosanus* or *N. jouteli* elevated rapidly during the first 4-h period then fluctuated and plateaued at around 16 h (Fig. 2). RH for chambers that received live termites of two *Cryptotermes* species also elevated during the 4-h period but plateaued at much lower levels than *C. formosanus* or *N. jouteli*. Increases in RH levels in chambers that received dead termites were more protracted than those with live termites, but they also plateaued by 16 h.

When the RH levels at 16 h were used as the RH equilibria in the chambers, those for live *C. formosanus* and *N. jouteli* were higher than those reached by two *Cryptotermes* species (Table 4). Termite

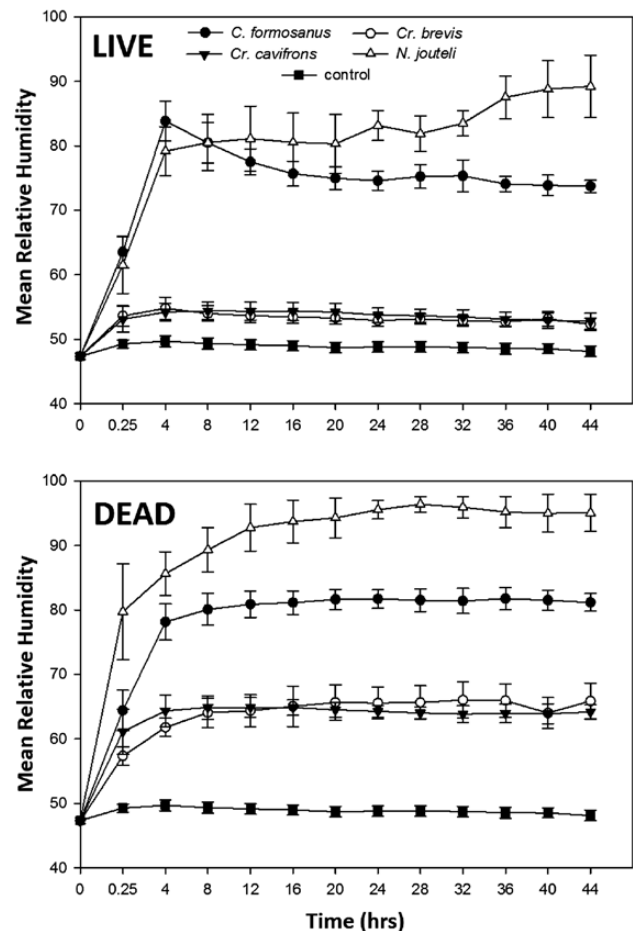


Fig. 2. Species-specific mean relative humidity-equilibria (RH-EQ) curves with SEM bars for live and dead termites of four species. Data at 16 h were used in the estimate of RH-EQ for all four species.

Table 4. RH equilibria (% ± SE) reached in confined chambers from evaporation of body water of 25 live or dead workers/pseudogates of four termite species after 16 h confinement^a

| | Termite species | | | | |
|------|----------------------|-------------------|----------------------|-------------------|--------------|
| | <i>C. formosanus</i> | <i>N. jouteli</i> | <i>Cr. cavifrons</i> | <i>Cr. brevis</i> | Control |
| Live | 75.7 ± 1.9Aa | 80.6 ± 4.6Aa | 54.4 ± 1.4Ab | 53.5 ± 1.0Ab | 49.0 ± 0.8Ab |
| Dead | 81.2 ± 1.8Ba | 93.7 ± 3.3Bb | 64.9 ± 1.2Bc | 65.1 ± 3.2Bc | 49.4 ± 1.0Ad |

^aMeans followed by the same uppercase letter within a column and same lowercase letter within a row are not significantly different at α = 0.05 (Tukey’s HSD post hoc test).

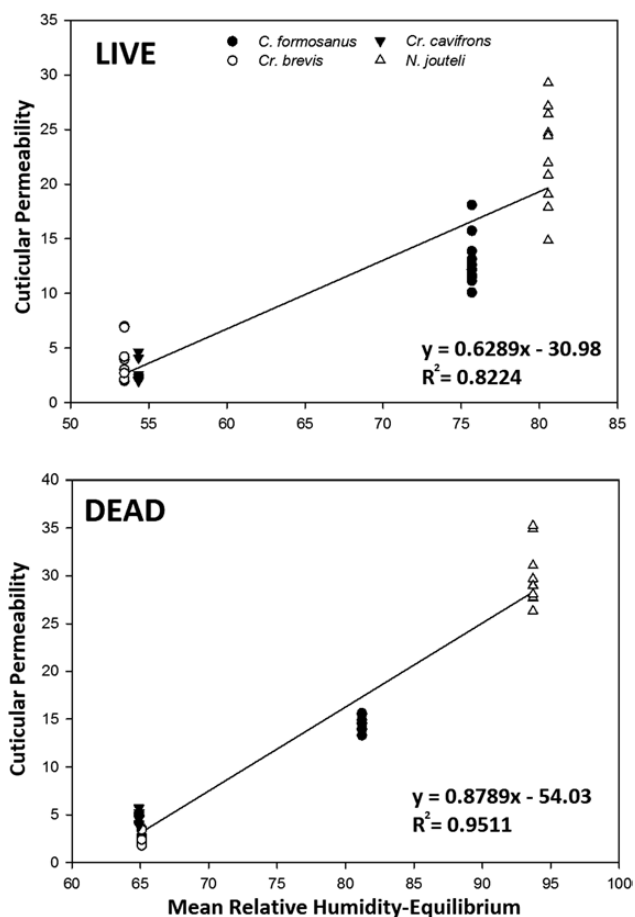


Fig. 3. Relationship between cuticular permeability value and the mean relative humidity-equilibrium at 16 h for live and dead termites of four species.

water retention mechanisms may include the physical structure of cuticular layers, behavioral manipulation of natural openings, and physiological means. At low RH environments, water escapes from the body cavity as the water vapor pressure moves toward equilibrium, i.e., the RH equilibrium that can be contained by the retention mechanism. RH equilibria, hence, represent the capacity of termite water retention mechanisms.

RH equilibria reached by four species (live) were significantly higher than control (Table 4), suggesting that even the xeric species such as *Cr. brevis* lost body water at ~49% RH and water loss did not stop until the chamber RH reached ~54%. The results indicated that water retention mechanisms of *C. formosanus* and *N. jouteli* that live in hydric habitats are more vulnerable to water loss than xeric species, especially *Cr. brevis*. *Cryptotermes*

cavifrons is found in relatively moist habitats and it is unclear as to why the RH equilibrium reached by this species is as low as *Cr. brevis*. RH equilibria for dead individuals of four termite species were significantly higher than those of live individuals, indicating dead termites lost more water after losing their physiological and behavioral means of retaining water. Yet, RH equilibria for dead termites of two *Cryptotermes* species were significantly lower than those of other two species, suggesting the physical structure of cuticular layers of the *Cryptotermes* species were more capable of retaining water. Among the dead individuals of four species, RH equilibrium for *N. jouteli* was the highest (93.7%), indicating that cuticular layers of this hydric species offer very little capability in water retention.

Results of this RH equilibria study generally agree with the CP values (Tables 3 and 4), and there are strong linear relationships between CP values and equilibria for both live and dead termites (Fig. 3), i.e., species with higher CP values also possess higher RH equilibria. Measurement of CP values has been problematic because of the difficulties in estimating surface areas of small organisms such as termites. Using an RH equilibrium, the rate of water loss from the body can be determined without depending on surface area estimates. Because RH equilibria represent termites’ capability in water retention, and because there is a strong linear relationship between RH equilibria and CP values, RH equilibria may offer simpler alternatives to CP estimates.

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