Light Sensitivity in Workers and Soldiers of the Formosan Subterranean Termite, *Coptotermes formosanus* (Isoptera: Rhinotermitidae)

by

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ABSTRACT

Photosensitivity of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, was tested in workers, pre-soldiers, and soldiers of various ages. Responses leading to possible foraging behaviors under laboratory bioassay conditions were also determined in response to various light intensities. Whereas workers and pre-soldiers avoid light of all intensities, soldiers while avoiding the light attain a defensive posture by lining up their heads pointing toward the edge of the light source. The tunneling assay further showed that subterranean termites avoid light, and foraging in exposed areas is facilitated by the construction of an opaque mud screen.

Keywords: *Coptotermes formosanus*, castes, light, phototaxis, foraging location.

INTRODUCTION

Most insects show certain characteristic responses to light. Termites in general avoid light, but the subterranean species, in particular, exhibit a strong tendency to stay away from light. Being cryptic species, they live in constant darkness, often hardly detected as they forage underground and in man-made structures. The workers, which constitute the most abundant caste in a colony, are responsible for foraging for food and yet they have no functional compound eyes. The presoldiers (an intermediate stage between workers and soldiers) and soldiers also lack apparent visual senses. Only the last nymph stage and the alates have functional compound eyes for the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, even though earlier nymphs have developing eyes. Cabrera & Rust (1996) reported that nymphs of the western drywood termite, *Incisitermes minor*, showed negative phototaxis. Based on the developmental stage of alates, Howse (1970) reported three different responses to light. Whereas premature

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and swarming alates were negatively and positively phototactic respectively, after dealation the alates showed negative phototaxis. Similar observations were reported for C. formosanus (Wang et al. 2002, Raina et al. 2003). Sakanošita & Oga (1971) suggested that in C. formosanus, light could act as an inhibitory factor for normal transition to primary reproductives.

Literature on photosensitivity of termite workers and soldiers is very scant. Active workers forage in darkness, possibly using cues other than light, such as pheromones, temperature and moisture gradients, for navigation. However, their sensitive behavior of avoiding light suggests that they may possess photosensitive areas other than compound eyes or ocelli. For example, in certain lepidopteran species, photoreceptors were found in reproductive organs (Arikawa & Aoki 1982, Giebultowicz et al. 1989).

Being a major pest of wooden structures and trees, the foraging behaviors of the Formosan subterranean termites have been extensively investigated. However, in all these investigations, either light intensity was not specified or was not low enough to match their cryptic environment (Reinhard et al. 1997, Campora & Grace 2001, Cornelius & Osbrink 2001, Puche & Su 2001, Reinhard & Kaib 2001). We present results of laboratory experiments to determine the responses of workers and soldiers of the Formosan subterranean termite to light of different intensities.

MATERIALS AND METHODS

Insects

Formosan subterranean termites were collected from bucket traps at three different locations in Orleans Parish, LA: City Park, University of New Orleans and USDA-ARS-Southern Regional Research Center. After collection, the termites were kept in plastic boxes (17 × 12 × 6.5 cm) with moist pieces of birch wood (4 × 1.25 × 0.5 cm) and maintained under constant darkness in an incubator held at 28 ± 1°C and relative humidity of 80 ± 5%.

Response to light and food consumption by workers

One half of each Petri dish (50 × 9 mm) was covered with aluminum foil to block all extraneous light. A 4.25 cm diameter filter paper disk (P5, Fisher Scientific, Suwanee, GA) was cut into two equal pieces and dried overnight in an oven at 60°C. Each half was weighed and the 2 pieces placed in the Petri dish. The filter papers were moistened with 200 μl distilled water and 30 workers were released into the Petri dish that was placed in a dark chamber (50 × 55 × 85 cm). The chamber was
illuminated with a 15 watt incandescent light bulb, shielded with one or two sheets of red-acetate paper to provide light intensities: 0 (no light), 0.6 (2 sheets), and 1.0 (1 sheet) lux. An additional setup was placed under normal laboratory fluorescent-light (for 60 lux). Light intensities were measured with a light-meter (AEMC Model 814, Boston, MA) before the record started. The experiment was replicated 5 times, for each light intensity and for each of the 3 test colonies. The temperature inside the chamber was monitored to be 28 ± 2°C during the experiment. The number of workers in the lighted area was recorded each hour for 24 h with a time-lapse video recorder (Panasonic Model AG-6740, Osaka, Japan) and a Mycroflex video imaging system (EmCal Scientific, Escondido, CA). After 24 h, each half piece of the filter paper was rinsed with distilled water to clean the debris, dried for two hours at 60°C, and then weighed to determine the feasible amount of food consumed.

**Response of pre-soldiers and soldiers to light**

 Newly formed pre-soldiers were regularly removed from the three test colonies for proper staging (Park & Raina 2003). Soldiers <2 d old, 4 d old, and >10 d old were selected for the test. The experimental set-up was similar to the one used for workers. The data were transcribed and analyzed based on the dependent t-test. ANOVA was used to determine the distribution of termites between the four lighting conditions. Descriptive statistics (Scheffe test) was used for comparison of the mean differences.

**Effect of light and tunneling**

A glass tube (33 cm in length x 6 mm in diameter) was filled with sand that was moistened with deionized water. The tube was covered with heavy-duty aluminum foil. Six 1.0 × 0.5 cm openings, located at random (3 at 5, 11, and 25 cm of the upper side and 3 at 16, 21, and 29 cm of the lower side of the tube) were cut out through the foil for allowing light to penetrate. The tube at each end was connected to a plastic container (6 cm in height x 4.2 cm in diameter). Both the containers were filled with a 1 cm layer of moist sand and one of them contained a piece of moist wood as shown in Fig. 1. The setup was suspended above a mirror to provide light from below. Workers and soldiers (150 and 10 respectively) were released into the sand-only container at the start of the experiment. The test carried out at 27 ± 2°C and 60 lux light intensity was terminated when the workers tunneled to the container with the wood. At this time, the aluminum foil was removed and the course of the tunnel was determined. The test was repeated with the tube rotated by 180° to reverse the position of the openings. The experiment was replicated 3
Fig. 1. Diagrammatic presentation of the set up to study the effect of light on tunneling by C. formosanus workers. L, fluorescent light (60 lux); M, mirror for reflection; S, container with sand; and F, container with sand and wood. Arrows indicate locations of the 6 openings for light.

times for each of the 3 colonies. For control, the tubes were covered with aluminum foil that had no openings.

RESULTS

Termite workers avoided the lighted side of the Petri dish at the light intensities equal to or greater than 0.6 lux. Based on the analyses of hourly recordings, an average of 84% workers stayed in the dark side as shown in Fig. 2. However, 16% of the workers constantly moved back and forth between the lighted and dark areas. The difference between the numbers of termites in the lighted and dark areas was significant for all light intensities ($t_{63} = 46.72, P < 0.001$ for 0.6 lux, $t_{45} = 29.31, P < 0.001$ for 1.0 lux, and $t_{53} = 78.63, P < 0.001$ for 60 lux, respectively). At 0.0 lux (no light or complete darkness), the location of termites could not be determined as it was below the level of camera sensitivity and attempts to determine the location were abandoned during the period of observation, since any light even for a brief period to count the termites, altered their behavior. ANOVA showed significant differences in the distribution of termites between the three lighting conditions ($F_{2,206} = 7.29, P < 0.001$). The results of the Scheffe test revealed that there was no significant difference between the means for 0.6 lux, and 1.0 lux. However, differences between mean value for 60 lux and with those of the other
two conditions were significant (Table 1). The results clearly indicated that workers of *C. formosanus* reacted strongly to light of even low intensity. There was significant feeding of the filter paper in the dark side than in the lighted side under all light intensities except for the no light condition (Fig. 3). Total food consumption varied noticeably among the three termite colonies (data not shown).

Similar to the workers, the pre-soldiers displayed negative phototaxis. Eighty two percentage of the pre-soldiers remained in the dark side ($t_{23} = -39.48, P < 0.001$). Soldiers < 2 d old also responded negatively to light as did the pre-soldiers and workers ($t_{19} = -9.06, P < 0.001$) (Fig. 4). Although soldiers, 4 d old or older, exhibited negative phototaxis, they lined up around the border between the lighted and dark areas with their heads pointing towards the lighted region. The statistics for the test with soldiers are $t_{6} = 12.50, P < 0.001$ for 4 days old, and $t_{113} = 5.919, P < 0.001$ for those older than 4 d.

The tunneling assay, conducted at 60 lux intensity, produced a clearly defined response by the workers, as illustrated in Fig. 5. In the absence of any light, the workers appeared to exhibit positive geotaxis.
Fig. 3. Weight of the filter paper (mg) consumed in lighted and dark regions of the Petri dish over a 24-hour period. The values are averages of 5 replicates and 3 colonies.

Fig. 4. Percent distribution of pre-soldiers (PS), and soldiers (S) of various ages in lighted and dark regions, observed over a 24 h period at 0.6 lux. The averages are for 3 colonies with 5 replicates per colony.
Table 1. Pairwise comparison of the difference in percentage mean values for the dark region at various light intensities (lux).

<table>
<thead>
<tr>
<th>Comparison pair</th>
<th>Mean difference ± SE</th>
<th>p-value</th>
</tr>
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<tbody>
<tr>
<td>0.6 vs 1</td>
<td>0.02 ± 1.65</td>
<td>1.00</td>
</tr>
<tr>
<td>0.6 vs 60</td>
<td>6.16 ± 1.50</td>
<td>0.000*</td>
</tr>
<tr>
<td>1 vs 60</td>
<td>6.18 ± 1.65</td>
<td>0.001*</td>
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* Significantly different

by confining tunneling activity to the bottom of the tube. First encounter with a light-opening did not generally result in an immediate turning response. However a subsequent exposure to light resulted in immediate change in the direction and away from the light. When the illuminated area was crossed the workers resumed normal behavior of positive geotaxis. Then, since the next illuminated areas to cross were nearby, the workers reacted immediately by moving upwards or to a side to avoid the areas.

**DISCUSSION**

Most insects possess different types of sensory organs and appendages such as compound eyes, ocelli, and antennae to detect various environmental cues. Among these, the compound eyes and ocelli are the primary sensory organs for detecting light. However, both the compound eyes and ocelli are absent in termite workers. When nymphs are developed they have non-functional or developing compound eyes and subsequently the alates have functional compound eyes in *C. formosanus*. Our results showed that Formosan termite workers exposed to different levels of light intensity exhibited strong negative phototaxis even at a very low level of 0.6 lux suggesting that alternate photoreceptor sites may be present in this insect.

As expected, there was a positive correlation between food consumption and the location of workers. Formosan termite workers preferred to stay and feed in a dark area even at the lowest light level. A proportion of workers (<20%) found in the lighted area at any given time during the test, was observed to move between the lighted and dark areas, particularly during the early part of the 24 h observation period. While under complete darkness the actual position of the workers could not be determined, it was inferred from the food consumption data that they were evenly distributed between the two test areas.

The established roles for workers and soldiers in a termite colony are foraging and defense of the colony respectively. In the case of the
subterranean species, most of the foraging is confined to dark areas such as below ground, behind walls in a house or inside of the host trees. Occasionally the workers are found foraging in open areas but this activity is accompanied with the construction of mud tubes that are essentially opaque to light. Construction of a mud tube, at any given time, is most probably undertaken by a small proportion of the total work force that may be constantly replaced by other members in the population. A majority of the workers stay back in the darkness. This behavior may have been reflective of the fact that we observed < 20% workers in the lighted area of the Petri dish.

The pre-soldiers, and soldiers < 2 d old, which play neither a foraging nor a defensive role, showed a strong preference for darkness. However older soldiers, as primary defenders of the colony, while expressing negative phototaxis even to 0.6 lux light, lined up against the lighted area just as they do in any natural opening in a termite gallery. This is also true when termite infested wood or shelter tubes are broken, the soldiers immediately appear at the exposed area. Thus light may be acting as a factor to evoke defensive reaction in the soldiers. At the same
time, defensive response is dependent on hardening of the mandibles and maturation of frontal glands in older soldiers. Moreover, these results imply that both pre-soldiers and soldiers of all ages have photoreceptors to detect light.

Results of the tunneling study revealed that besides avoiding light, workers of *C. formosanus* appear to show a positive geotaxis. In most cases it took a second encounter with light to respond negatively to it but they always returned to the bottom of the tube. Delayed response may indicate some learning on the part of workers although this can be proven with further experimentation.

It has been suggested that in open foraging species no outside directional stimuli such as light and gravity are used to make up for the directional ambivalence of the odor trail (Jander & Daumer 1974). In addition, for experiments with subterranean termites it will be useful to consider light conditions, even red light of low intensity because they are very sensitive to physical variations such as lighting system for experiments and disturbance resulted in removal from the main nest. Still, the nature and location of photoreceptors in subterranean termite workers and soldiers remain to be identified.

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REFERENCES


