Regulation of soil moisture by mound-building termites

(*Odontotermes obesus*)

A Thesis

submitted to

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by

Shruti Gangasagare

Registration Number: 20191140

Indian Institute of Science Education and Research Pune

Dr. Homi Bhabha Road,

Pashan, Pune 411008, INDIA.

Date: April, 2024

Supervisor: Prof. Sanjay P. Sane

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INDIAN INSTITUTE OF SCIENCE EDUCATION AND RESEARCH PUNE

Certificate

This is to certify that this dissertation entitled "**Regulation of soil moisture by mound-building termites (*Odontotermes obesus*)**" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study carried out by **Shruti Gangasagare** at National Center for Biological Science under the supervision of **Prof. Sanjay P. Sane**, Department of Biology, during the academic year 2023-2024.

Prof. Sanjay P. Sane

Committee:

Prof. Sanjay P. Sane

Dr. Nixon M. Abraham

This thesis is dedicated to my mother.

Declaration

I hereby declare that the matter embodied in the report entitled '**Regulation of soil moisture by mound-building termites (*Odontotermes obesus)***' are the results of the work carried out by me at the National Center for Biological Sciences under the supervision of Prof. Sanjay P. Sane, while affiliated with the Department of Biology, Indian Institute of Science Education and Research, Pune, and the same has not been submitted elsewhere for any other degree. Wherever others contribute, every effort is made to indicate this clearly, with due reference to the literature and acknowledgment of collaborative research and discussions.

Shruti Gangasagare

20191140

27 March 2023

Contents

Abstract

Mound-building termites build large structure made entirely from soil. These mounds enclose their colonies and protect them from predators and natural elements. In addition to the termite colony and their brood, the mound also houses a fungus that is cultured by the termites, which in return helps the termite digest wood. For survival of the termites and the symbiotic fungus, the internal environment of the mound must maintain its temperature, humidity, and oxygen levels. It is also essential that termites be able to repair mounds if they are damaged. All of these tasks require a continuous supply of water. It is well-known that termite build long-lasting mounds in both water-logged and arid regions, which suggests that they must be able to sense and regulate soil moisture levels within the mounds. However, very little is known about how termites are able to regulate the moisture levels within their mounds. In large part, this lack of knowledge stems from the fact that it is very difficult to film termites within their subterranean environs. To address this question, we developed laboratory-based experiments in which we were able to directly visualize the water-transportation by termites. We next manipulated the water levels in soil patches and quantified the ability of termites to build under variable soil moisture conditions. These experiments reveal that termites actively transport water depending on the soil moisture levels, and that they show distinct time dynamics of the water transport. Our study provides novel insights into water transportation and soil moisture regulation by termites.

Acknowledgments

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Thanks to Sree Subha Ramaswamy for guiding me throughout the project. This study was started by simple observations done with Subha and Srijani Mitra, which encouraged me to continue this project.

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List of Figures

Contributions

Contributor name	Contributor role
Sanjay Sane, Sree Subha Ramaswamy, Shruti Gangasagare	Conceptualization Ideas
Girish Kumar G.S., Mitali Patil, Shruti Gangasagare, Sree Subha Ramaswamy, Amritansh Vats, Sreekrishna VarmaRaja	Methodology
Girish Kumar G.S., Sree Subha Ramaswamy, Shruti Gangasagare	Software
Shruti Gangasagare, Simran Virdi	Presentation
Sanjay Sane	Validation
Girish Kumar G.S., Mitali Patil, Shuchita Soman, Shruti Gangasagare	Formal analysis
Shruti Gangasagare	Investigation
Mitali Patil, Shruti Gangasagre	Resources
Shruti Gangasagare	Data Curation
Shruti Gangasagare	Writing - original draft preparation
Anza Simon, Madhuri Srinivasan, Mitali Patil, Shuchita Soman, Sree Subha Ramaswamy	Writing - review, and editing
Sree Subha Ramaswamy, Shruti Gangasagare	Visualization
Sanjay Sane	Supervision
Sanjay Sane	Project administration
Sanjay Sane	Funding acquisition

Introduction

Termites are widely recognized as ecosystem engineers due to their ability to shape and modify terrestrial environments through foraging and nesting activities (Jones et al., 1997). They play a crucial role in converting dry and seemingly inhospitable habitats into more conducive ecosystems by actively transporting soil and water (Turner, 2011). Their activities contribute to the formation of microhabitats with increased moisture levels, thereby supporting diverse biological communities and ecosystems.

Recent insect phylogenies firmly place termites as a monophyletic group within cockroaches (Blattodea). However, unlike cockroaches, termites are eusocial similar to Hymenopteran insects such as ants, bees, and termites. Their eusociality enables them to form intricate societies composed of several cooperating individuals (Boomsma & Gawne, 2018). Eusocial insects are characterized by a division of labor, with distinct roles within a social structure that includes overlapping generations and cooperative care of the young (Wilson, 1971). Like other eusocial insects, termite colonies also have distinct castes which have different functions. These include sterile, eyeless, and wingless major and minor workers which help in growth and maintenance of the colony, soldiers which defend the colony with their sharp mandibles, and fertile, wing- and eye- individuals, who can fly and mate, thereby ensuring the continuation of their colony (Boomsma & Gawne, 2018).

The life cycle of termites begins when male and female winged termites (alates) pair up, mate, and subsequently shed their wings. Following this, they burrow into the ground where the female lays eggs. These give rise to sterile workers (classified as major and minor), soldiers, and alates which are future reproductives. Whereas the major and minor workers construct and maintain the mound, alate termites disperse and swarm, to disperse, and reproduce during the mating season. Except for the alates, all members of the termite colony lack compound eyes and wings (Noirot, 1985).

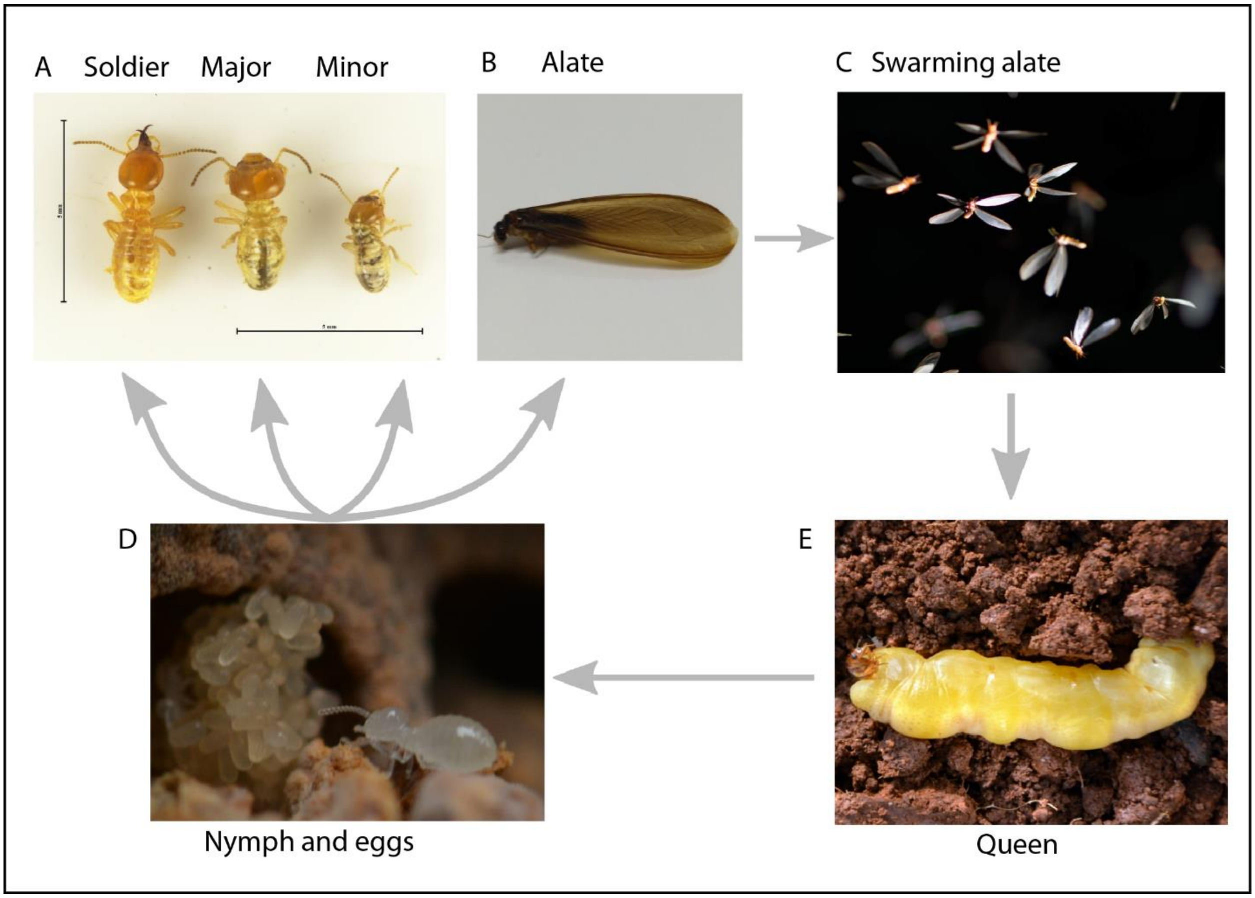

Fig 1.1 Life cycle of termites. **A)** The image shows all the major castes including soldiers, major and minor workers, **B)** alates, **C)** alates while swarming, **D)** nymphs and eggs, and **E)** queen. PC: Abin and Subha

Mound-building termites

All experiments were conducted on the subterranean termite species *Odontotermes obesus* (Arthropoda, Insecta, Blattodea, Termitidae) which are abundant in the South Indian peninsula (Rao & Revanasiddappa, 2002). NCBS, situated within the GKVK agricultural college, hosts several wild mounds of *O. obesus*. The mounds built by this termite species are easily recognizable and can reach up to a few meters in height, vastly larger than the size of individual termites of approximately 3-4 mm (Harris, 1956; Zachariah et al., 2017). These mounds shield termites from predators and unfavorable climatic conditions, and can withstand extreme weather conditions for decades (Zachariah et al., 2017). The mounds are thought to have complex ventilation systems that enable control of internal temperatures (Andréen & Soar, 2023). Continuous reshaping within termite mounds may be influenced by transitory flows of air rather than continuous ones, which may impact respiratory gas exchange within the mounds (Andréen & Soar, 2023). The mounds consist of a royal chamber for the queen and a fungal garden (Ocko et al., 2019) which is located within the core of the mound. The termites grow fungus inside their mounds using their partially-digested excrement. These are housed in combs that range in color from gray to yellow and made of decomposing plant matter (da Costa et al., 2019). These *Termitomyces* fungi are continually tended by termites (da Costa et al., 2019), and exist exclusively within their mounds.

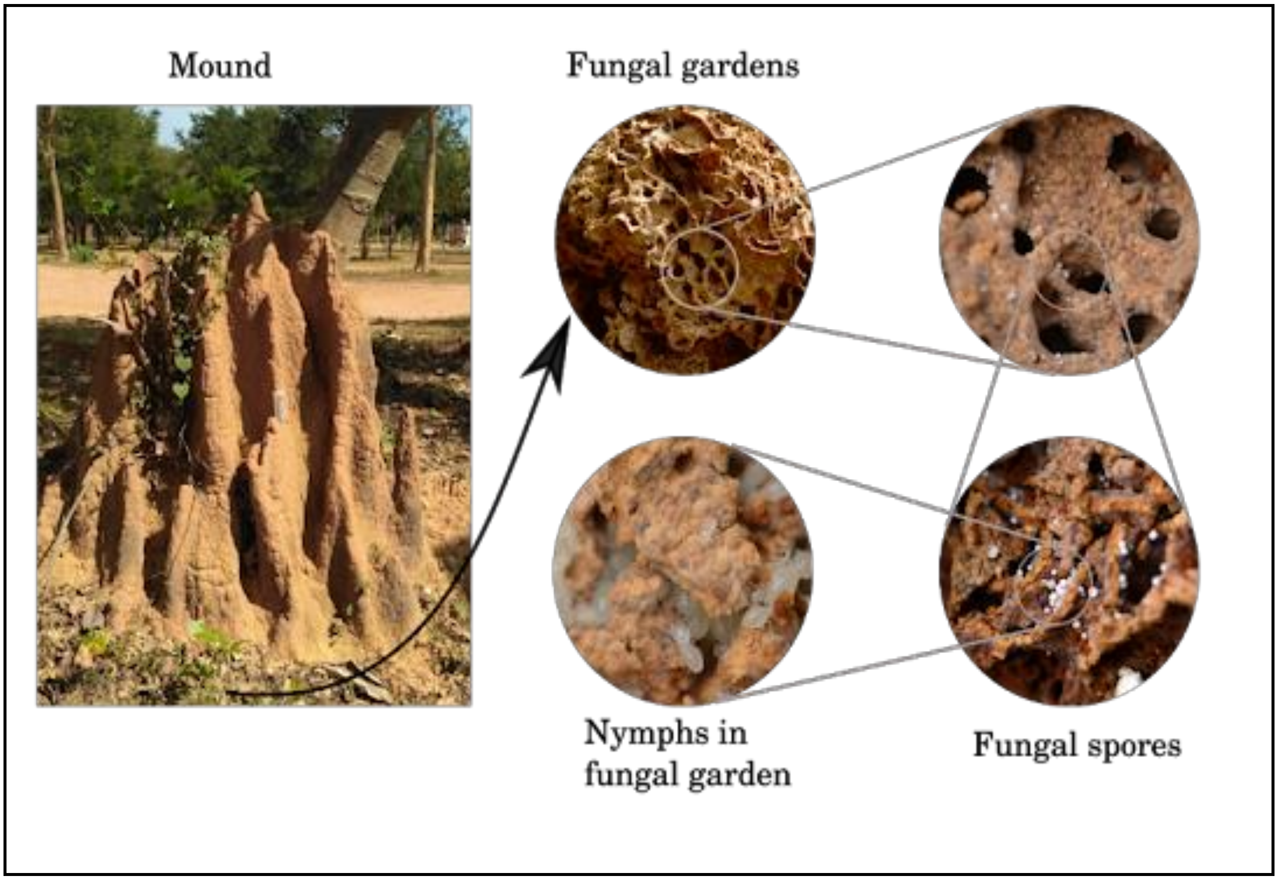

Fig 1.2 Mound structure. The image shows a mound (made of soil) and a subterranean fungal garden. The fungal garden is made of masticated cellulose which serves as a substrate for the fungus to grow. The fungal garden consists of spores of fungi, and further shows eggs and nymphs of termites resident in the fungal gardens PC: Sree Subha Ramaswamy

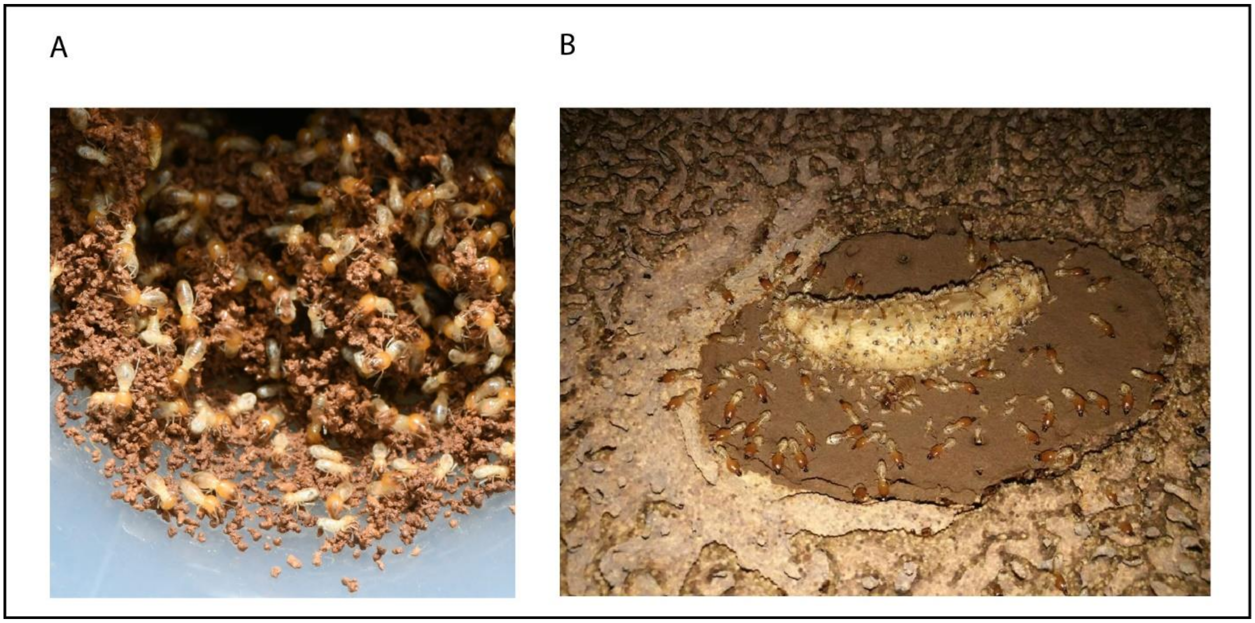

Fig 1.3 A) Termites depositing boluses. **B)** Royal chamber PC: Royal chamber (Wikipedia)

Additional food reserves may be stored in these defendable and controlled microcosms, which is essential to tide over seasonal food scarcity or when environmental factors limit foraging.
In *O. obesus* major and minor termite worker castes build mounds with soil that is moist. During the building process, termites aggregate soil particles, mix them with their body fluids, and roll them with their mandibles to generate tiny boluses (singular: bolus) (Kandasami et al., 2016), which are the building blocks or bricks of construction (Kandasami et al., 2016; Zachariah et al., 2017). It is thought that termite secretions may function as a biocement when combined with damp soil during the bolus-making process (Zachariah et al., 2017).

Role of water in the life history of termites

Moisture is key for the survival of mound-building termites (Forschler et al., 1995), and essential for the upkeep of the mound and its structure. Soil is a complex ecosystem where water plays a crucial role in various processes, such as the cycling of nutrients, microbial activity, and plant growth processes (Lee & Foster, 1991). By engaging in mound-building and related soil processing, termites maintain a delicate balance of water fluxes inside the mound by ensuring a consistent moisture supply for termite activity and fungal growth, including in arid environments (Dangerfield et al., 1998).

On the other hand, excess water can also cause problems. For instance, rainwater can cause weathering of the outside walls of mounds (Price, 1995), increasing the likelihood of them sustaining damage. The strength of the soil thus plays an important role in maintaining the integrity of the outer walls of mounds. Moreover, maintaining the fungal garden requires the mounds to have consistently high humidity levels inside the mound (Schmidt et al., 2023). The fungal garden needs a relatively low CO_2 concentration as the metabolism of the fungus garden is highly sensitive to and dependent on CO_2 levels (Schmidt et al., 2023). Elevated CO_2 concentration can harm the growth of fungal gardens in variable ways (Schmidt et al., 2023). The internal temperature of the mound must also be maintained as *Termitomyces* can only withstand extremely low temperatures (Wood, 1988). In addition, effective gas exchange mechanisms are necessary due to the high metabolic requirements of fungus (Vesala et al., 2019).

From the above, it is evident that termites, particularly fungus-growing termites, must have the ability to sense and redistribute moisture within the soil. They can bring moisture to the surface by continuously building. For that, they utilize secretions as a cementing material to place freshly laid soil in addition to water (Kandasami et al., 2016). Water accounts for a substantial fraction of the soil transported by termites, ranging from 10% to 15% (Jones et al., 1997). A remarkable feature of termite behavior is their capacity to disrupt deep soils and build extensive networks of tunnels (de Bruyn & Conacher, 1990). These modifications enhance soil fertility and production, while also also improving soil water retention capacity (Arshad, 1982). By creating channels and pathways within the soil, termites facilitate water penetration into deeper soil layers, thereby promoting soil moisture retention and availability for plant uptake (Arshad, 1982). Termites in open habitats have been observed to transfer more water through their mound structures than those in forested habitats, indicating their role in regulating water dynamics across different ecosystems (Chen et al., 2019). Thus, the ability of termites to transport significant amounts of water through their activities contributes to the overall moisture content and availability of water within soil environments.

The subterranean lifestyle of termites poses significant challenges for water management. Termites lose water to evaporation through buccal and anal openings, spiracles, and their cuticles. The relatively thin cuticle of subterranean termites might make them vulnerable to rapid desiccation in dry to relatively moist surroundings (Edney, 1977; Hadley, 1994). Thus, maintaining a steady water supply is crucial to their survival. Despite that, some subterranean termite mounds are found in desert areas (Hernández-Teixidor et al., 2024). Because mound-building termites survive across various environmental conditions, their ability to build and maintain mounds is puzzling, especially as the source of their water supply is unclear. Even if water is accessible, it is unknown whether and how this species can transport it.

In this project, I explored how termites transport water for mound-building. Based on previous observations that termites transport water, I developed a lab-based assay to measure the water transport behavior. We examined the quantity of water transported as well as the timescales of the behavior at varying soil moisture conditions (20%, 30%, and 40%). The results show that there is less need for water transport at the 40% soil moisture level, which shows that the 40% soil moisture is enough to maintain the mound. At 40% soil moisture levels, the termites made distinctly identifiable structures which were not observed at lower soil moisture. Compared to 20% soil moisture condition, the termites ingested and started to transport water within 30 minutes. We show these water-transporting results using various metrics in our results chapter.

Materials and Methods

Study species and site

All experiments were conducted using *Odontotermes obesus* termites collected from termites mounds at the National Centre for Biological Sciences (NCBS) and Gandhi Krishi Vignana Kendra (GKVK) campuses in Bengaluru, India.

Sample collection

To collect the termites from the mound, we made a hole (~3 cm diameter) in the mound and covered it using a 50 mL centrifuge tube. This prompted the termites to build within the tube walls by depositing soil. This building process indicated the presence of active termites in the mound, which allowed us to collect both the termites and the soil processed by them. It took about two to three hours for the termites to fully cover the tube walls. After the tube walls were covered with a layer of soil, we removed the tube from the mound, tapped out the termites in a container, and scooped out the soil from the tube for subsequent experimental purposes. After collection, we separated termites from the soil by using a paint brush and kept them in an open container. This container was then stored for around an hour in a room where the temperature and humidity were maintained at 23^0C and 75% relative humidity (RH), respectively using humidifier. In our assay, only the major caste of termites were used to minimize variability. Major workers are visibly larger than minor workers, which makes their separation and handling easier. After an hour, we made groups of 30 termites, and each group was put into a different panel in the filming arena for subsequent experiments. We ran our experiments at 23 ± 1^0C and $70 \pm 5\%$ RH. We oven-dried the mound soil (which is processed by termites) at 60^0C for 48 hours to remove all water. Specific quantity of water was then added to dried soil.

Experimental Setup

To visualize the termites as they transported water, we modified an assay that had been previously developed in the lab (Ramaswamy, manuscript in prep). This assay contained a cuboidal plexiglass arena that was open at the top, measuring 29 cm x 17 cm x 8 cm (Fig 2.1A). The arena was divided equally into four panels, each measuring 17 cm x 7 cm. Each panel was separated by a plexiglass wall to prevent termites from crossing over into the adjacent panels. At either end of these arenas, there are detachable wells (30 mm in diameter, 1.5 mm in height) supported by a thick mesh under them. One of these wells hold soil, and the other holds a reservoir of water. Previous research (S. Ramaswamy manuscript in prep) had established that at 30% soil moisture levels, the building capacity of termites was maximal. Based on this result, the first set of experiments were conducted with soil patches of 20%, 30%, and 40% w/w of water to dry soil.

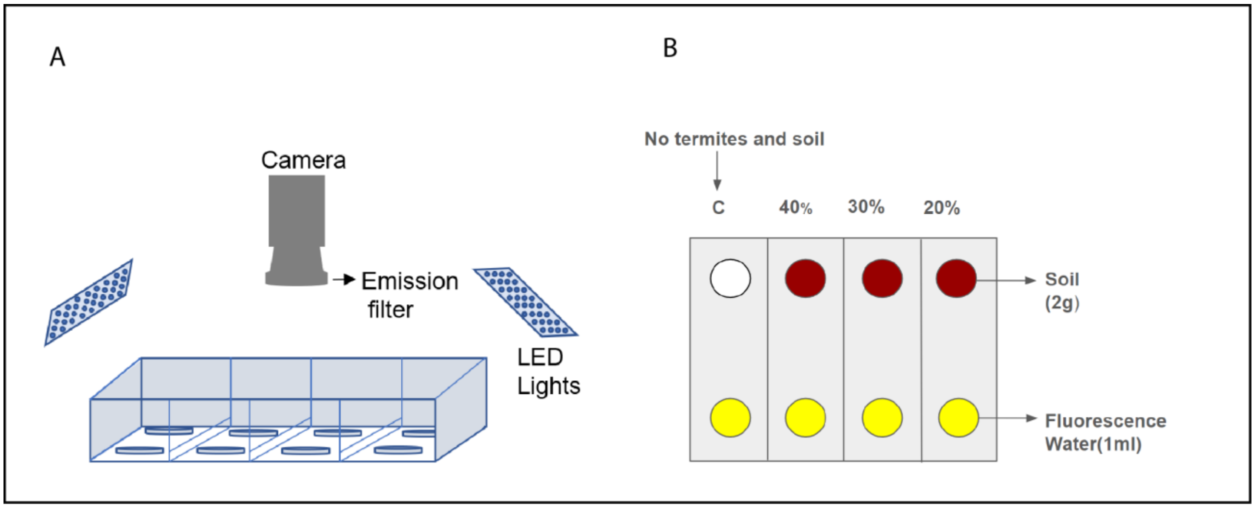

Fig 2.1 A) Schematic of a setup from the front view **B)** Schematic of a setup from the top view

The well at the other end contained water which was provided using moistened tissue paper. This water was mixed with 1µL/mL of fluorescein (Excitation: 440–460 nm, Emission wavelength: 517 nm). When the arena was illuminated by 470nm blue LED light, the fluorescein-laced water glowed and allowed us to track and film the termites which had interacted with or imbibed the water, as glowing spots of light. Groups of 30 major termites were added to the center of each panel, and the observation period was set to 4 hrs.

Measurement of water loss

Because the temperature and humidity around the arena were maintained at constant levels, we assume the evaporation rate for all the lanes is the same. Water loss was measured by weighing the water well before the initiation of the experiment and after finishing the experiment. We also conducted a control experiment in which we measured water loss exclusively due to evaporation, by providing the water body without termites or soil in the fourth lane (refer to schematics).

Later, this value was subtracted from all other water bodies of different lanes to account for water loss due to termite intake only. Because each lane has a patch of different soil moisture content at one end, we were able to assess how much water was transported, over and above the water that evaporated, for different soil moisture levels.

Videography

We recorded the termite movements using either a SONY FDR-AX700 4K Handy-cam (Sony Corporation) or a DSLR with a field lens (focal range 18 - 140mm) (Nikon D7500). An emission filter of 500 - 560 nm band-pass was used on top of the lens to film the water transport activity. Three LED panels containing 160 LEDs each (470nm emission, 5mm through-hole) covered the whole arena and provided illumination at approximately 250 lx of light intensity (CENTER 337 Light Meter). This emission filter selectively transmits the emitted fluorescence light while blocking the transmission of other wavelengths, including the emission wavelength of 470nm of the LEDs. The recording was done with 1920 x 1080 resolution at 25fps for 4hrs.

Image Acquisition

We acquired an image once every 15 min which was then analyzed as follows. The arena was divided into three equal regions – soil region, water region, and middle region. Across the images, we counted and tabulated the number of termites with and without fluorescence in each region. Using different metrics, these numbers were further used to calculate water drinking and transporting activity.

Percentage of termites visible: It is important to note that not all termites were visible to the cameras, especially when they built overhanging structures that blocked our view. Such termites are termed as *hidden termites*. This meant that we could only count the percentage of visible termites, which could change with time (Fig 3.3 from results).

Number of termites building: The number of termites that were actively building could be assessed by counting the number in the soil region (Fig 3.6 from results).

Number of termites actively drinking water: To assess which termites had interacted with water, we counted the total number of termites with fluorescent abdomens. The abdomen of termites fluoresces only if they have imbibed water from the water body laced with fluorescein. The hidden termites were not counted because their abdomens were not visible (Fig 3.5).

Number of termites transporting water: To assess how many termites transported water from the water patch to the soil patch, we counted termites on the soil patch with fluorescing abdomens (Fig 3.7).

Statistics

A normality test was done for the dataset. As sample size is 6, we used non-parametric tests. A pairwise comparison using a two-tailed Mann-Whitney U test was done to assess the significance of water loss between 20-30%, 30-40%, and 20-40% of soil moisture. (Fig 3.2).

Results

Termites uptake water from the water body

To understand water transportation in termites, we first standardized the fluorescein concentration in the water body to ensure that it was not averse to termites. Higher fluorescein concentrations in water (2µL/mL, 3µL/mL, and 4µL/mL) elicited no response from termites which rejected such water. Through iterations, we observed that termites readily imbibe water from the water body at 1µL/mL conc of fluorescein added to distilled water. The fluorescein fluoresces under blue light has an excitation wavelength of 440–460 nm (Fig 3. 1A). This method allowed us to track the termites that had consumed water from the water patch.

Termites transport water to the soil patch from the water body

The second step was to observe if the water imbibed by the termites from the water patch was deposited on the soil patch. In the experiment, we provided soil patches of different moisture levels with a water body for each soil patch. We observed that termites imbibed the fluorescein-laced water, moved to the soil patch and actively built there. The movement of such termites could be easily tracked due to the fluorescein in their abdomens (Fig 3.1B). Was the transported water used in subsequent construction? If so, then we may conclude that termites transport water to facilitate construction. Indeed, our experiments indeed showed that the fluorescein-laced water from the water patch was deposited on the soil patch during construction activity (Fig 3.1C).

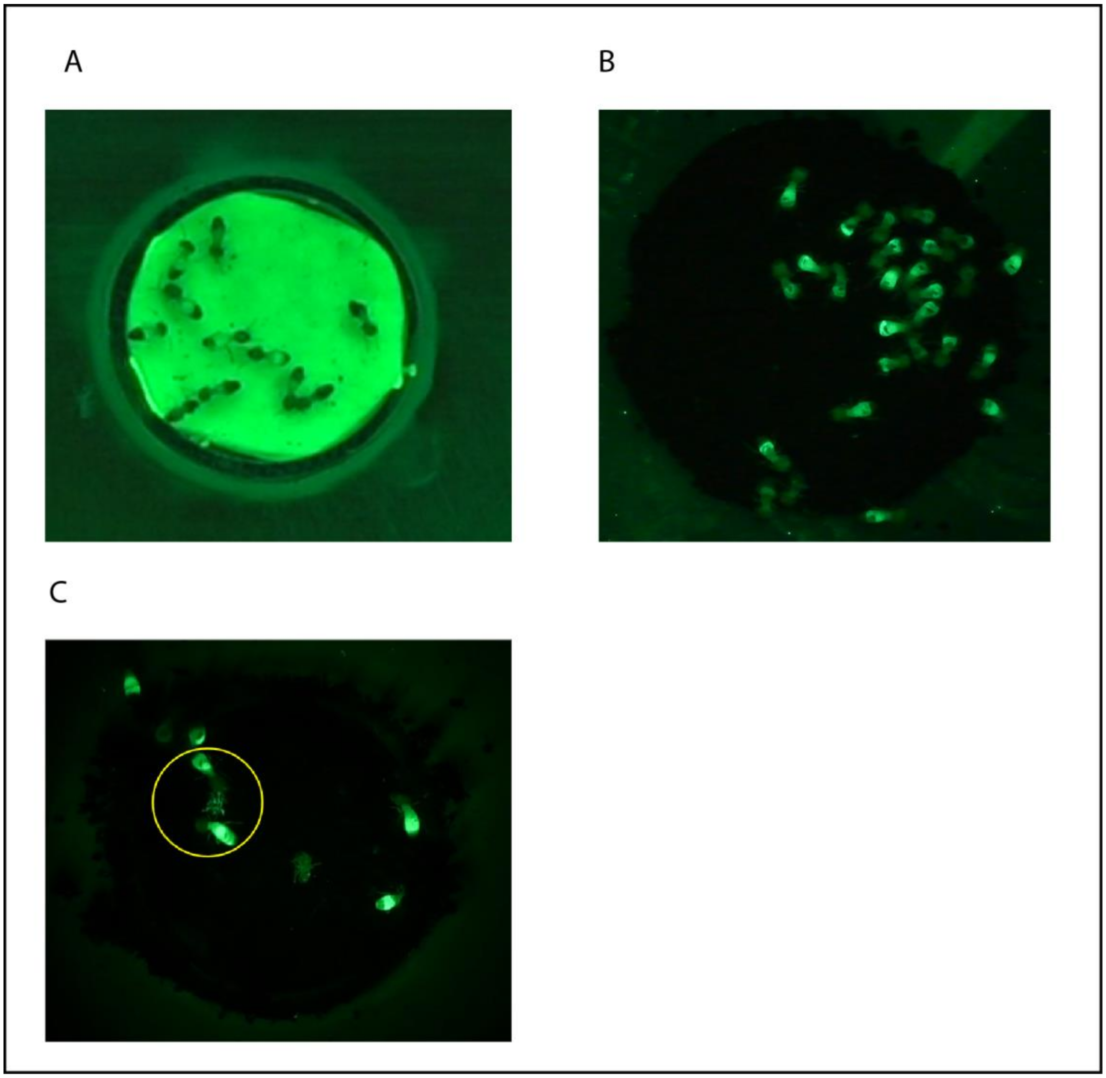

Fig 3.1 A). Termites uptake water from the water body and have a fluorescing abdomen when observed under blue light. **B).** Termites with fluorescing abdomen on a soil patch. **C).** The circled area shows one such instance of water deposition onto the soil patch.

Amount of water transported by termites

The water loss due to evaporation alone (Fig 3.2A-control) was subtracted from our readings for water content to obtain the water loss due to transportation by termites (Fig 3.2B). The median water transport by termites is 37% in soil moisture content of 20%, 26% in soil moisture content of 30%, and 6% in soil moisture content of 40%. This demonstrates that water transported from the water body to the 20% soil moisture patch was greater than the water transported to the 30% patch, which in turn was greater than the water transported to the 40% patch.

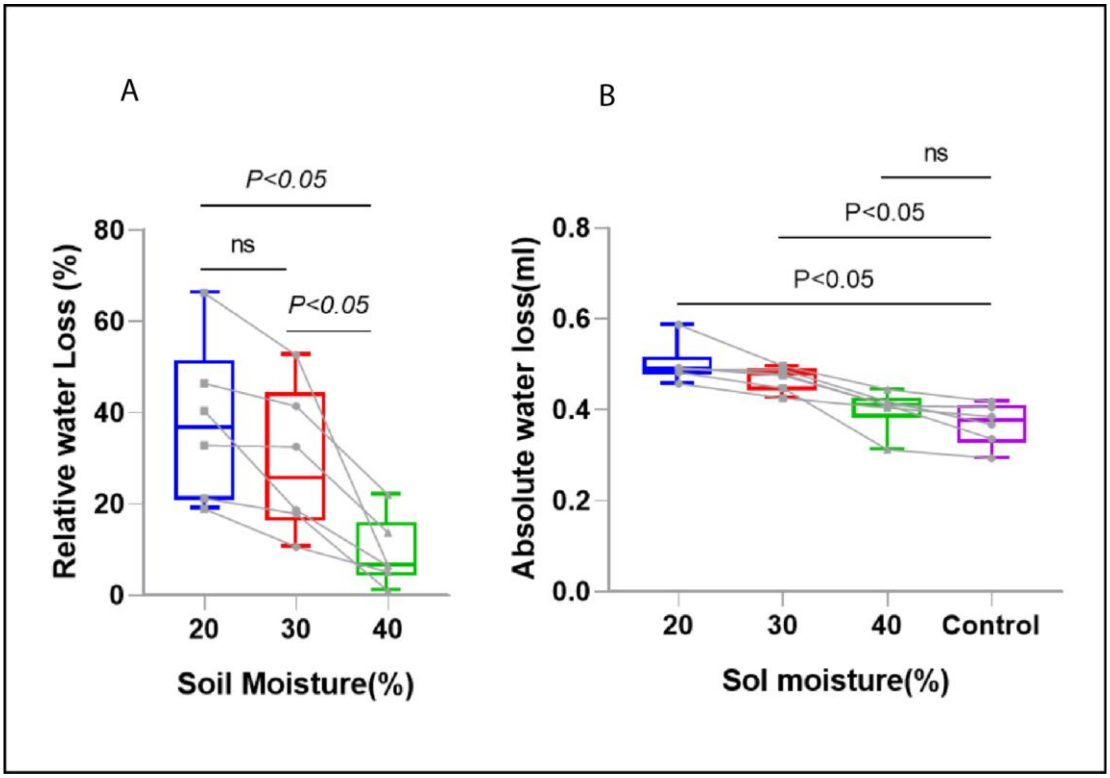

Fig 3.2 Water loss due to consumption by termites. **A)** Absolute Water loss in mL from the water body across the different soil moisture conditions. The evaporation control is for ambient evaporation of water during the experimental time. The connecting lines show the result from the same trial for different soil moisture conditions. **B)** Relative water loss across the various soil moisture panels. The value of water evaporation has been subtracted from each corresponding trial. The connecting lines show the result from the same trial for different soil moisture conditions. The grey dots show every trial (N=6). Statistical analysis using Mann- Whitney U test was used.

The structures built on the soil patch determine the visibility of termites

Throughout the observation, termites built various structures including dome-like structures (Fig 4.2 from discussion) which were overhanging and led to termites being hidden. The number of hidden termites thus indicate more overhanging structure. To account for this in our analysis, we measured how the number of visible termites changed as a function of time. Unlike in the case of 20% soil moisture lane in which all termites were always visible, the termites in the 40% soil moisture lane decreased in number (presumably because they were hidden under the overhanging structure), and then reappeared perhaps because they climbed atop the structures that they had built.

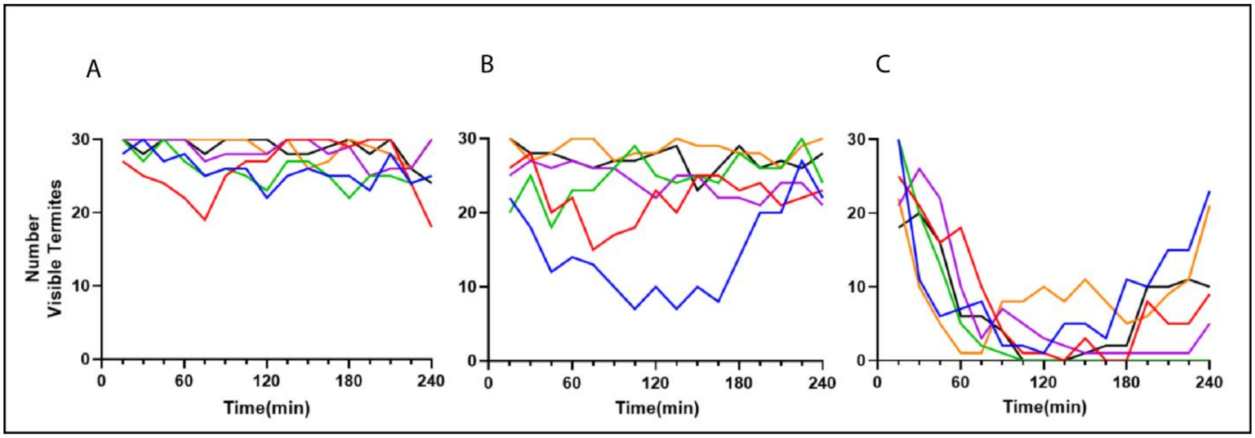

Fig 3.3 Number of visible termites in all three panels across the experimental duration. **A)** 20% soil moisture condition, **B)** 30% soil moisture condition, and **C)** 40% soil moisture condition across different time points. The various colors are different trials (N=6).

Water transport starts at different time points in different soil-moisture conditions

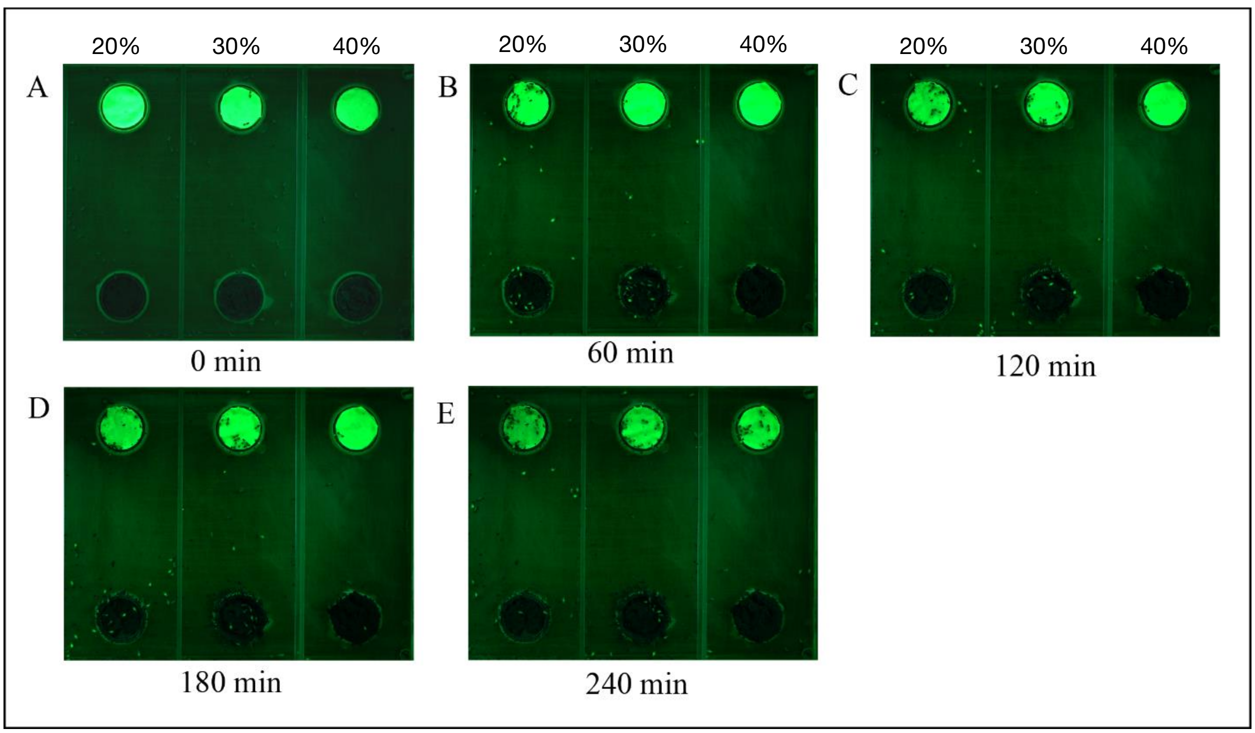

Fig 3.4 Images of the experiment at every 60th min time interval are shown.

Fluorescence-based measurement of water transport in termites

Concomitant with the measurements of water loss, we also counted the number of termites that were fluorescent due to water ingestion. Consistent with water loss measurements, the number of fluorescent termites in the 20% soil moisture lane were greater than the number in the 30% soil moisture lane, followed by the number in the 40% soil moisture lane which only starts to increase after 120 mins.

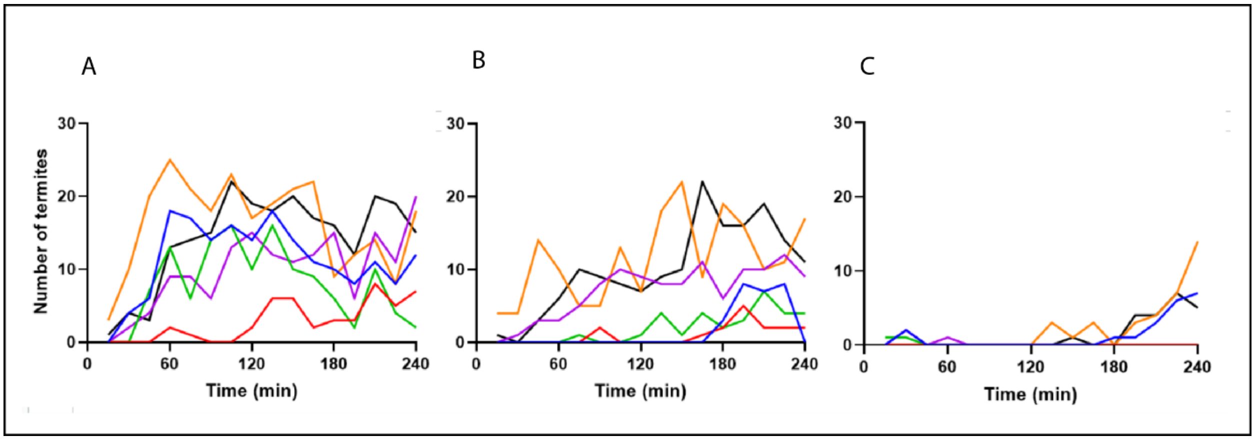

Fig. 3.5 Number of termites that have ingested water from the water body: **A)** 20% soil moisture condition, **B)** 30% soil moisture condition, and **C)** 40% soil moisture condition across different time points. The various colors are different trials (N=6)

Termites in 40% soil moisture condition show maximum building activity

We counted the number of termites present on each soil patch as a measure of building activity as a function of time. The termites were photographed and counted every fifteen minutes. We observed maximal building in the patch with 40% soil moisture (Fig 4.2). However, these termites were static on the patches, and not moving about. Hence, they were building on the moist soil patches, rather than transporting water from the water patch.

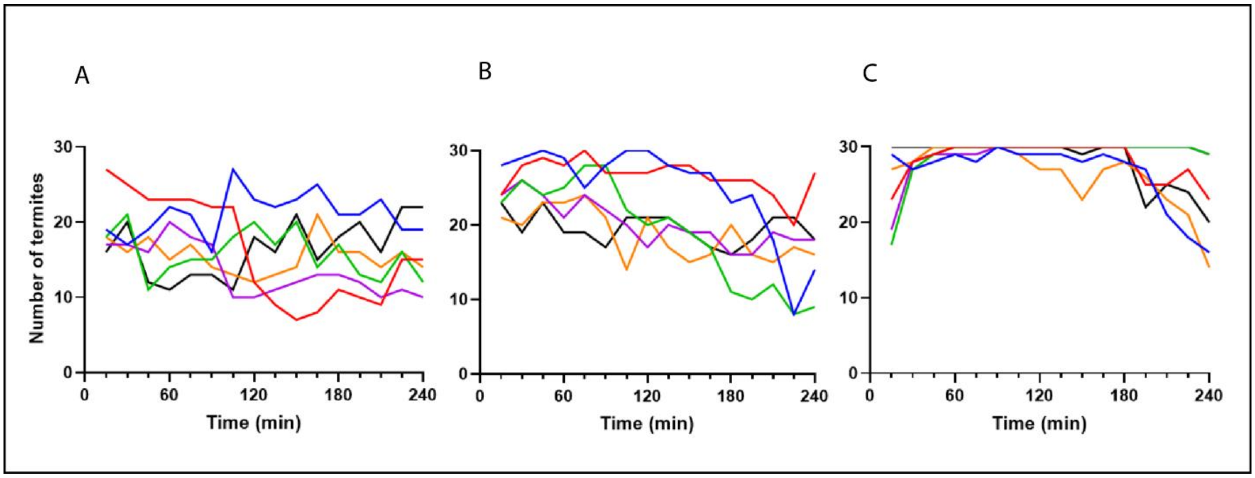

Fig. 3.6 Number of actively building termites in **A)** 20% soil moisture condition, **B)** 30% soil moisture condition, and **C)** 40% soil moisture condition across different time points. The various colors are different trials (N=6)

Termites in 20% soil moisture condition actively transport and build

We counted the number of termites with fluorescent abdomens, and again photographed and counted them every 15 minutes. These data show that there are more fluorescent termites present on the 20% soil moisture patch as compared to the 40% patch, which suggests that these termites had actively transported water from the water patch for the purpose of construction.

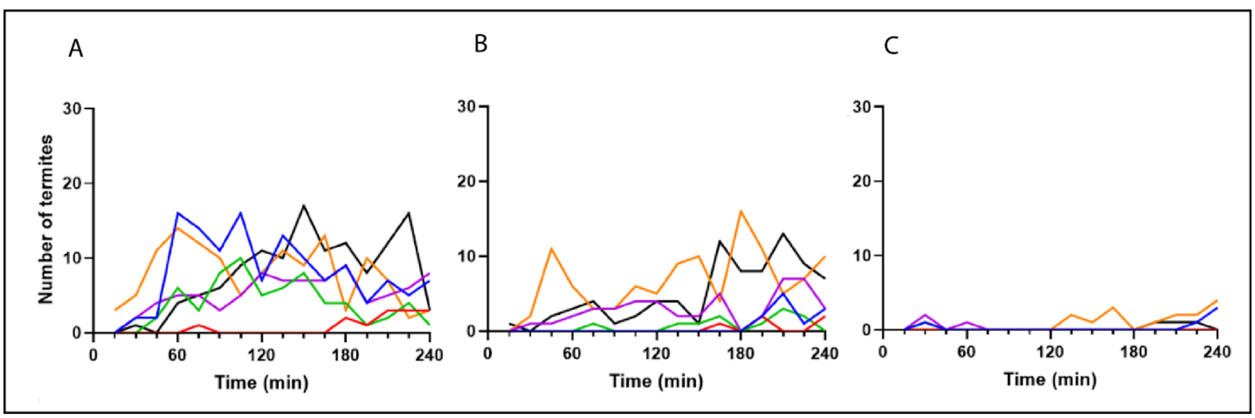

Fig. 3.7 Number of termites that are actively transporting and building on soil patch. **A)** 20% soil moisture condition, **B)** 30% soil moisture condition, **C)** 40% soil moisture condition across different time points. The various colors are different trials (N=6)

Discussion

Water transportation in termites during building

O. obesus termites build mounds of soil, which house their entire colony. During construction, the soil is continuously masticated, regurgitated, rolled up into boluses and deposited. Termites also continuously reshape the interior part of mound which requires a continuous supply of materials. Proximity to a water source or water-logged areas could facilitate access to these materials, as termites not only forage for food but also gather soil for bolus formation. Like ants, termite species transport water in their abdomens for various activities, however the specific water regulation mechanisms employed by *O. obesus* remain unexplored.

The results reported here clearly demonstrate that termites ingest and transport water from water-rich patches to drier patches and use the water for construction. The series of experiments described here show that when soil patches are drier (20%) than optimal (30%), termites tend to transport water from the water source to the patch, whereas when the patches are wetter (40%) than optimal, they build overhanging structures on site, without transporting any water. Further, we were also able to track their movements in time for these various conditions to obtain the temporal dynamics of their movements. Water transport was least frequent (6%) in conditions with 40% soil moisture, whereas at 20% soil moisture, a significantly higher volume of water (37%) was transported by the termites (see Fig 3.2). This investigation sheds light on the adaptive strategies *O. obesus* employs to manage water resources.

Construction in various soil treatments

A prior study in our lab investigated how termite structures vary with water content alone when they are forced to build in specific soil moisture conditions between two plates. The maximum number of galleries and structures in the “double plate assay” occur at 30% moisture content (Ramaswamy, in prep). However, in the double plate assay, water content was consistently maintained, preventing termites from altering the soil moisture. These results reflected termite behavior and construction in a static moisture setting, capturing termite-built structures in a 2D context due to the presence of plates on either side.

Building upon this, our experiment compared 3D structures to those observed in the previous study. We found that at 20% and 30% soil moisture levels, the structures termites constructed were similar to those previously observed. However, at 40% soil moisture, we observed distinct types of construction. Termites removed soil from the plate, forming it into boluses to create a dome-like structure atop the plate. Under this dome-like structure, termites in the 40% soil moisture condition continued to build, later creating small holes in the dome to emerge and forage for water. Contrarily, in other soil moisture conditions, we observed the formation of walls and tunnels using the soil. These novel findings underscore the adaptability of termite construction techniques to varying environmental conditions.

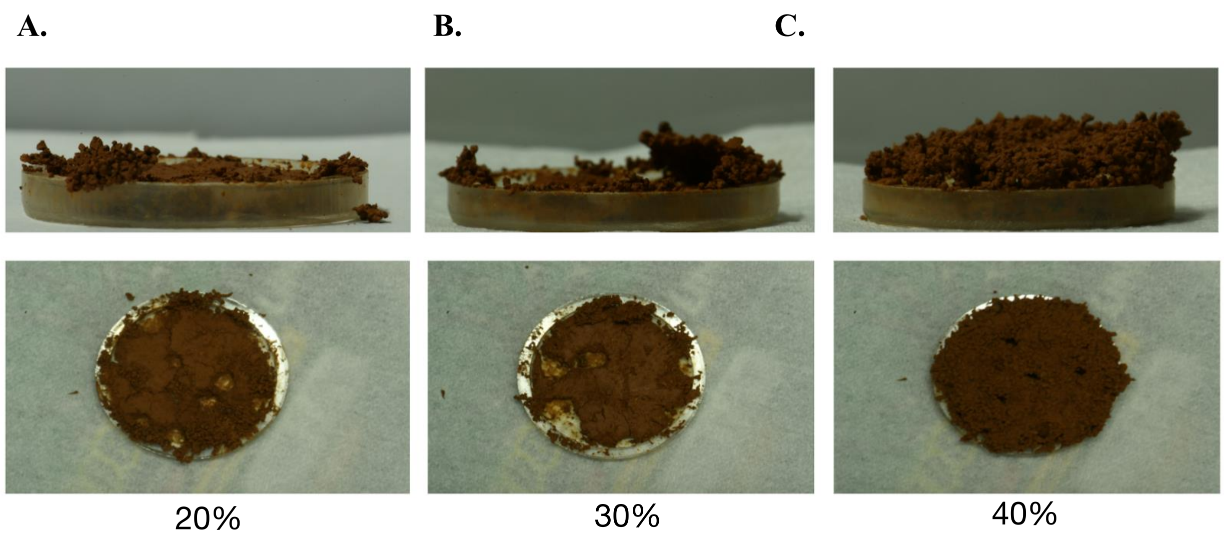

Fig 4.1 Side view and top view of the construction done by termites in different soil moisture conditions. **A)** 20% soil moisture condition, **B)** 30% soil moisture condition, **C)** 40% soil moisture condition

Temporal dynamics of water transport

Water uptake and transportation activities were predominantly observed at 20% soil moisture levels, followed by 30% and 40%. Our choice of the various conditions soil moisture levels of 20% mimic arid conditions, while 40% indicates rainy areas, and 30% represents neither arid nor rainy. These moisture conditions and changing seasons significantly influence termite behavior, affecting their building, water ingestion, and water transport over time. Despite efforts to control temperature and humidity in our experiments, maintaining consistent soil moisture proved challenging due to water evaporation from the soil surface. The construction activity of termites exacerbates this issue by bringing soil particles to the surface, increasing evaporation risk. At 40% soil moisture however, termites emerged after building the dome, which underscores the importance of environmental factors. This phenomenon is particularly relevant in diverse climates like that of the Indian subcontinent, where temperature and humidity vary widely, possibly affecting termite foraging strategies for both food and water. Our study focused on major worker termites, whose larger size enables them to carry greater volumes, contrasting with potentially different behaviors observed in minor worker termites. Investigating minor workers could unveil further intriguing insights into termite behavior and environmental adaptation strategies.

Future Directions

The experiments described in this thesis may be viewed through the lens of how collective building occurs under varying ambient conditions, and how decisions are made about excavation and deposition in specific sites. Although we have not investigated communication between termites, some form of structure-based communication may be an essential feature in such cooperative construction activity (Sane et al, 2021). Another important aspect that emerges from this study is the possibility of humidity sensing in termites, especially as the worker termites lack eyes. Their ability, demonstrated here, to build different structures under variable soil moisture conditions provides a mechanistic basis of adaptive decision making under variable conditions.

Our research also throws light on termite mound maintenance across diverse environmental conditions. How is this accomplished under natural conditions? Future research should look into the internal moisture levels of mounds in the wild throughout the seasons. Using soil moisture sensors in and around the mound that could provide detailed recordings of how moisture is regulated within mounds under varying climatic conditions over the year would provide valuable long-term data. This approach would shed light on the ability of termites to adaptively manage mound conditions in response to different temperatures and seasonal changes.

Given the significant variation in land water content across seasons—from over 60% during rainy periods to as low as 0-10% in summer—the strategies termites use to maintain mound integrity under such extremes present a compelling area of inquiry. Moreover, cataloging the number of mounds in various regions, alongside the climatic conditions of these areas, would offer valuable insights. The species under study is itself known to build five different distinct mound architectures in the same environment. A comprehensive survey considering the count, size, shape, and construction material of mounds across different locales could reveal patterns in mound variability.

Collectively, this data would not only enhance our understanding of termite engineering and environmental resilience but also contribute to broader ecological and biological knowledge. Such studies are essential for appreciating the complex interplay between organisms and their habitats, offering lessons on sustainability and adaptability relevant beyond the study of termites.

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