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Termite Foraging and Preference of Soil Type and Moisture Content in Laboratory Bioassays

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ABSTRACT

Termites (*Coptotermes acinaciformis*) were tested for their preference of different soil types in a laboratory condition at different soil moisture levels. The soil types provided were Topsoil, Fine sand, Potting mix and Peat at moisture levels of 0, 5, 10, 15 and 20% for 30 days. The experimental apparatus involved individual termites foraging from nesting jars connected to four sets of standing perspex tubes filled with the four soil types attached to the jar lid on top at each moisture level. Foraging activities were observed at 12 hour intervals to avoid disturbance while the number of days taken by termites to penetrate and forage inside each soil column was analyzed as a measure of preference by termites. Soil type had a significant effect on termite preference whereas soil moisture content did not have any significant effect. At lower moisture levels of 0 and 5%, termites preferred Fine sand. Topsoil was preferred at moisture levels of 10, 15 and 20%. Termites built distinct tunnels and tunneling branches in Fine sand, most of the time starting from top to bottom, and covered them with dark clay particles brought from the nesting jars. However, they transported soil particles from Topsoil columns to the nesting jars to build foraging layers on top. The average rate of soil transport from a Topsoil column was higher at higher moisture levels.

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INTRODUCTION

Termites construct intricate networks of underground tunnels and soil covered tubes to access resources as well as protect themselves from predators and harsh environmental conditions while foraging (Lee and Wood, 1971; Lee and Su, 2010). Their preference for specific soil types determines successful start of their colony, establishment and expansion, foraging behavior, territory, distribution and access of food resources (Cookson and Trajstman, 2002; Cornelius and Osbrink, 2010; Lee *et al.*, 2008). In laboratory conditions, they were observed to increase their tunneling activities when concentrations of sand particles were increased (Houseman and Gold, 2003). Apparently they forage through soils by following gaps, surface irregularities and other materials, roots, food, etc. or any other preformed tunnels in the soil in order to conserve energy and time before starting to construct their own tunnels (Evans, 2003).

The ability of termites to transport water into dry soils is influenced by the water holding capacity of the soil which in turn determines the availability of free water for termites (Ahmed, 2000; Cornelius and Osbrink, 2010). Cornelius and Osbrink (2010) observed that termites could not successfully colonize wood blocks located on dry clay substrates because water molecules hold more tightly to fine particles of clay when compared to the coarser particles of sand. In fact moisture is so critical that dry soil has been used as a barrier against termite penetration (Cornelius and Osbrink, 2011). Location and number of termites in a particular foraging place is usually higher in higher moisture content (MC) (Ahmed, 2000; Wong and Lee, 2010). In a study on the effect of moisture in a sand substrate on the behavior of termites (*Mastotermes crassus* and *Coptotermes gestroi*), Wong and Lee (2010) discovered higher number of termites in 20 % moisture level dish than in those with lower MC. However, at 25 % moisture level less activity and presence of termites was observed due to saturation of the sand substrate. A medium range of 10–15% MC was reported as the preferred range to conquer baits located at the top end of a sand substrate for *C. acinaciformis* (Ahmed, 2000).

Generally, termite activities increase with increase in soil MC (Arab and Costa-Leonardo, 2005; Su and Puche, 2003; Wong and Lee, 2010) unless the soil is saturated, drastically limiting their movement (Ahmed,

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2000; Su and Puche, 2003; Wood, 1988). Early tunneling activities are usually concentrated primarily in areas of higher MC. Rate of tunneling, distance and area explored increase with increase in MC (Su and Puche, 2003). After being released into a homogenous sand filled arena, *Coptotermes frenchi* tunneled slowly in the dry part of a sand substrate before concentrating into and increasing their tunneling activity by about five times after discovering wet sand (Evans, 2003). Su and Puche (2003) observed a positive correlation between tunneling activity of termites and MC and reported a 1 % increase in MC resulting in an increase of tunneling areas at 6.26 cm^2 and 7.17 cm^2 for *Coptotermes formosanus* and *Reticulitermes flavipes*, respectively. Arab and Costa-Leonardo (2005) mentioned that *C. gestroi* explored more areas at soil MC of 15 % and above in a sand substrate by building more secondary tunnels. Wong and Lee (2010) reported the species *M. crassus* and *C. gestroi* tunneled significantly further in sand with 20 % than 0 % MC.

Termites transport water from moist areas to relatively drier substrates and improve the microclimate by creating and maintaining a humid environment while softening their food material for easy consumption (Ahmed, 2000; Arab and Costa-Leonardo, 2005; Evans, 2003; Su and Puche, 2003; Wong and Lee, 2010). They construct galleries in dry soils using moisture carried from wetter soils and retain it in the galleries during evaporation and hence maintain continuous supply (Evans, 2003). This helps them colonize food sources located in dry soils and it determines their success in conquering new areas (Wong and Lee, 2010). Two weeks after successfully establishing their foraging activities in their favorite range (10 – 20 %), Ahmed (2000) reported that *C. acinaciformis* conquered drier moisture ranges of 2.5 % and 5 % in a laboratory apparatus. After conquering places of higher MC, termites modify or control drier environments cancelling the effect of any moisture gradient due to drying (Ahmed, 2000; Arab and Costa-Leonardo, 2005; Su and Puche, 2003).

Termites are more likely to aggregate in moist top soil and clay (mainly fine texture) as they can retain moisture in their galleries for extended periods of time and avoid dehydration due to evaporation. However, soils with more organic matter like Peat moss and Potting soil are chosen when termites move from moist to dry soil owing to the higher water retention capacity of these soils and the readily available water (Cornelius and Osbrink, 2010). Cornelius and Osbrink (2010) also observed that *C. formosanus* termites in replicates with clay and top soil built shelter tubes up the sides of the tanks while those in sand replicates not only built shelter tubes into the air with no contact with the tank walls but also spread the sand particles all over the surface to help them move up the tank walls. Individual termites climbed up the tank using the sand particles spread on the wall but were exposed to the air. However, because the tanks were kept in an incubator with 97 % relative humidity, the sand particles may have maintained their MC and allowed termites to obtain moisture easier than in soil or clay, thus successfully climbing without constructing shelter tube.

The objective of this study was to extend this knowledge base and determine optimum MCs for termite foraging in different soil types in a laboratory condition; to describe and quantify soil transport rate and percentage surface cover in different soil type – MC combinations; and to compare the time it takes for termites to penetrate and forage different soil types at different MCs.

MATERIALS AND METHODS

Termite:

Termite species of *Coptotermes acinaciformis* were collected from two mounds of field colonies in Gove Peninsula (12°17′S 136°49′E), in the town of Nhulunbuy, 600 km east of Darwin, Northern Territory, Australia. The mounds were selected randomly and were then opened by circumventing cable ropes around their perimeter and pulling through using a vehicle to break the outer hard surfaces and open up the mounds. The distance between the two mounds was deemed big enough that it was assumed that they constituted two different colonies. The termites were carefully collected manually from the broken mounds on the field using sieve meshes to separate them from mound soil materials and nest debris. Approximately two spoonfuls of termites (40 g) each containing mostly of workers and soldiers were placed in transparent glass jars (100 mm wide and 300 mm long) after filling the jars with soil material from the mound and inserting chips of wood blocks (20 X 20 X 5 mm) as food. Water was sprinkled into the jars and they were brought back to the laboratory, at the University of Melbourne, Burnley campus, Melbourne, stored and kept in the dark at room conditions of 27 ^oC Temperature and 75 % Relative Humidity. The jars with termites from the first mound were considered as Colony I and termites from the second mound as Colony II and were marked accordingly. Immediately before starting the experiment, 10 ml of water was sprinkled into each jar to make sure that termites have enough moisture for the duration of the experiment and encourage them to forage into the soil columns from an optimum environment.

Soil Types:

Four different soil types were used for the study: Top soil, Fine sand, Potting mix and Peat. All soil types were composed of heterogeneous soil or organic material (Table 1). The Top soil used was sandy loam soil, sometimes sold as Turf Blend soil. The Fine sand was quarried sand sold as a coarse grade washed sand and is composed of 70 – 90 % particles of size range of at least 1.18 mm and 10 % of 4.75 mm. The Potting mix was prepared from Composted Pine bark while the Peat used was Canadian sphagnum Peat particularly characterized by its ability to hold large amount of water, up to 20 times its dry weight in water.

Fig. 1: Selected termite mound of *C. acinaciformis* was opened by pulling through a circumvented cable rope and manually collecting and sorting termites from the broken mound.

Table 1: Soil types used for the experiment and their composition.

Soil Type	Source	Composition
Top Soil	Fulton's, Victoria	Sandy loam soil, Turf blend 30% Fine sand
Fine sand	Rocla, Victoria	Coarse grade washed sand, 70-90% >1.18mm, 10% 4.75mm
Potting Mix	Debco, Victoria	Composted pine bark, Medium grade 4-6mm
Peat	Canadian sphagnum Peat	Anaerobically composted leaves and stems of Peat Moss plant

Moist soil preparations:

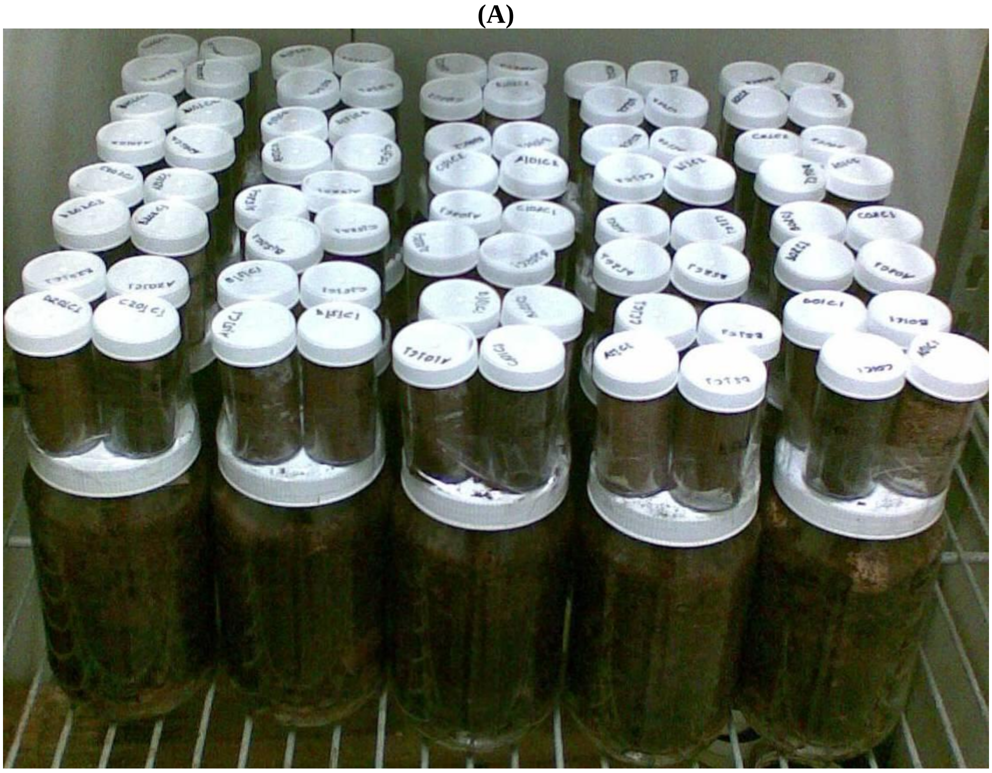
All soil materials were air dried for three weeks to bring the soil moisture in equilibrium with the surrounding air. The MC of each soil was then measured by taking soil samples for oven drying overnight and reweighing. Depending on the air dry MC of each soil type, a sample was oven dried overnight to be used as 0 % MC while a calculated amount of water (using mass/mass ratio) was added to bring each of the other samples to the desired 5, 10, 15 and 20 % MCs, respectively.

Each sample was thoroughly mixed and placed in a sealed container and left overnight to equilibrate. At the end of the equilibration period a subsample of the soil was placed in clear perspex tubes, filling up to 5 cm level and leaving the upper 2 cm for placing a wood block used as food. As it was not practical to add exactly the same amount of soil particles to each column due to heterogeneity of the soil types, the weight of each soil column used in each case was recorded.

Experimental apparatus and design:

The experimental setup (Figure 2 A and B) consisted of 40 jars, 20 for each colony (C1 and C2). Each jar was connected on top of its plastic lid cover to four vertically standing clear perspex tubes (700 mm long and 350 mm diameter) filled with one of four soil types (Topsoil, Fine sand, Potting mix and Peat). They were placed next to each other randomly to avoid any bias. The soil columns were glued and firmly attached to the lid cover and connected via 2 mm opening holes drilled through the base of each column at the centre and on to the lids. Termites had to move through the opening holes connecting the jars with the soil columns in both directions. Before filling each column with the soil type of specific moisture content (0, 5, 10, 15 and 20 %), a 350 X 350 mm square tissue was placed just above each opening hole in the column to prevent soil falling into the jar while making it easy for the termites to cut and open through during penetration. Dry wood blocks of 0.5 X 2 X 2 cm were placed on top of each soil column to encourage termites to forage through the whole column to access them. Prior to the start of the experiment, the wood blocks were weighed and numbered. Finally each column was closed with a lid, before commencing the experiment to avoid moisture loss and termite movement outside the column. The presence of lid also made observation of the condition of the wood blocks and termite activity easier.

(A)



(B)

Fig. 2: (A) A glass nesting jar filled with moist soil mound material and *C. acinaciformis* with a lid cover connected to four vertically standing clear perspex columns filled with four soil types. (B) Experimental setup for the study of termite preference of soil type and MC in laboratory bioassay.

Observations were made every 12 hours (in order to minimize disturbance to the termites) to assess daily termite movements, foraging activities to initiate or/and penetrate as well as tunneling activity within soil columns. Termite soil spots into or around opening holes of the underside of the lids were used as indications of whether termites have initiated and explored a soil type while penetration into a soil column, number of hours it took and activity inside were used as indications of soil preference. Inspection of termite foraging activity involved examination of the underside of the plastic lid cover of the jars to look for any termite activity or movement, soil spots on the underside and on the opening holes, any opening or termite penetration into the soil columns, any formation of tunnels on the surface of the soil columns and soil particles removed from the columns. At the end of the experiment wood blocks were inspected if they have been covered with soil particles, which probably is an indication of the beginning of termite consumption. Finally they were cleaned and re-weighed to determine wood consumption.

Statistical Analysis:

The treatment consists of two colonies of termite species (*C. acinaciformis*), four soil types, and five levels of soil moisture in a 2 X 4 X 5 factorial design in an apparatus modified from Ahmed (2000), Cornelius and Osbrink (2010) and Cornelius and Osbrink (2011). Four air-dried soil types were moistened prior to installation in test columns of transparent perspex jars, using % mass/mass, to achieve different treatment levels of soil type – MC. Topsoil, Fine sand, Potting mix and Peat were used for the experiment at five different MCs- 0, 5, 10, 15 and 20 %.

Statistical analysis was performed using Minitab 16 Statistical Software. Observations of termite penetration and foraging were made at 12 hour intervals. Time taken by termites to penetrate a soil column and start foraging inside was recorded. The mean number of days under which termites managed to penetrate individual soil columns through the bottom openings of each column were compared and analyzed using analysis of variance (ANOVA) tests for factorial designs at $\alpha = 0.05$. Fisher's least significant difference LSD test at $\alpha = 0.05$ was used to separate individual means of average number of days under which termites penetrated soil columns within a soil type or MC variable. Weight loss of the wood blocks placed at the top of each soil column was also compared to analyze wood consumption rate of termites in different soil types and moisture levels.

RESULTS AND DISCUSSION

Foraging Activity in different soil types:

During the first day of observation, termites immediately foraged up towards the inside surface of the lid cover hovering in and around the opening holes. No particular trend was observed in the way termites started foraging neither was prior preference shown to a particular soil type at any MC. Similar trends in foraging behavior were reported by Su *et al.*, (1984) for *C. formosanus* and by Campora (2001) for *Reticulitermes flavipes*.

Termites move soil particles to transport soil and moisture, build foraging galleries underground or on surfaces and cover them to create dark and moist environments (Cornelius and Osbrink, 2010). Unlike some other insects, termites lack sticky pads on their feet and, thus, encounter difficulty foraging over smooth surfaces. They use transported clay materials and their own excreta to cover the surfaces and forage easily (Skaife, 1955).

Tunneling usually includes excavation, loading, transportation and deposition of soil particles (Lee and Wood, 1971). When termites penetrated **top soil** column, they started their foraging activity from the bottom centre of the soil column, immediately excavating and transporting soil particles to the nesting jars and building galleries at the top of jars or the inside surface of the plastic covers (Figure 3). The excavation and transport of Topsoil left hollow spaces at the bottom of the column and hollowing continued upwards as the excavation continued. Depending on the MC, the top part of the soil column either remained intact above the hollow created at the bottom of the Topsoil column or collapsed under its own weight or the weight of wood block sitting on top. In Topsoil at 15 and 20 % MCs, a thin layer of soil (approximately 0.5 cm thick) formed at the top of the soil column carrying the wood block. This layer of soil remained intact for most of the time till the end of the experiment amid all the excavation and soil transport beneath.

In the case of **Fine sand** columns termites foraged towards the opening holes by transporting clay materials from the nesting jar. This may be in order to carry moisture and improve moisture holding capacity of the sand for further exploration as well as cover the tunnels constructed near the surface with dark clay materials (Lee and Wood, 1971; Turner *et al.*, 2006). Early during the termite foraging, spots of clay soil materials were observed beneath the surface of lid covers (Figure 4). These spots were used as indications on the progress of termite foraging at a particular time especially in cases where Topsoil was not the preferred soil type. Their presence indicated how far and how often termites foraged towards the opening of a certain soil type. More mud cover or darker spots were observed when termites foraged a number of times to penetrate the opening hole and forage inside or close it for partitioning depending on the MC and soil preference. However it may not indicate termite penetration or preference per se as termites may penetrate a certain opening hole without frequently travelling (hence less spots) if the soil type happened to be the preferred type. In most cases where Topsoil was preferred, transport of soil was in the opposite direction and soil particles were deposited at the top of the jars or beneath the lid cover where the spots would have been built. Thus thick galleries were formed beneath the lid cover, quickly covering the spots, making them less visible and hence less useful as indicators of progress in termite foraging in these particular cases.

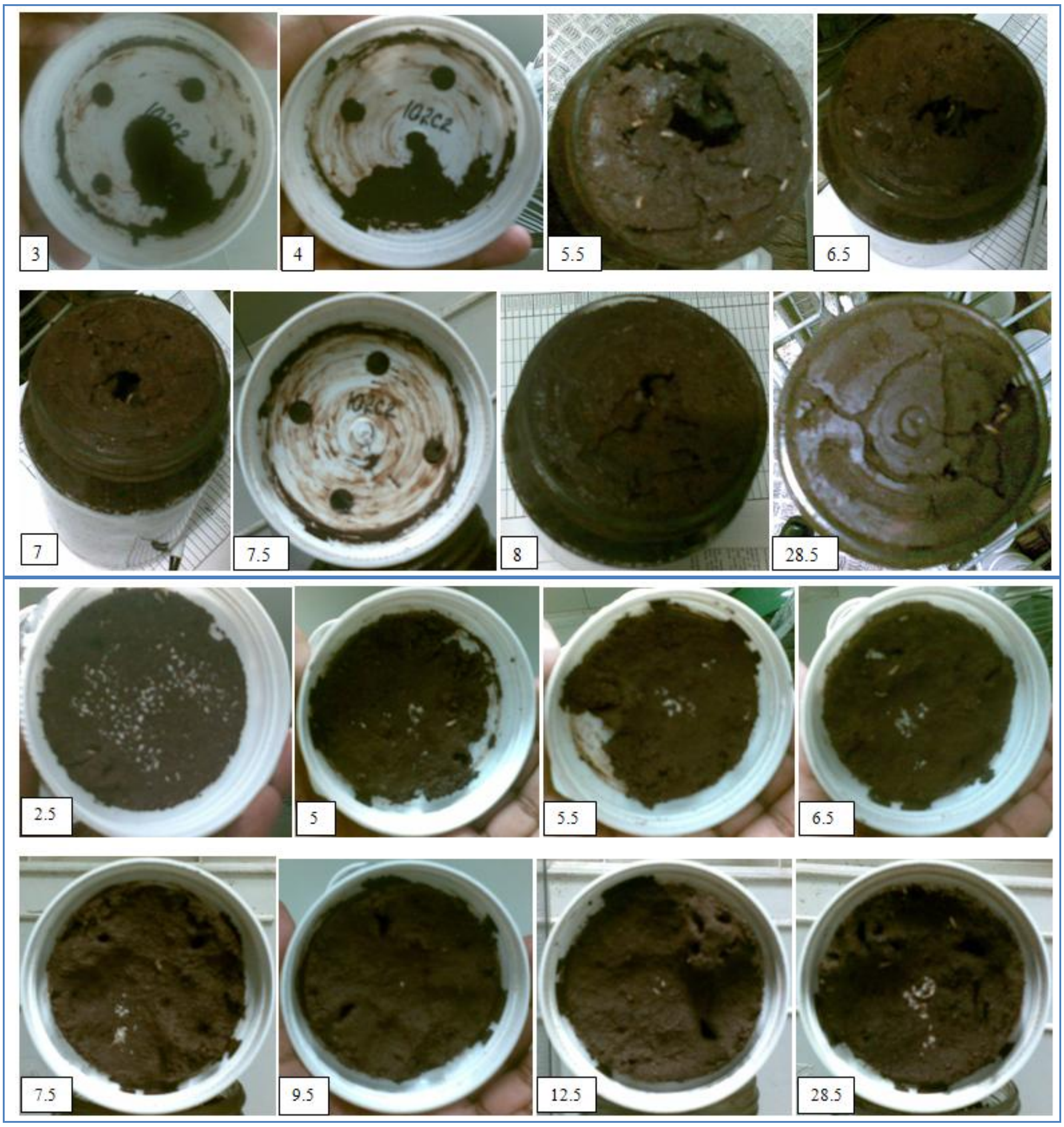


Fig. 3: Termites excavated top soil column at 10 % (Top) and 20 % (Bottom) MC, transported the soil particles to the nesting jar and built foraging galleries by depositing them inside the lid cover surface and/or at the top of the nesting jar. The figure shows accumulation of soil particles and development of soil galleries at the top of nesting jars or beneath lid cover at different days during the study period.

Termites also moved soil particles and pushed them aside within the Fine sand columns to create space for their movement to access wood blocks on top. Similar behaviors were also reported by Lee and Wood (1971) and Li and Su (2009) for other termites.

The random start of foraging by individual termites and distribution of clay spots or materials on the inside surface of most of the plastic lid covers probably confirmed the fact that termites randomly forage when searching for food and other substrates (Su *et al.*, 1984). Termite foraging also followed lines on the edge of the lid cover as these edges were usually darker (especially at the start of foraging) than the other surfaces and most of the time the first ones to be covered with clay materials carried from the nest jars. This might prove the fact that termites also follow physical guidelines during foraging to access a food source (Swoboda and Miller, 2004).

In **Potting** columns termites built tunnels with distinct shapes including V shapes, diagonal, zigzag, irregular and horizontal ones. The most prominent ones, horizontal tunnels, were usually formed at the base of the column covering the whole diameter. High activity of termites was observed on the surface around the wood block and on the tunnels built and in both cases the surfaces were ultimately covered with spots of clay.

The columns of **Peat** were heterogeneous in their composition in terms of the range of particle sizes. There is always some space in between the particles and together with the light weight of the material and relatively low bulk density, termites foraged through the columns relatively easily. However, due to the requirement of higher MC for such soil types in order to sustain termite activity, they were either foraged at higher moisture levels or at a later date during the experiment. This is probably after termites have modified and altered the soil MC by carrying moisture from the nest (Ahmed, 2000). In all the cases termites foraged easily and created distinct vertical and horizontal tunnels and covered the surfaces with clay materials brought from the nest jars.

Although termites were more likely to explore and forage on the first opening hole they encountered, they were observed to explore one or more opening holes at the same time. At any particular MC, most of the foraging activity was concentrated in the column of preferred soil type for that MC, but simultaneous foraging was also observed in other soil types especially late in the study period. Concurrent use of different food sources has also been reported by Arab and Costa-Leonardo (2005).

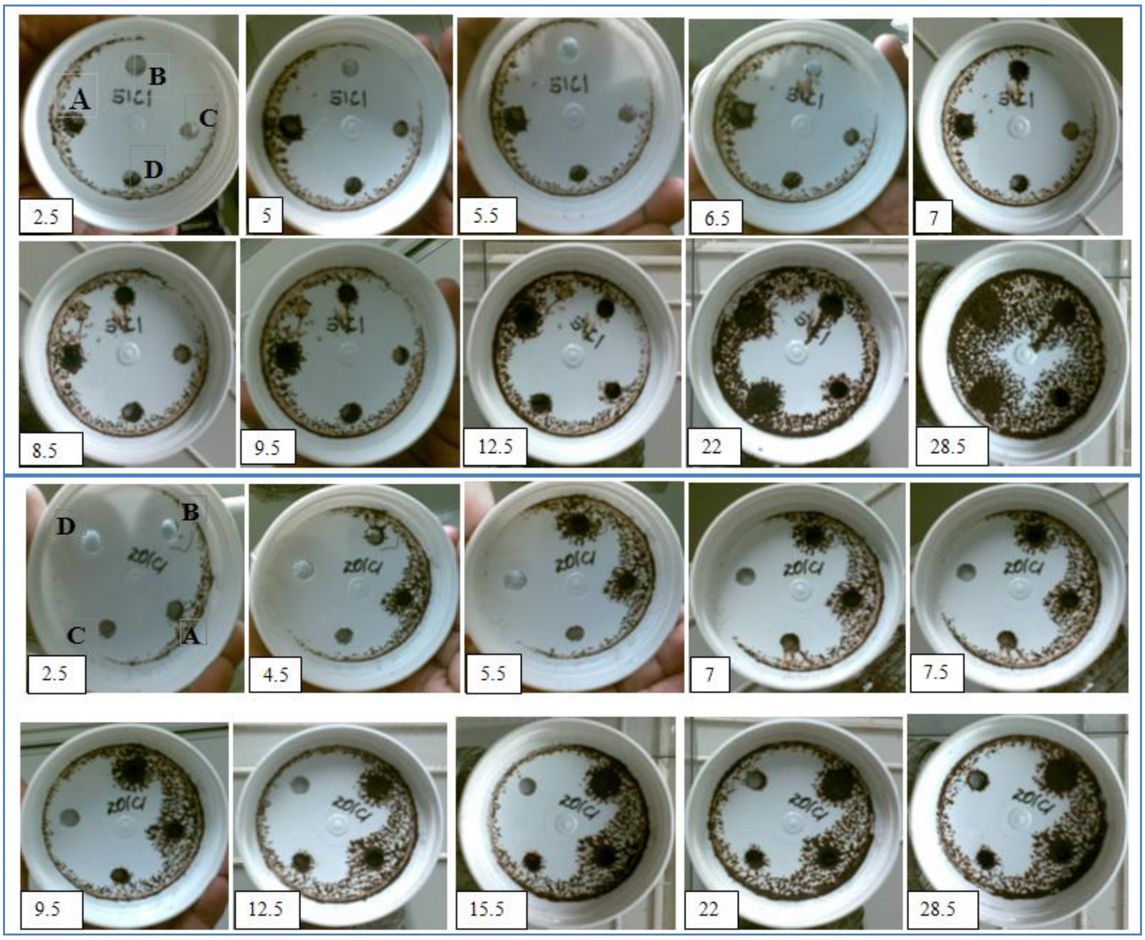


Fig. 4: Soil spots developed during termite foraging at different days during the experiment from a nesting jar to openings on lid cover connected to columns of four soil type at 5 (Top) and 20 % (Bottom) MCs, respectively, via openings at the base. A= Top Soil; B=Fine sand; C=Potting Soil; D=Peat Soil.

In columns with Fine sand (Colony II) at 5 %, Topsoil at 15 % (Colony I) and 20 % (Colony II) MCs, termites penetrated the openings shortly (within 12 hours) after the experimental apparatus was setup. Inside the Fine sand columns they foraged along the entire length of the column and built tunnels close to the surface starting from the top of column towards the bottom. However, inside the Topsoil columns they started excavation at the bottom going upwards, picking and transporting soil particles into the nesting jar usually depositing them at the top or beneath the surface of the lid cover building distinct soil layers or galleries (Figure 3).

Soil MC:

In the control soil (**0 %** MC) termites managed to penetrate and forage through the whole column of Fine sand starting at the top downwards and built distinctly visible vertical tunnels close to column surfaces. First, they covered the surfaces of tunnels already constructed and then eventually most of the upper 65 % of the surface of the column with clay materials transported from the nest jar (Figure 5). Termites sealed opening holes of Potting, Peat and Topsoil columns at the beginning or some time during their foraging activities with clay transported from nest jars. The only exception was in the first replicate where opening holes in Fine sand column remained open while individual termites penetrated and foraged inside the column. It has been reported that termites show behaviors of physical partitioning in order to separate different moisture levels (Green *et al.*, 2005), avoid physical encounters with other colonies or delineate boundaries (Li *et al.*, 2010). In this particular case sealing might have prevented moisture loss or movement from nest jars to the drier substrates of Potting, Peat and Topsoil columns. Evidently these soil types would otherwise need more water than the Fine sand due to their higher water holding capacity which also restricts its availability. Termites are also more likely to obtain water from sand at this MC than from other soil types (Lys and Leuthold, 1994).

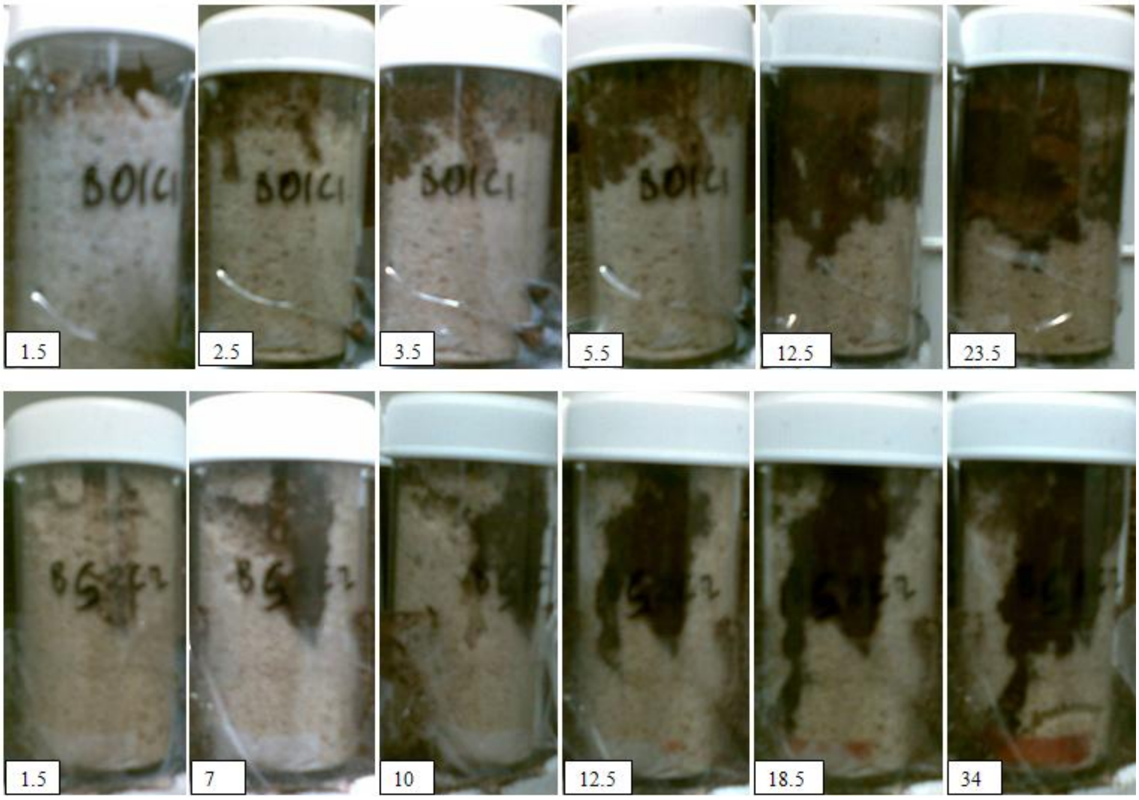


Fig. 5: Tunnel construction and development with time in Fine sand columns at 0% (top) and 5% (bottom) moisture levels by foraging termites and coverage with clay materials transported from nesting jar.

In Fine sand at **5 %** MC, some activity was observed by termites from Colony I albeit with no formation of significant tunnels or clay transport. However, the opening holes of Topsoil, Potting and Peat soil columns were sealed for most of the time. Termites from Colony II built tunnels with distinct vertical V-shapes and branches running from top to bottom in Fine sand columns while sealing the opening holes in Potting and Peat soils. Termites also managed to penetrate Topsoil columns at this moisture level and continued excavating and transporting soil particles as can be observed from the soil accumulation beneath the lid cover surface of the jars as well as reduction in the height of the soil in the column after each activity of soil transport.

Two types of soil transporting were highlighted during the study. The first one involves transport of clay materials from nesting jars into the Fine sand, Potting and Peat columns in order to transport soil moisture and darken surfaces. The second one involved transport of soil particles from the Topsoil column back to nesting jars. This could be due to the need for moisture back in the nest jar or rather more likely due to the preference of top soil particles in the construction of galleries. However, it varied depending on the MC of Topsoil. Therefore, the amount of soil particles transported from Topsoil columns to nesting jars was calculated in order to analyze whether soil MC affects the rate of soil transport (Table 2). At 5 % MC, only termites from colony II showed some transport activity, and they managed to transport 10% of the particles in Topsoil columns in 29 days at a rate 0.19 g of soil per day (g/day).

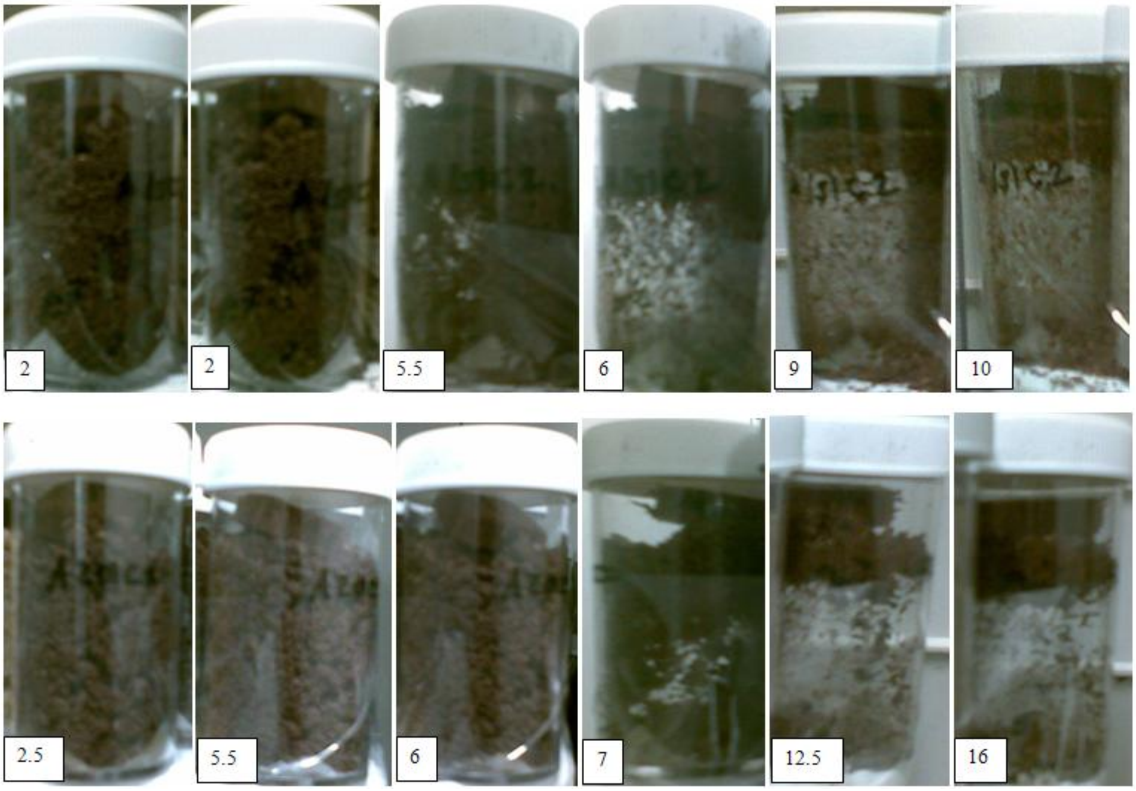


Fig. 6: Soil excavation with time in Topsoil columns at 15 % (A) and 20 % (B) moisture levels and development of hollowing with time as foraging termites transport Topsoil particles to the nesting jar.

At **10 %** MC, termites showed little or no interest in Potting, Peat and Fine sand soils. However, they continued foraging inside and transporting soil particles from Topsoil column and accumulating them beneath the lid cover or at the top of the nesting jar. When termites excavated in Topsoil columns and remove soil particles and transported them to the nest jar, the soil remaining in the column collapsed after some time during the foraging activity. This is probably due to the lower moisture level which was not enough for soil particles in Topsoil column to hold together and remain intact. At this moisture level, termites transported soil particles from Topsoil column to nesting jars at an average rate of 0.34 g/day.

At **15 %** MC, termites in Colony I sealed the opening holes in Potting and Peat soil columns for all or most of the time during the study. At the same time they started transporting soil particles from Topsoil columns (0.18 g/day) as soon as they penetrated the columns. In Colony II, however, termites started foraging as well as transporting soil particles from Topsoil column relatively earlier and completed it faster, literally emptying one of the columns within four hours (13 g/day), which was the highest rate recorded during the experiment. The average rate of soil transport (at 15% MC) was 3.4 g/day which was relatively higher than at 10 % MC. Potting columns were not preferred by both colonies, while very late in the study period, some termite activity was observed in Fine sand columns. Termites also managed to forage in Peat columns later during the study.

Termite alates were observed in the distinct horizontal tunnels at the base of the column as well as in the long vertical tunnels close to the perspex column surfaces. Termites started excavation from the column base and foraged upwards, transporting soil particles to the nesting jar, wide hollow spaces were created beneath the soil remaining at the top. At the end of the foraging period, a 0.5 cm layer of Topsoil remained intact at the top in two cases carrying the wood block.

In all the cases at **20 %** moisture level, termites excavated and transported soil particles from the Topsoil columns to the nesting jar, except for the first replica for Colony I, where they only penetrated later in the experimental period. Termites in one replicate in Colony II literally emptied the Topsoil column in a relatively short period of time (6 days) at a rate of 8.65 g/day, leaving a thin layer of soil (0.5 cm) at the top carrying the wood in the other two replicates. The average rate of soil transport was 2.86 g/day. Little or no activity was observed in Fine sand and Potting soils. Termites were active in Peat soil foraging all over (except in one replicate of Colony I) constructing horizontal tunnels at the base and a vertical one reaching the top along the surface.

Table 2: Soil transport rate (g/day) and percentage transported by foraging termites from Topsoil columns at different soil MCs.

MC (%)	Colony	Soil Weight before Foraging (g)	Soil Weight after Foraging (g)	Number of Foraging days	Soil Transported (%)	Soil Transport Rate (g/day)
0	I	52.0	52.0	29	0	0.00
		52.0	52.0	29	0	0.00
	II	52.0	52.0	29	0	0.00
		52.0	52.0	29	0	0.00
5	I	55.0	55.0	29	0	0.00
		55.0	55.0	29	0	0.00
	II	55.0	49.5	29	10	0.19
		55.0	49.5	29	10	0.19
10	I	50.0	40.0	31	20	0.33
		50.0	45.0	29	10	0.17
	II	50.0	45.0	29	10	0.17
		50.0	30.0	30	40	0.68
15	I	52.0	52.0	24	0	0.00
		52.0	47.0	29	9.6	0.18
	II	52.0	5.2	34	90	1.40
		52.0	0.0	4	100	13.00
20	I	50.8	50.8	29	0	0.00
		50.1	5.0	34	90.1	1.35
	II	52.1	5.2	33	90.0	1.44
		51.9	0.0	6	100	8.65

In summary, at lower (0 and 5 %) moisture levels termites were more active in Fine sand columns than in any other soil type. In the control soils (0 % MC) no excavation or transport of soil particles from Topsoil to nesting jar was observed by termites while little/ no excavation and transport of soil particles were observed in Topsoil at 5% MC. The opening holes in the Potting and Peat soils were sealed from the beginning or for most of the time during the study with clay materials from the nesting jar indicating that termites showed less preference towards these soil types. It can be concluded that termites preferred Fine sand at 0 and 5% moisture levels. This confirms with the fact termites prefer sandy soils at lower MCs as water is more readily available and easier to extract from sand particles which hold water particles less tightly than other soil types at this MC (Ahmed, 2000).

At higher moisture levels of 10 %, 15 % and 20 % termites preferred Topsoil more than any other soil type. In most cases they concentrated their excavation and transport activities in Topsoil column and built foraging galleries at the top of nesting jar or just underneath the lid cover. The average soil transport was highest at 15% MC with a rate of 3.65 g/day followed by 2.85, 0.33, 0.09 and 0 g/day at 20, 10, 5 % moisture levels and control soil, respectively. Similar trends were reported by Evans (2003) where termites of *C. frenchi* foraged five times more in wet sand than when they did in a dry one.

Termites built well defined distinct tunnels with or without branches in Fine sand columns at 0 % and 5 % moisture levels usually starting from the top to bottom. In Topsoil columns at 10 % MC, where termites excavated and transported more soil particles, the soil remaining in the column collapsed under its own weight or the weight of the wood block sitting on top. This could probably be because the MC was not enough to hold parts of the remaining soil column together. However, in Topsoil columns at higher MCs, 15 and 20 %, termites excavated and transported soil particles from the columns to nesting jars starting from the bottom up, leaving at the top a thin layer of intact soil particles carrying the wood block placed at the top.

In all MCs, termites covered surfaces of columns with clay materials from the nesting jars in the spaces where tunnels were built, as in Fine sand columns, or where hollow spaces were created after removing Topsoil particles, as in Topsoil columns. At almost all the MCs Peat soil was the least preferred soil type. In most cases the opening holes beneath the tube containing Peat were either sealed for most of the time or been opened with no or little penetration and termite activity.

Penetration:

Termite penetration into soil columns and their foraging activity was monitored at 12 hour intervals as mentioned above. Penetration was considered when termites opened a hole and moved into a soil column, formed visible tunnels along the surface of soil column, and/or removed soil particles from soil column and created hollow spaces visible to the naked eye.

In soils at lower MCs (0 % and 5 %), the average number of days under which *C. acinaciformis* penetrated Fine sand columns was significantly lower than for the other soil types ($P<0.05$)(Figure 7). In the control soil they penetrated Fine sand column within 4 days on average, while it took around 5.4 days equally for the other soil types. At 5 % MC, termites penetrated Fine sand column significantly earlier than Potting and Peat columns ($P < 0.05$) but not Topsoil ($P > 0.05$). The average number of days under which termites penetrated Fine sand column was 2.1 whereas they penetrated Topsoil, Potting and Peat columns in more than five days, 5.2, 6.3 and 6.5 days, respectively. At the higher (10 – 20 %) moisture ranges, it took fewer days for termites to penetrate Topsoil columns than it did for the other soil types. However, the difference was only significant at the 10% soil moisture level ($P < 0.05$) where the average number of days were 4, 4.2, 5.7 and 4.4 for Topsoil, Fine sand, Potting and Peat columns, respectively. At 15 % MC, there was no significant difference between the average number of days termites took to penetrate the different soil columns ($P > 0.05$). At 20 %, however, termites penetrated Topsoil significantly earlier than they did in Peat soil. There was no significant difference between either of Topsoil or Peat and Fine sand and Potting soil ($P > 0.05$).

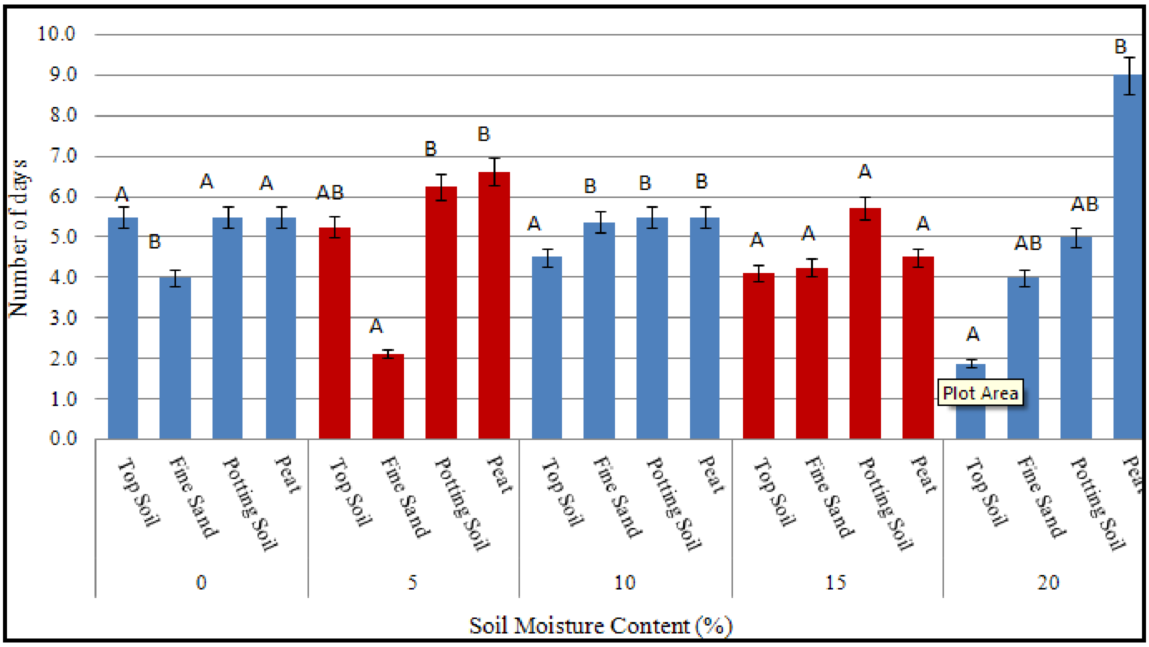


Fig. 7: Comparison of the average number of days under which termites penetrated four soil types at five different moisture levels. Different letters indicate significant differences (=0.05) within moisture levels using Fisher's LSD t-test.

In conclusion, termites penetrated Fine sand column earlier than any of the other soil columns. The average number of days it took termites to penetrate Fine sand column and start foraging was 3.6. It was significantly lower than that of Potting (5.6 days) and Peat (6.2 days) soils. Significant difference was also observed between the average number of days taken for termites to penetrate Topsoil (4.3 days) and Peat soil. No significant difference was observed between Fine sand and Topsoil, Topsoil and Potting, and Potting and Peat soils.

At the end of the study period almost all soil types were penetrated by termites. In the case of Potting soils distinct vertical tunnels running the whole height as well as horizontal tunnels at the base were formed along the surface of the column. Alates were observed in tunnels formed in columns preparing for flying out of the nesting jars.

When the average number of days under which termites took to penetrate Topsoil columns were compared within a moisture level, the only significant difference observed was between the control soil and Topsoil at 20 % moisture level ($P < 0.05$)(Figure 8). No significant difference was observed between the control soil or 20 % MC and all other soil types. The earliest time under which termites penetrated Topsoil column was 1.8 days at 20 % MC whereas the latest was 5.4 days at the control soil. In Fine sand columns termites penetrated earliest at the 5 % MC (2.2 days) which was strangely significantly different to the latest time (5.3 days) recorded for the 10% MC ($P < 0.05$). There was no significant difference in the number of days under which termites took to penetrate either the 5 % or 10 % MC and the rest ($P > 0.05$). In the Potting and Peat columns at different moisture levels, the average number of days for termite penetration ranged between 5 – 6.2 days and 4.4 – 9 days, respectively. There was no significant difference between all the moisture levels ($P > 0.05$).

Overall the earliest average time under which termites penetrated any of the soil columns was 3.6 days for Fine sand, followed by 4.2, 5.7 and 6.2 days for Topsoil, Potting and Peat soils, respectively. Termites penetrated Fine sand column significantly earlier than Potting and Peat soils ($P < 0.05$), but not Topsoil (P >

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0.05). They also penetrated Topsoil at a significantly earlier time than Peat soil ($P < 0.05$) but not Potting soil ($P > 0.05$). No significant difference was observed either between Potting and Peat soils or the overall average number of days under which termites penetrated soil columns at different MCs ($P > 0.05$)(Figure 9).

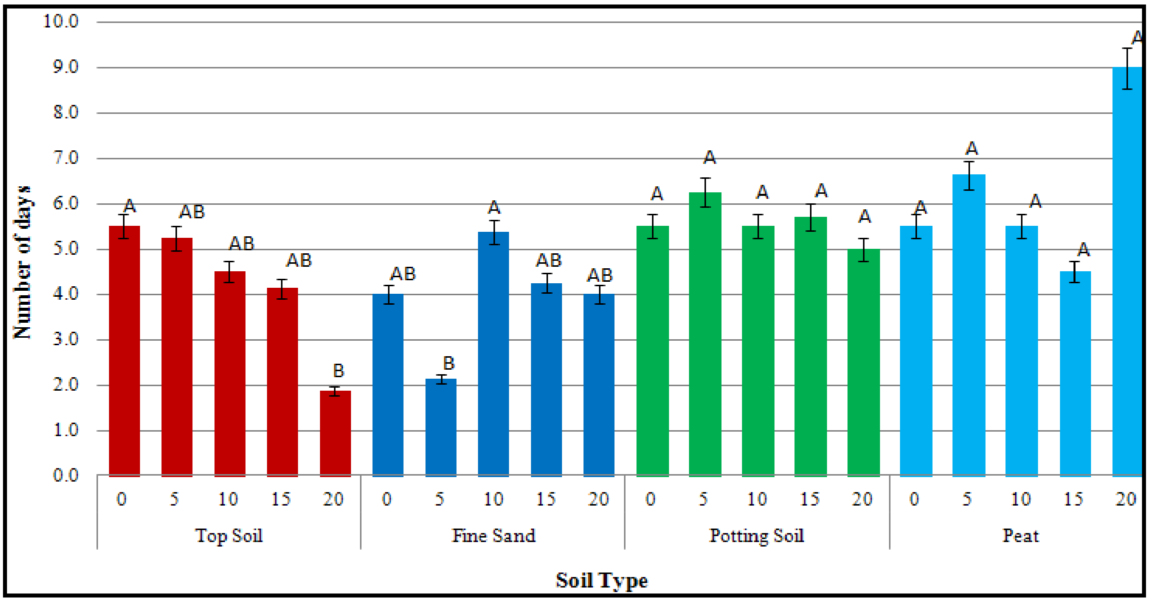

Fig. 8: The number of days under which termites penetrated four soil types at five different MCs. Different letters indicate significant differences ($\alpha = 0.05$) within moisture levels using Fisher's LSD t-test.

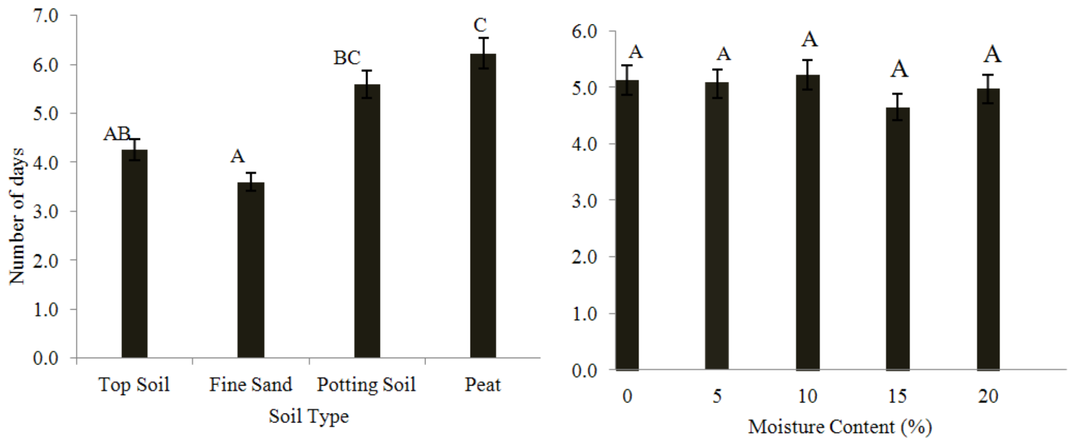

Fig. 9: Comparison of the average number of days under which termites penetrated four soil types and five different moisture levels in a laboratory experimental setup. Different letters indicate significant differences ($\alpha = 0.05$) within moisture levels using Fisher's LSD t-test.

Most termite species cover the foraged material with sheet galleries before they start feeding (Tschinkel, 2010). In the soils where termites managed to penetrate and either build tunnels or transport soil particles from, they covered the wood blocks with soil particles but did not start feeding on the wood itself. In columns of Topsoil where termites left a small intact soil ring on top, they couldn't reach the wood material sitting on the Topsoil. There was no difference in the weight of wood blocks before and after termite exposure. However, in soil columns where termites managed to penetrate through the soil and reach the wood blocks, soil coverings/spots could be observed around the wood blocks. It showed that termites cover wood blocks with soil/clay materials before they start any consumption. However, the experimental time period may not have been long enough for termites to actually start feeding. It was also not possible to deduce if termites didn't feed on the wood block in the soil columns because there was enough food within the nesting jars.

Conclusions:

It was concluded that soil type had a significant effect on termite preference whereas soil MC did not have any significant effect. Termites penetrated earlier, built distinct tunnels and tunneling branches in Fine sand, most of the time starting from top to bottom, and covered them with dark clay particles brought from nesting jars. However, they transported soil particles from Topsoil columns to the nesting jars to build foraging layers. The average rate of soil transport from a Topsoil column was higher at higher moisture levels. At lower moisture levels of 0 and 5%, termites preferred Fine sand. Topsoil was preferred at moisture levels of 10, 15 and 20%. Peat soil was the least preferred soil type and in most cases opening holes beneath tubes containing Peat were either sealed for most of the time or been opened with no or little penetration and termite activity. Termites covered surfaces of columns with clay materials from nesting jars in the spaces where tunnels were built, as in Fine sand columns, or where hollow spaces were created Topsoil columns after removing Topsoil particles.

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Appendix:

Table 1: Summary table of average number of days under which *C. acinaciformis* penetrated columns of four soil types at different moisture levels attached to a nesting jar in laboratory

MC (%)	Soil Type	Mean Penetration and St Dev
0	Topsoil	5.5 ± 0a
	Fine sand	4 ±1.92b
	Potting Soil	5.5 ±0a
	Peat	5.5 ±0a
5	Topsoil	5.3 ±0.3ab
	Fine sand	2.1 ±3.3a
	Potting Soil	6.25 ±2.5b
	Peat	6.625 ±2.4b
10	Topsoil	4.5 ±0.7a
	Fine sand	5.4 ±0.3b
	Potting Soil	5.5 ±0b
	Peat	5.5 ±0b
15	Topsoil	4.1 ±4.6a
	Fine sand	4.2 ±2.2a
	Potting Soil	5.7 ±1.1a
	Peat	4.5 ±2.4a
20	Topsoil	1.9 ±2.1a
	Fine sand	4 ±1.2ab
	Potting Soil	5 ±1.2ab
	Peat	9 ±8.3b

Different letters in the same column indicate significant differences on the mean average number of days termites taken by termites to penetrate a soil column among MC (Fisher's t- test; $p < 0.05$).

Table 2: Analysis of Variance table for average number of days termites took to Penetrate soil columns: (Factorial).

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Soil	3	70.312	70.312	23.437	4.21	0.011*
Moisture Content	4	3.099	3.099	0.775	0.14	0.967
Colony	1	55.001	55.001	55.001	9.89	0.003*
Soil*Moisture Content	12	102.656	102.656	8.555	1.54	0.151
Soil*Colony	3	12.879	12.879	4.293	0.77	0.517
Moisture Content*Colony	4	66.495	66.495	16.624	2.99	0.03*
Soil*Moisture Content*Colony	12	53.11	53.11	4.426	0.8	0.652
Error	40	222.5	222.5			
Total	79	337567				

*Significant at $\alpha = 0.05$ using ANOVA