TERMITES, WATER AND SOILS

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INTRODUCTION

Soils are not simply present in a habitat: they are the product of a dynamic balance between agents of soil construction and soil degradation. Arid conditions, like those that prevail over much of Namibia, pose special problems for soil building because arid soils can be hostile environments for creatures like earthworms, which are important agents of soil construction in wetter environments (Lee and Foster, 1991). In Namibia, termites are among the most important agents of soil building, particularly termites like the fungus-cultivating Macrotermes that build large mounds (Figure 1).

Termites are unlikely candidates for this role because they are, as a rule, intolerant of dry conditions (Abushama, 1974). *Macrotermes*, however, can thrive in environments with annual rainfall as low as 250 mm, where other kinds of termites cannot survive (Figure 2; Deshmukh, 1989). *Macrotermes* can survive in such harsh conditions because they are adept at creating humid environments for themselves in their subterranean nests. Their ability to do so is tied in with their capabilities as agents of soil construction (Dangerfield *et al.*, 1998; Turner, 2006a; 2006b).

THE DYNAMIC MOUND OF *MACROTERMES*

Macrotermes mounds are prominent features of the landscapes of northern Namibia. The mound serves an important physiological function for the colony: it is a wind-driven lung, which intercepts wind-borne kinetic energy and uses it to drive air flows through the mound's complex internal network of ventilatory tunnels (Turner, 2000; 2001; 2002).

Although the mound appears to be static and substantial, it is in fact a remarkably dynamic and fluid structure. Wind and rain continuously erode soil from the mound surface. To maintain the mound's structure, and the physiological function it serves, termites offset erosion losses with a continuous transport of soil to the mound surface. This surface deposition is evident as patches of roughly textured soil on the smoother, eroded surface of the mound. When the soil is freshly deposited, it is conspicuously darkened by moisture in the salivary glue they use to fix it in place (Figure 3).

The quantities of soil moved by termites are substantial. Pomeroy (1976), for example, estimated that *Macrotermes natalensis* colonies in Uganda move as much as a cubic metre of soil annually to the surface. *Macrotermes michaelseni* in Namibia are likewise prodigious movers of soil, moving several kilograms of wet soil to the mound surface per day (Table 1). Remarkably, colonies in an open habitat move nearly four times more soil to the surface than colonies in a wooded habitat.

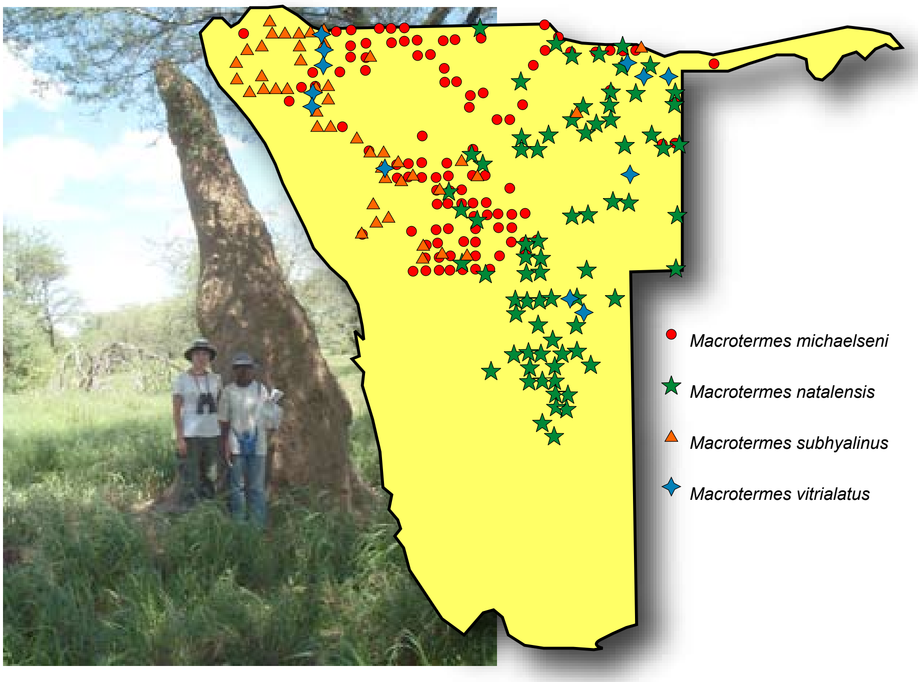

Figure 1. *Macrotermes* in Namibia. *Left:* A mound of *Macrotermes michaelseni* in an acacia woodland; Wendy Park (l) and Grace Shihepo (r). *Right:* Distribution of the four *Macrotermes* species extant in Namibia.

SOIL TRANSPORT IS COUPLED TO WATER TRANSPORT

Termites transport more than soil to the surface, however. They also transport water – in the form of moisture in the salivary glue they use to fix newly deposited soil in place. Water constitutes roughly 10–15% of the total mass of newly deposited wet soil (Table 1). Because termites in open habitats move four times more soil to the mound surface than termites in wooded habitats do, termites in open habitats also move more water through the mound: roughly 25 kg in the open habitat, compared with roughly 6 kg for the wooded habitat.

Table 1. Soil transport to the surface of *Macrotermes michaelseni* mounds in northern Namibia during the 2004/5 rainy season

Type of habitat	Soil transported for all mounds (n = 5)			Soil transported average per mound		
	Wet mass (kg)	Dry mass (kg)	Water mass (kg)	Wet mass (kg)	Dry mass (kg)	Water mass (kg)
Open habitat						
Total for the season	908.4	785.7	120.7	190.0	164.4	25.2
Average per day	17.1	14.8	2.3	3.6	3.1	0.5
Maximum per day	41.0	36.6	5.8	8.2	7.3	1.2
Days of soil transport out of days surveyed	53/81					
Wooded habitat						
Total for the season	252.3	222.4	30.4	51.6	45.5	6.2
Average per day	5.1	4.5	0.6	1.1	0.9	0.1
Maximum per day	14.8	13.0	1.8	3.0	2.6	0.4
Days of soil transport out of days surveyed	49/81					

Note: Soil and water transport were quantified by collecting and weighing soil transported daily to the surface of five Macrotermes michaelseni mounds at the study site located at the Omatjenne Agricultural Research Station near Otjiwarongo. Samples were collected early in the morning when new deposition was still fresh and wet. Water content was quantified by the difference between wet weight of the freshly collected soil and the soil's weight after it was dried. Our survey spanned nearly 80 days (24 January through 4 April 2005) of the 2004/5 rainy season, and compared soil transport between two habitats: open grassland and acacia savanna. Because this survey only accounted for about 80% of the duration of the 2004/5 rainy season, these figures probably underestimate the annual soil transport by 20–25%. Nearly all soil transport by Macrotermes colonies occurs during the rainy season.

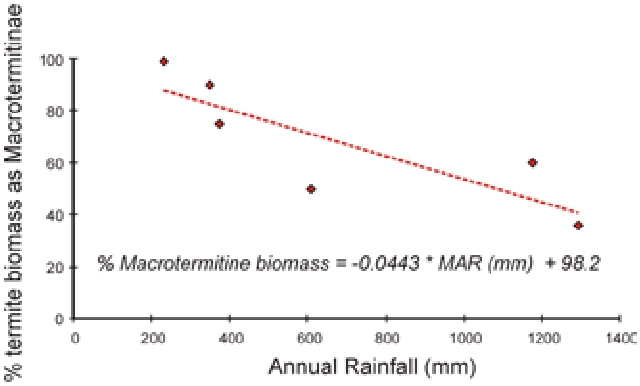

Figure 2. *Macrotermes* dominates the termite fauna in arid environments (Deshmukh, 1989).

Nearly all new soil deposition takes place during the rainy season, and movement of soil appears to be tied to patterns of rainfall (Figure 4). During the 2004/5 rainy season, there were three episodes of heavy rainfall: one each in January, February and March (Figure 4). At the beginning of the census, which followed the January rainfall episode, new soil deposition was evident on all mounds surveyed. During the dry interval that followed, the proportion of mounds with new deposition declined. After the February rainfall episode, soil deposition increased again, and then declined during the ensuing dry interval. Soil transport increased again following the March rainfall episode (which was the last of the season), and declined to nil as the dry season set in.

Figure 3. New soil deposition on a *Macrotermes* mound. *Left:* One evening's new deposition, darkened by moisture. *Right:* Detail of patches of new soil deposition.

SOIL TRANSPORT IS COUPLED TO THE COLONY'S WATER BUDGET

Thus, in a fundamental way, soil transport through the mound is tied to water transport. That fundamental connection is probably the regulation of the colony's water balance.

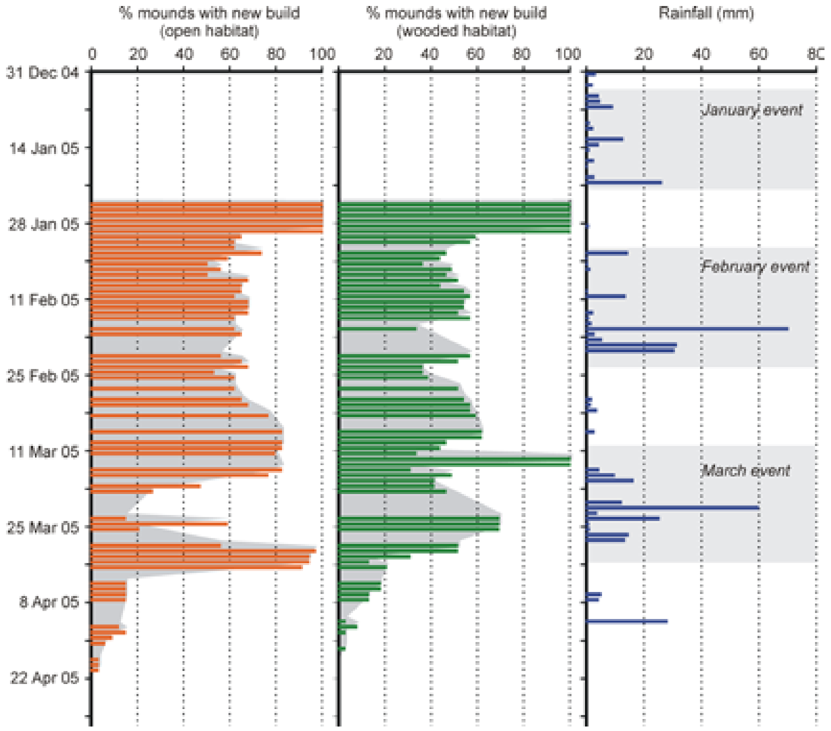

Figure 4. Incidence of new soil deposition on the surface of *Macrotermes* mounds through the 2004/5 rainy season. Forty mounds in an open habitat and forty in a wooded habitat were visited each day from mid-January 2005 to mid-April 2006. Each day, each mound was scored for whether or not it had evidence of new building on its surface. This daily survey was carried out in the early morning when newly deposited soil was still moist and conspicuous. Surveys were not carried out on rainy mornings. Bars represent the proportion of mounds in each habitat that showed evidence of new building.

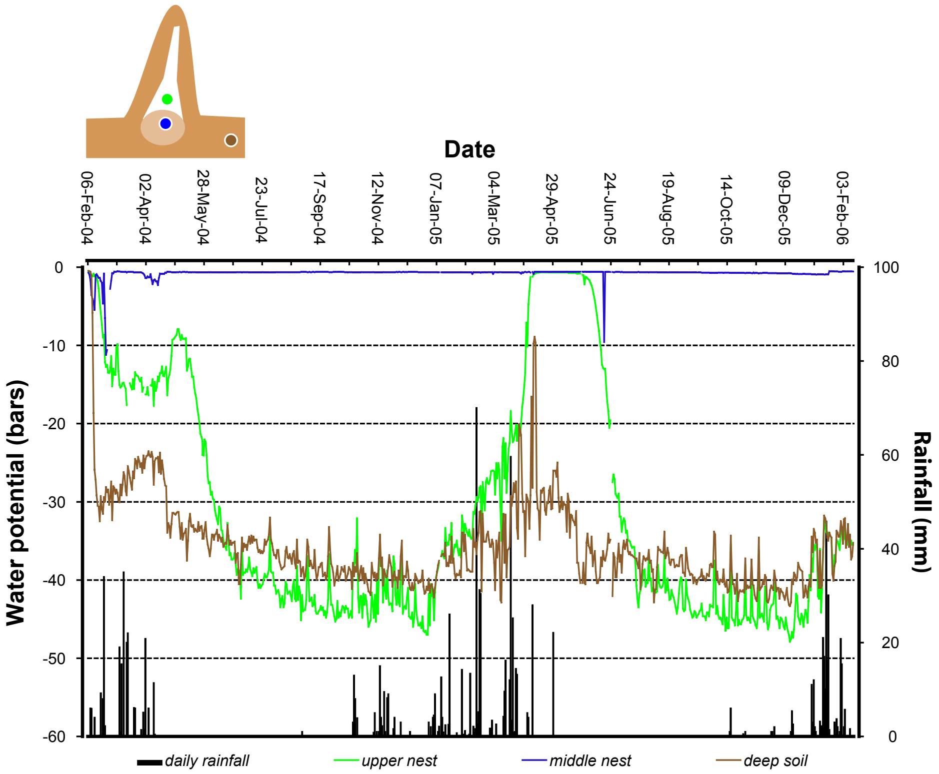

Figure 5. Moisture in a mound and nest of a *Macrotermes michaelseni* colony and in nearby soils. Soil moisture was measured with gypsum block soil moisture sensors. Rainfall was measured with a conventional rain gauge. Water potential is a measure of the total potential energy available, expressed in units of pressure, to drive water movement. Water potential in soils is generally negative, i.e. it is a suction pressure and indicates the tendency of soil to draw water into it. The more negative the water potential, the more strongly soil will draw water into it.

Macrotermes and the fungi they cultivate are intolerant of desiccating conditions. Termites are agents of homeostasis, however, surviving in harsh environments by creating regulated environments that are suitable to their needs (Turner, 2004; 2006a). Among the things they regulate is nest moisture, and their capacity for this is impressive. Since 2004, soil moisture within the nests and mounds of two *Macrotermes michaelseni* colonies was observed, as was the moisture in adjacent soils. One set of observations is shown in Figure 5. As would be expected, deep soils (1 m deep) dry considerably during the dry season and become charged with water again during the rainy season. The same is true of mound soils near the top of the nest. Within the nest itself, in contrast, moisture is high and steady throughout the year.

In any regulated system, the maintenance of a particular property – in this instance, nest water potential – is the outcome of a balance of flows of water into and out of the nest (Figure 6). In the *Macrotermes* nest and mound, there are four major avenues of water flux:

- Evaporation from the mound surface
- Passive movement of water into the nest from adjacent soil, conveyed mostly as liquid water percolating into the nest following rainfall events
- 'Active transport' from the nest to the mound surface, mostly as liquid water conveyed in salivary glue, and
- 'Active transport' into the nest, in the form of liquid water carried up in moist soils from below the ground.

All these avenues for water flux are coupled to the modification and movement of soils around the colony. For *Macrotermes* colonies, this soil modification occurs on a massive scale. For example, termites forage by excavating so-called foraging tunnels a

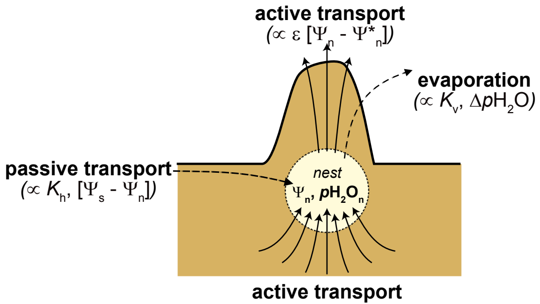

Figure 6. Major elements of the water balance of a *Macrotermes* nest.

few centimetres below the ground surface. These tunnels provide a network of soil macropores that promotes the infiltration of s into soils (Lobry de Bruyn and Conacher, 1990). These networks are extensive: the foraging territory for a *Macrotermes* colony can extend as much as 70 m from the nest, and one nest's foraging tunnel network often abuts those built by adjacent colonies (Abe and Darlington, 1985). Termites also modify deep soils extensively. Below the nest, for example, soils are commonly perturbed in a spindle-shaped lens that can extend 12–15 m below the surface (Figure 7; Boyer, 1973; 1975a; 1975b). Those soils are often more porous and richer in clays than the parent soil, which helps them retain water. Among the modifications wrought by this perturbation is an excavation of deep calcite layers to form a saucer-shaped depression below the nest where perched water from an extensive surrounding area can drain and be readily available to the termites in the colony (Figure 7; Lepage *et al.*, 1974; Lebrun, 1976). Indeed, the vertical transport of water and soil may be more extensive than this: numerous anecdotal reports suggest that *Macrotermes* will range as deep as 100 m in search of water (Yakushev, 1968; Lepage, 1974; Lepage et al., 1974; West, 1970). This extensive soil engineering essentially makes the *Macrotermes* colony a massive water-gathering system that enables them to survive in arid conditions (Figure 5). Termite species with lesser capabilities for soil engineering will not survive (Figure 2).

The movement of water from the nest to the surface seems to indicate a regulatory process at work. In Figure 8, soil moisture is plotted at several localities within a *Macrotermes michaelseni* mound. Obviously, the mound is very dry during the dry season. As the rainy season proceeds, however, moisture spreads through the mound. This is not due to direct wetting of the mound by rain: even heavy rains will wet the mound surface only to a depth of a few millimeters, whereas soil moistures were measured at depths of 10 cm or more. Rather, the mound becomes moister throughout because termites convey moist soil up into the mound from the wetter nest and deeper soil horizons.

These movements of soil are clearly tied to rainfall (Figure 8). Prior to the 2004/5 rainy season, there were two small rainfall episodes: a 1 mm event in September 2004, and a week-long episode in October 2004 (28 mm). The latter prompted the emergence of a swarm of alates. Following these episodes, there was a steady increase of soil

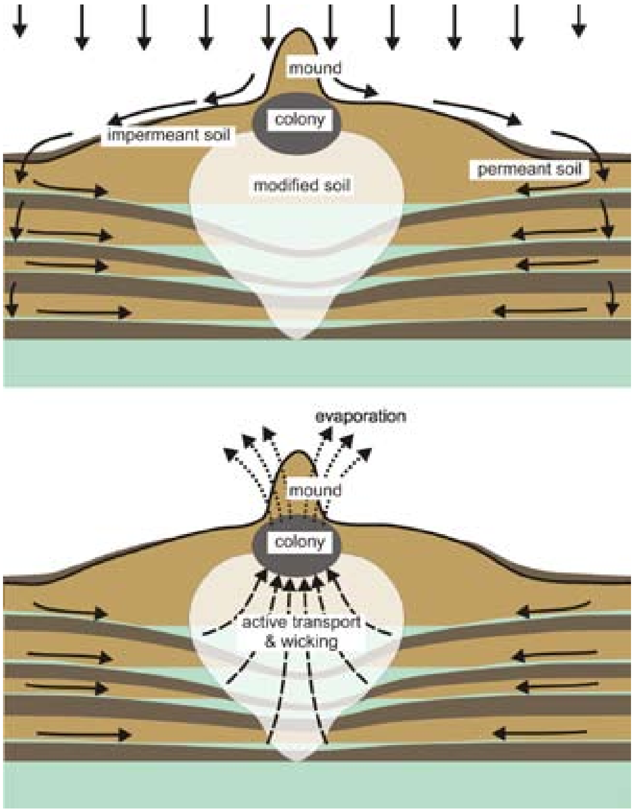

Figure 7. Boyer's scheme for termite-mediated modification of the hydrology of arid savanna soils. Top: Collection of water in a basin-shaped perched water table excavated below the colony. Bottom: Termite-mediated movement of water and soil through the colony and mound.

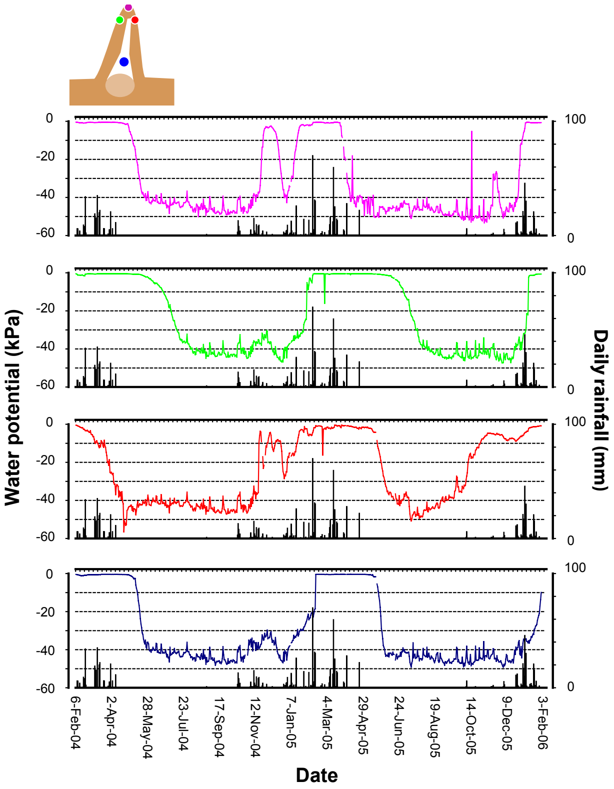

Figure 8. Seasonal patterns of soil moisture within a Macrotermes michaelseni mound. Gypsum block soil moisture sensors were placed in the chimney above the nest (blue), on the north-facing surface (red), the south-facing surface (green), and top (magenta) of the mound. The black bars indicate daily rainfall.

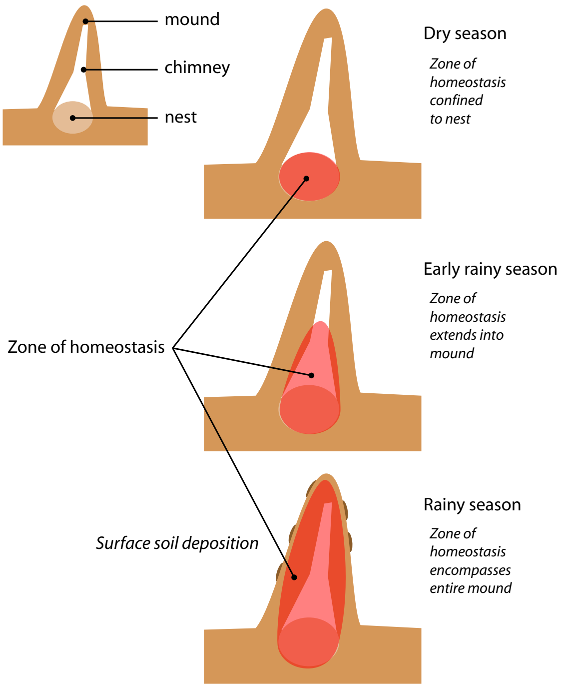

Figure 9. The seasonally expanding zone of moisture homeostasis in a Macrotermes colony.

moisture in the mound – first in the chimney above the nest, then in the upper parts of the mound several weeks later (Figure 8). Eventually, moisture throughout the mound comes to be regulated, just as it is throughout the year in the nest (Figure 5). This *zone of homeostasis*, confined to the nest during the dry season, expands during the rainy season to eventually encompass the entire mound. At this point, soil deposition to the mound surface begins.

This explains why soil movements to the surface of mounds in open habitats are much greater than they are in wooded habitats (Table 1). Open habitats are windier and sunnier, and the air is dryer, which prompts greater evaporation of water from the mound surface. If moisture of the mound surface is regulated, termites will have to transport more water to the surface to offset these losses. Because moisture is conveyed in wet soil, surface deposition will likewise be greater.

TERMITES, WATER AND SOILS

Termites are important conveyors of soil and water through arid habitats in Namibia. *Macrotermes* colonies extensively modify the hydrology of arid soils, turning them into a massive water-gathering system that enables them to survive in arid conditions (Figure 5). This ultimately depends upon termites acting as vertical conveyors of soil and water, bringing moist soil up from deep soil horizons. This soil is enriched as it passes through the colony, and ultimately erodes off the mound and onto the ground surface, where it helps maintain the high veld productivity that can support high stocking rates (Bachelier, 1971; Arshad, 1982). These termites may be the stock farmer's best friend.

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