

## Chapter 17

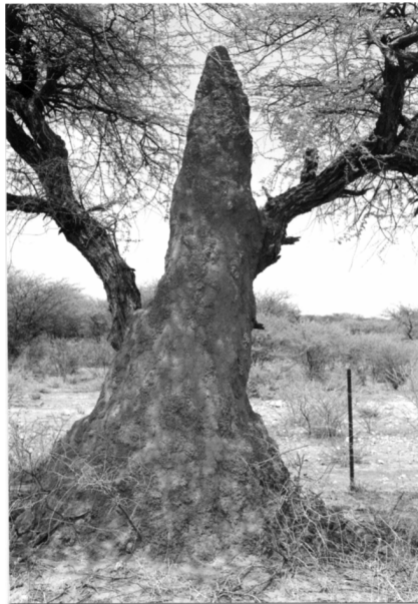
### TERMITES AS MEDIATORS OF THE WATER ECONOMY OF ARID SAVANNA ECOSYSTEMS

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#### 1. Introduction

Large termite mounds, constructed by colonies of various species of macrotermitine termites (Isoptera, Termitidae, Macrotermitinae), are dominant features of the arid and semi-arid savannas of southern Africa. These mounds can populate a savanna in very high densities, generally one to four colonies per hectare, containing biomass of termites and symbiotic fungi that exceeds the typical biomass of vertebrate and non-termite arthropod herbivores in these systems. Termites' construction of nest and mound turns over savanna soils at substantial rates, and, like other central-place foragers, they convey significant quantities of inorganic and organic matter into their nests, concentrating it there. In short, macrotermitine termites are “ecosystem engineers”, structuring and controlling to a large extent the flows of energy and matter through tropical savannas (Dangerfield et al. 1998).



**Figure 1.** A representative mound of *Macrotermes michaelseni* in northern Namibia, built up around an *Acacia mellifera* tree.

This chapter concerns one aspect of these termites' engineering activities: their possible roles as mediators of the water economy in arid savannas. It is inspired by an observation made in the course of ongoing research on respiratory gas exchange in nests of *Macrotermes michaelseni* (formerly *M. mossambicus*), in northern Namibia (Turner 2000; 2001). These termites' habitat is designated as mixed mopane/acacia savanna, which is characterized by a mixture of grasses, geophytes and patchy assemblages of broad-leaf (commonly

*Colophospermum mopane*) and narrow-leaved (commonly *Acacia* spp) trees (Ruelle et al. 1975). As in most tropical savannas, rainfalls in northern Namibia are strongly seasonal, with intense summer rains interspersed with strenuous winter drought. During winter, most trees there either drop their leaves or allow them to die on the branch. A few trees, however, retain green vegetation throughout the year. Invariably, these trees are associated with termite mounds (Figure 22.1), suggesting that termite colonies provide a local source of water that sustains the trees well into the dry season. How termites provide this water has broad implications for ecosystem function in dry tropical savannas.

## 2. Water balance in arid savannas

The water relations of arid savannas have been extensively documented elsewhere and in other chapters in this volume (Chapters 2-4), so only a few salient points will be made here.

Tropical savannas experience strongly seasonal rainfalls (see Chapter 15 for a discussion on precipitation patterns in tropical savannas), which arise from a combination of convective disturbances and frontal storms. In southern Africa, annual rainfalls are generally higher in the east and decline toward the west, reflecting a longitudinal shift in the relative importance of frontal vs. convective storms. Toward the east, frontal storms predominate, fed by inputs of water vapor from the Indian Ocean. The influence of frontal systems diminishes to the west, leaving convective disturbances as the most common source of rainfalls. This brings with it a strong interannual and spatial variation of rainfall. Thus, dryer savanna habitats must cope not only with annual and frequent multiyear droughts, but with significant spatial droughts as well.

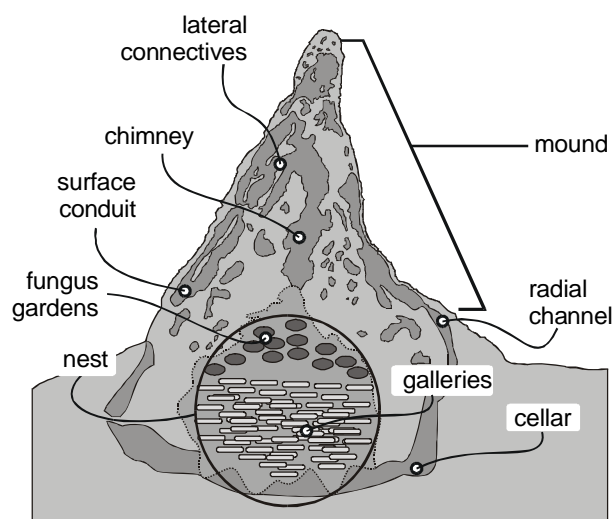
The surface water balance in tropical savannas is dominated by evapotranspiration and infiltration, while runoffs generally are minuscule (Nicholson et al. 1997). Evapotranspiration is by far the dominant surface flux, which varies through the year between rainfall equivalents of 70 mm mo<sup>-1</sup> in summer to roughly 15 mm mo<sup>-1</sup> during winter. Rainfall exceeds evapotranspiration during summer, while the reverse is true in winter. Consequently, there is a net storage of water in soils during summer, which may then be tapped by plants or animals into the dry season. Once these stores are exhausted, production of above-ground biomass declines and standing biomass dies and dries. The dry and dead vegetation represents a store of fixed water in cellulose that can be a significant source of metabolic water for herbivores like termites.

## 3. Natural history and colonial physiology of *Macrotermes* colonies

The termite fauna of arid savannas is dominated by the fungus-cultivating Macrotermitinae (Termitidae). The macrotermitine termites are characterized by large body size (2-3 times heavier than other types of termites), large colony populations (1-2 million workers per colony, one to two orders of magnitude more populous than other types of termite colonies), and cultivation of symbiotic fungi (*Termitomyces* spp) in the nest, on specialized structures called fungus combs (Batra and Batra 1979; Thomas 1987; van der Westhuizen and Eicker 1990; Veivers et al. 1991). The fungi and fungus combs are part of an extracorporeal digestive system for the colony, in which raw cellulose forage is digested into more readily digestible sugars and oligosaccharides (Martin and Martin 1978). The fungi also provide fixed nitrogen and other nutrients (Rouland-Lefevre 2000). Together, the termites and fungi comprise a superorganismal metabolism rivalling that of many ungulate herbivores. Metabolic rates of *Macrotermes jeaneli* colonies, for example, have been estimated at about 55 watts, similar to that of a small goat: some estimates put the figure as high as 210 watts (Darlington et al. 1997). This metabolic effervescence helps make *Macrotermes* the dominant component of the termite fauna in many African savannas (Dangerfield et al. 1998; Deshmukh 1989).

## TERMITES AS MEDIATORS OF THE WATER ECONOMY

The colony's high collective metabolism requires a considerable rate of respiratory gas exchange, which is regulated by the mound superstructure (Figure 22.2; Turner 2001). The mound is essentially an organ of extended physiology, a device to capture wind energy for powering ventilation of the nest (Turner 2000b). It is also an adaptive structure, its architecture being adjusted by the termites to balance ventilation with the colony's respiratory demands. This confers upon the nest environment a considerable degree of homeostasis, regulating nest concentrations of oxygen and carbon dioxide, and importantly, water vapor (Turner 2001).



**Figure 2.** Cross section through a mound and nest of *Macrotermes michaelseni*, showing locations of nest and fungus garden, and basic layout of the network of ventilatory tunnels. From Turner (2001).

#### 4. Water balance of *Macrotermes* colonies

The air in an active *Macrotermes* nest is much more humid than the atmosphere. During the summer, when the colony is most active, water vapor partial pressures ( $p_{H_2O}$ ) in a *M. michaelseni* nest are on average 3.4 kPa, typically 2.6 kPa above atmospheric humidity (Table 22.1). In winter, humidity is lower, primarily because temperatures within the nest are cooler than. There is also a slight daily variation in humidity, again due mostly to daily variations of temperature within the nest. Nest humidity appears to be actively regulated, and is comparatively steady with respect to variations of atmospheric humidity, more so in the active summer season than the more dormant winter (Turner 2001). This tendency to nest homeostasis has significant consequences for soil water in and around the nest.

**Table 1.** Humidity and humidity gradients (expressed as water vapor pressure) driving evaporation in colonies of *Macrotermes michaelseni* in northern Namibia. Values are reported as mean (standard deviation): sample size. After Turner (2001).

Humidity (kPa)	Winter	Summer	Morning	Afternoon
Nest	2.58 (0.29)	3.40 (0.43)	2.99 (0.50)	3.08 (0.65)
Environment	0.35 (0.21)	0.83 (0.56)	0.65 (0.51)	0.55 (0.47)
$dp_{H_2O}$ (nest - env)	+2.23 (0.23)	+2.57 (0.47)	+2.34 (0.37)	+2.53 (0.46)

The high nest humidity drives a considerable rate of water vapor loss from the nest. Darlington et al (1997) estimated average evaporation rates equivalent to 5 liters per day (1,825 l y<sup>-1</sup>) from the nests of *M jeaneli*, with some nests evaporating nearly 13 l water d<sup>-1</sup> (4,750 l y<sup>-1</sup>). Weir (1973) reported similar rates of evaporation from the mounds of *M subhyalinus* (12 l d<sup>-1</sup>, or 4,380 l y<sup>-1</sup>), although he suggested that evaporation in large colonies can amount to as much as 25,000 kg water per annum. Weir (1973) and Darlington et al. (1997) made their measurements at different times of the year, so it is unclear whether these rates are reflective of sustained rates of evaporation through the year. It is likely that they are, however. In nests of *M michaelseni*, for example, the p<sub>H<sub>2</sub>O</sub> differences driving evaporation do not vary appreciably between summer and winter (Turner 2001; Table 1). Average rates of air turnover within *M michaelseni* nests also do not differ significantly between summer and winter (Turner 2001). Because evaporation rate is the product of water vapor partial pressure difference and the nest-to-atmosphere vapour conductance, the absence of a discernible seasonal difference in either suggests evaporation rate will not differ appreciably between summer and winter.

## 5. Sources of water for termite nests

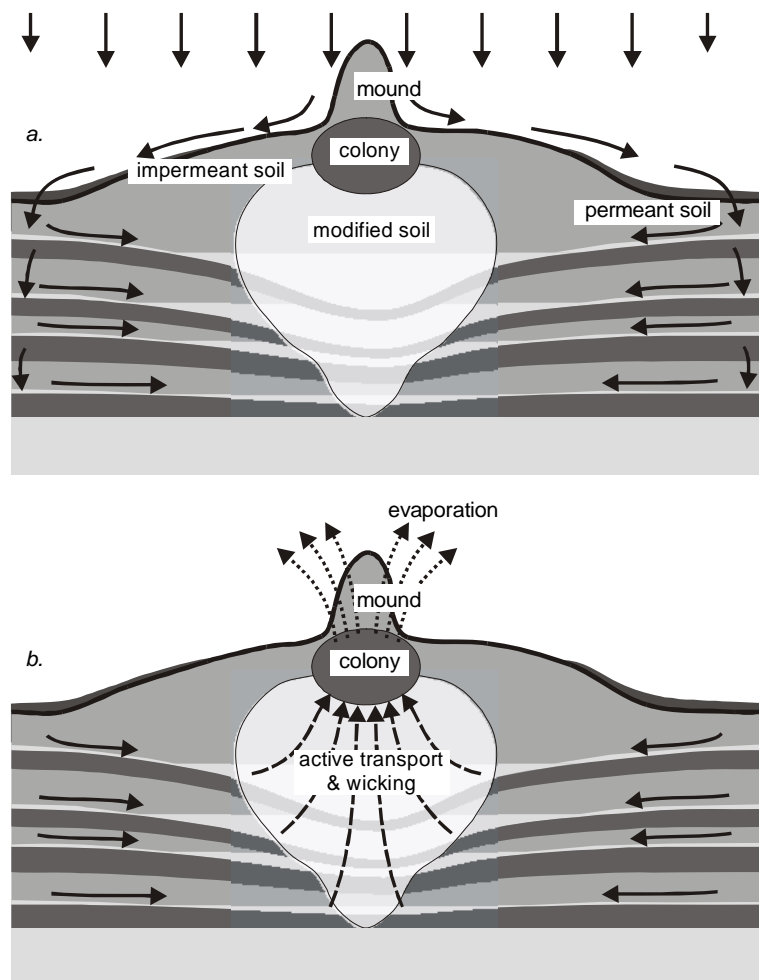
To maintain a specific nest humidity, evaporation from the nest must be offset by inputs of liquid water into the nest. There are three likely sources of such water: water released from metabolism, matric water wicked in from superficial or deep soils, and water brought up actively from deep soil horizons.

By any estimation, metabolic water accounts for a small proportion of the nest's total water inputs (Darlington et al. 1997). A colony's rate of metabolic water generation can be calculated from its metabolic rate: for typical oxidative respiration, metabolic water is generated at a rate of about 25 µg per joule energy consumed. Metabolic rates for *Macrotermes* colonies have been estimated to range from about 50 to 200 watts (Darlington et al. 1997). For a colony metabolic rate on the high end of that range (200 W), this corresponds to a generation of roughly 190 kg metabolic water per year, or about 10% of the colony's annual evaporation: actual inputs are probably smaller. Preformed water in soil must therefore make up the other 90% of water inputs to the nest.

How soil water gets into the nest has long been a matter of controversy (Lee and Foster 1991; Lobry de Bruyn and Conacher 1990). In 1947, Milne suggested that capillary action in the nest's soil matrix wicks in water from deeper soils. He suggested this might explain the high concentrations of carbonate minerals often found in mound soils, but offered no evidence for or against his inference. However, Watson (1969; 1971) followed movements of soil water below mounds of *M bellicosus* and *Odontotermes badius*, in what was then Rhodesia, (traced using <sup>51</sup>Cr tracers injected into soil water), and could not show the upward movement of water that (Milne 1947) had predicted. The enrichment of minerals in the nest that Milne sought to explain could therefore not be the result of wicking. More likely, the distribution of minerals arose through differential leaching: poor leaching in soils directly below mounds in juxtaposition with strongly leached soils in the intervening spaces between mounds (Watson 1969). On the other hand, termite colonies transport immense quantities of coarse-grained soils outward and upward from the nest (Pomeroy 1976), which leave behind in the nest a fabric of fine-grained silts and clays (Arshad 1981). These are molded together by salivary glues that tend to readily mineralize (Mermut et al. 1984). Water could conceivably be wicked into the nest by the very strong matric potentials that characterize fine-grained soils like clays (Campbell 1977). Wicking of water into the nest in this way is a double-edged sword, however. Strong matric forces might draw water in, but also hold the water tightly, making it unavailable for the nest occupants. In any event, the many reports of moist soils within nests, and the tendency of colony-associated trees to stay green through periods of drought (Turner, personal observation, Konaté et al. 1999) indicate that termite

## TERMITES AS MEDIATORS OF THE WATER ECONOMY

mounds and colonies are, if anything, at higher water potentials than surrounding soils. Weir (1972; 1973) and Watson (1969) have also suggested that the extent of mineral accumulations observed in mound soils would require periods of continuous occupancy of mounds for centuries. Mound re-occupancy does occur among the macrotermites, albeit rarely (<10% of extant colonies; Pomeroy 1976). Nevertheless, continuous occupancy of nests for centuries by subsequent generations of termite colonies is not unheard of. For example, a peculiar landform in the winter-rainfall regions of the Karoo in South Africa, known in the vernacular as *heuweltjies* (Afrikaans for “little hill”), arises from just such a pattern of ongoing colonization of a particular patch of ground by a species of harvester termite, *Microhodotermes viator* (Lovegrove 1991; Moore and Picker 1991). It remains unclear what effects termite colonies might have on the movements of matric water in soils: the macrotermitine termites colonize such a wide diversity of soils and climatic regimes that no generalizations can safely be drawn at present.



**Figure 3.** Scheme of pedology and hydrology of soils around a *Macrotermes bellicosus* colony, after Boyer (1975). a. Patterns of runoff and percolation of rainfalls and their catchment as perched water tables (light shading) by impermeant layers in the soil (dark shading). b. Patterns of soil water movement and evaporation that maintains a particular humidity within the nest.

Termites also construct extensive underground networks of tunnels and cavities, and it is likely that the resultant changes in soil hydrology will affect movement of water through the nest. The construction of a mound involves translocating several cubic meters of soil from deep horizons to the surface (Pomeroy 1976), and this must open commensurate void space and macropores in the soil below the mound. A typical mound of *M. michaelseni*, for example, occupies a volume of 5-7 m<sup>3</sup>, of which roughly 80% is soil excavated from deep soils and brought up into the mound (Turner 2000a). Because soils within mounds tend to be compacted compared to surrounding soil, the actual subterranean void space is probably more capacious (Arshad 1981). The mound is also a dynamic structure, with roughly a cubic meter of soil per year being transported up to replace soil lost from the mound through erosion (Pomeroy 1976). Finally, foraging tunnels around colonies of *Macrotermes* can radiate for 50 m or more into surrounding soils, and these also involve a substantial upward transport of soil. All this activity increases the volume of soil macropores, which enhances rates of infiltration and retention of rainfalls around the mound (Mando 1997; Mando et al. 1996), as is the case for soils in the Chihuahuan desert of North America, where termites generally enhance infiltration and water retention (Elkins et al. 1986).

At the nest itself, however, the local enrichment of clays and other fine-grained soils (Arshad 1981, Holt and Lepage 2000) makes soils there relatively impermeable. For example, a nest of *M. michaelseni* is typically surrounded by an impermeant clay barrier that protects it from periodic flooding (Dangerfield et al. 1997) and from aardvark attack (Turner, personal observation). Soils below *Macrotermes* nests also show a remarkably low leach rates (Watson 1969), suggesting an enhancement of runoff, rather than infiltration, at the mound itself.

The overall picture suggests that *Macrotermes* nests impart a complex hydrology to savanna soils. The most comprehensive assessment of this comes from the work of Boyer (1973; 1975a; b), who showed extensive and widespread effects of nests of *Macrotermes bellicosus* and *M. natalensis* on pedology and hydrology of savannas in the Central African Republic. Below the nest, there is a zone of extensive modification of soils that can extend to depths of 10-12 meters (Figure 22.3). From this zone, termites draw soil for mound construction. The continual disturbance of the soil there, along with biogenic deposition of calcite, forms impermeable depressions below the mound into which perched water tables can drain (Figure 22.3). Above and around the nest proper, the relatively impermeant layers of soil there promote runoff, eroding the relatively friable surface layers of the mound onto a broad, comparatively impermeant, outwash pediment that can radiate ten to twenty meters from the mound. In soils beyond the outwash pediment, infiltration is enhanced by the colony's extensive networks of foraging tunnels there, charging both perched and permanent reservoirs of ground water. These ultimately drain back to the impermeable depressions below the colony.

Water may also be brought into the nest through a peculiar form of active transport. Termites are known to bring soil up into the nest and mound from considerable depths, so that soils in the nest and mound soils often differ considerably from the ambient surface soils (Watson 1972; 1974; 1977). For example, soils in northern Namibia commonly comprise coarse iron-rich sands overlaying a calcite base: it is not uncommon to see chalky-white mounds emerging from these reddish sandy soils (Turner, personal observation). Termites' tendencies to bring soils up from deep horizons has led some to suggest mounds could serve as useful probes for detecting mineral-rich ores below the surface. For example, *Macrotermes* mounds in the Kalahari are enriched in zinc, drawn presumably from zinc-rich horizons that lay several meters below the surface (Watson 1970; 1972; West 1970). There are also many anecdotal reports of mound soils being enriched in gold, brought up from deep alluvial deposits (Gleeson and Poulin 1989). If the soil carried up by termites from deep horizons is damp, this amounts to a form of active water transport: movement of water against a water potential difference, driven by the colony's metabolism. This, rather than wicking, might account for a considerable rate of water movement into the nest and mound. Its

## TERMITES AS MEDIATORS OF THE WATER ECONOMY

magnitude is completely unknown.

Whatever its magnitude, active transport of water into the nest can be undertaken at surprisingly little cost to the colony, and might be a major effector in the regulation of nest humidity. The energy cost,  $Q$  (J) of transporting water into the mound from deep reservoirs can be estimated from gravity potential ( $\Psi_g$ ;  $\text{J kg}^{-1}$ ), itself the product of gravitational acceleration,  $g$  ( $9.8 \text{ m s}^{-2}$ ) and the height,  $h$  (m), the water is lifted:

$$\Psi_g = g h \quad (1)$$

and the mass,  $M$  (kg), lifted:

$$Q = M \Psi_g \quad (2)$$

The cost of transporting, say, 1800 kg of water up 5 m into a mound (equivalent to the estimated annual evaporation from colonies of *M. jeanelli*; Darlington et al. 1997), requires an expenditure of roughly 88 kJ. Spread over a year, this amounts to a power demand of only 2.8 mW. Upward transport of soil is about as cheap. Densities of silica sands and clays range from  $1800 \text{ kg m}^{-3}$  (bulk density) to  $2600 \text{ kg m}^{-3}$  (density of the parent rock). Assuming termites transport roughly a cubic meter of soil into the mound each year (Pomeroy 1976), this amounts to lifting roughly 1800-2600 kg into the mound annually. If the soil is lifted on average 5 m upwards, the work done raising this quantity of soil by 5 m amounts to 88-127 kJ, or roughly 4 mW. Even if one assumes an extremely low conversion efficiency of muscle work to transport work of, say 1%, these rates correspond to metabolic expenditures of roughly 600 mW, roughly 1% of the estimated 55-210 W metabolic rate for *M. jeanelli* colonies (Darlington et al. 1997).

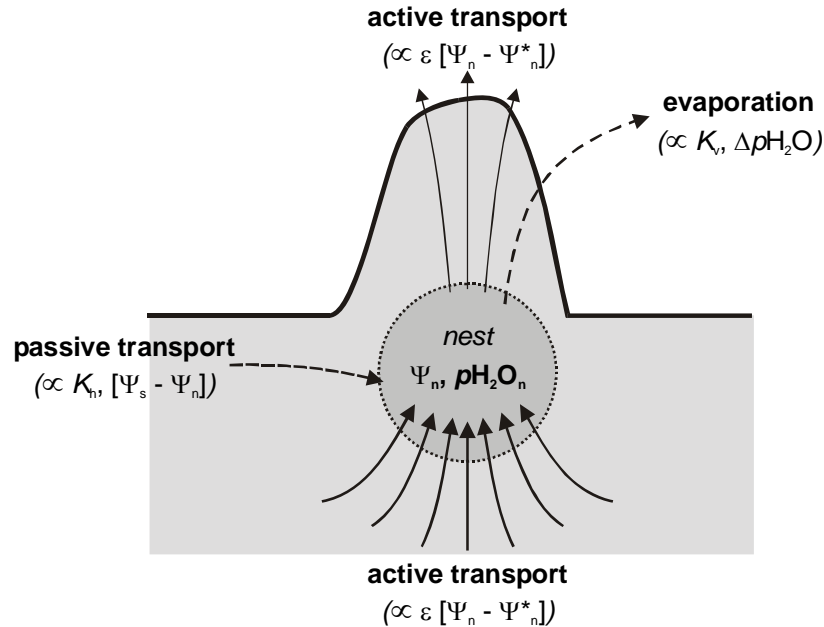
### 6. Termites as homeostatic water gatherers in savanna ecosystems

Irrespective of the mechanistic details, evaporation from *Macrotermes* mounds is sustained by what seems to be a substantial water input from surrounding soils. During the rainy season, rainfalls shed from the mound and relatively impermeant soils surrounding it charge perched and permanent water tables in the more permeable soils between mounds. These form a reservoir that the colony can then tap during dry periods, using a combination of passive and active transports of water into the nest, ensuring a relatively steady evaporative flux through the year. In short, a *Macrotermes* colony can act as a “water gatherer”, a physiological system that draws water from a broad expanse of soil centripetally to the colony. In this sense, a termite colony is physiologically akin to a tree, with an extensive system of conduits for the centripetal transport of water.

If water gathering by termites is driven by the demands of nest homeostasis, it would confer upon the colony a certain independence from seasonal, interannual and spatial variation in the hydric environment (Figure 22.4). In wetter environments, for example, a specific nest humidity can be achieved by a combination of a mound’s high evaporative conductance and rapid translocation of wet soil from the nest to the mound surface. The same humidity in dryer environments can be maintained through a combination of building mounds with low evaporative conductance, limited transport of damp soil to the surface, and more intense transport of soil water into the nest. Because *Macrotermes* colonies can bring more metabolic power to these tasks than can other termites, they are able to colonize dryer habitats than any other termite species. In sub-Saharan Africa, for example, *Macrotermes* spp come to dominate termite biomass as habitats become dryer and dryer (Figure 22.5; Deshmukh 1989).

Nest homeostasis regulates more than nest humidity, though, and this poses challenges for balancing regulation of various nest properties against one another. For example, maintaining the colony’s fungal symbionts requires that  $\text{CO}_2$  concentrations within the nest be kept within narrow

limits (Batra and Batra 1979). Nitrogen fixation within termite nests also is compromised by high oxygen concentrations (Curtis and Waller 1996). Finally, colony temperatures are also steady (Korb and Linsenmair 1998a; b; 2000), although this derives largely from damping by the capacious thermal sink of the soil rather than active regulation. Thus, nest homeostasis involves managing fluxes of a variety of materials - oxygen, carbon dioxide, water vapor - and energy, and regulation of one may conflict with regulation of others. For example, a colony in a dry environment that maintains humidity by reducing the mound's gas conductance might be faced with a compromised ventilatory exchange of the CO<sub>2</sub> or oxygen upon which the colony's fungal symbionts depend. Conversely, a mound that is sufficiently porous to support the proper exchange rates of oxygen and carbon dioxide will also support high rates of water vapor flux, and along with it, the risk of nest desiccation.

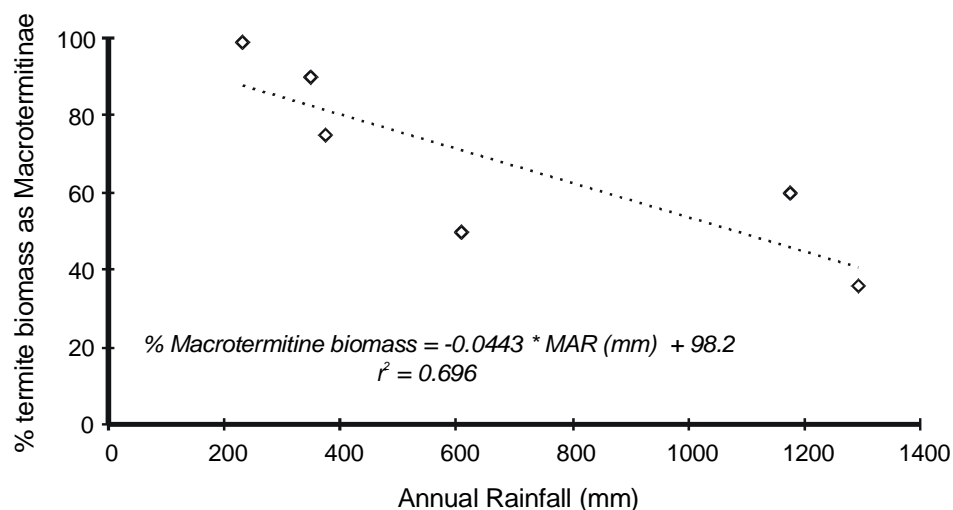


**Figure 4.** Scheme of managing water balance in a *Macrotermes* nest. The nest's water balance is geared to regulating nest humidity ( $pH_2O_n$ ) and water potential ( $\Psi_n$ ). Evaporation is proportional to the mound's vapor conductance ( $K_v$ ), which the termites manage by altering mound architecture, and the water vapor partial pressure difference between nest and atmosphere ( $\Delta p_{H_2O}$ ). Water can be transferred into the nest from perched water tables in soils, driven by the difference in water potential between nest and soil ( $\Psi_s - \Psi_n$ ), and limited by the soils' hydraulic conductance ( $K_n$ ). Water can be conveyed actively into the nest from deep soils, or to the surface from the nest by transport on damp soil. This will be regulated by an error signal ( $\varepsilon$ ), which reflects the difference between actual nest humidity ( $\Psi_n$ ) and a "target" nest humidity ( $\Psi_n^*$ ).

Such tradeoffs between multiple exchanges usually arise when sources and sinks of the various materials are linked. In the case of the respiratory gases, carbon dioxide, oxygen and metabolic water vapor, all are linked by the stoichiometry of respiration, and anything which affects the exchange of one similarly affects exchange of the others. Such tradeoffs can be avoided by uncoupling the links between the various fluxes. This, in a roundabout way, is the rationale for drinking of liquid water by animals. There is no inherent reason why animals need to drink - the kangaroo rat is the quintessential example of an animal that balances its water budget with metabolic water inputs alone - but not drinking means tying water balance inextricably to the

## TERMITES AS MEDIATORS OF THE WATER ECONOMY

stoichiometry of respiration, and elaborate mechanisms of water conservation and retention are necessary for this to work. Most animals avoid the problem by coupling water vapor flux to both metabolic water and an external source, namely drunk liquid water. Through access to an additional capacious source, high water flux rates can be maintained without simultaneously disrupting flux rates of oxygen and carbon dioxide, and hence their concentrations within the body. Water gathering by termites is the superorganismal equivalent of drinking, coupling high evaporative fluxes to the relatively capacious source of soil water, enabling the simultaneous regulation of all the respiratory gases. Plants, of course, make similar tradeoffs, and like termite colonies, resolve the conflicts by decoupling water flux rates from gas flux at the leaf (see Chapter 4 for more details on plant physiology).



**Figure 5.** Proportion of termite biomass that is represented by *Macrotermitinae* in savannas with various annual rainfalls. After Deshmukh (1989).

What impact water gathering has on savanna systems will depend, of course, upon how rare is the resource of soil water. In wetter savannas, “drinking” by termite colonies is unlikely to have much impact on the soil water balance, and hence the availability of soil water to other organisms. Certainly, wetter environments support a higher diversity of other termites, and termites there have lesser impacts on differential soil leaching and other functions that depend upon rainfall. In environments where the inputs of rainfall are less, and the desiccating forces greater, the draw on soil water by macrotermitine termites will be proportionally greater, with larger consequences for the soil’s hydric environment and the organisms that depend upon it. Substantial ecological consequences might follow, exemplified by the observation that inspired this paper. Northern Namibia hosts some of the dryer savannas in Africa, with annual rainfalls averaging about 250-450 mm. Trees in this environment associated with termite mounds would appear to have a clear competitive advantage over trees that are not (Konaté et al. 1999). What other ecological consequences might follow in an ecosystems dominated by such a powerful draw on scarce soil water? Questions abound, but very few answers are at hand.

Water gathering also has implications for our understanding and ability to predict climate in tropical savanna systems. Climate models depend strongly upon measurements that assume some degree of homogeneity to the flux processes upon which climate depends. For example, expected transpiration is often calculated from a variant of the Penman equation, which estimates evaporation from air temperature, local humidity, ground cover and so forth (Campbell 1977;

Nicholson et al. 1997). Increasingly, these parameters are sensed remotely from various satellite platforms, with resolutions typically in the km<sup>2</sup> range, and the results validated against commensurably homogeneous habitats on the ground, like agricultural fields. Despite the great strides in remote sensing, however, none are capable of resolving the kind of hydrological patchiness that *Macrotermes* nests in a habitat might impart. Let us assume, for the sake of argument, that a *Macrotermes* mound evaporates roughly 5 liters of water per day (Darlington et al. 1997). This water leaves the soil through the “footprint” of the mound’s basal area, estimated to average roughly 4 m<sup>2</sup> (Turner 2000a), yielding a focal water flux density of 1.25 kg m<sup>-2</sup> d<sup>-1</sup>, or about 457 kg m<sup>-2</sup> y<sup>-1</sup>. This is numerically identical to a “rainfall equivalent” of 457 mm y<sup>-1</sup>. Throughout the year, this amounts to a monthly evaporation from the mound’s footprint that is equivalent to 38.1 mm rainfall. Contrast this with estimates of monthly evapotranspiration from a semi-arid savanna, which range from roughly 75 mm mo<sup>-1</sup> in summer to less than 20 mm mo<sup>-1</sup> in winter (Nicholson et al. 1997). Notice that a conservative estimate of the mound’s annual evaporation have been used: Weir’s (1973) more extravagant estimate of 25,000 kg of water evaporated annually from nests of *M. subhyalinus* in Tanzania corresponds to an evapotranspiration rate of more than 500 mm mo<sup>-1</sup>, roughly equivalent to the *annual* evapotranspiration estimated from climate measurements (Nicholson et al. 1997). This suggests that the development and validation of microclimate models would have to account for the extreme patchiness associated with the presence of termite mounds.

## 7. Acknowledgments

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## TERMITES AS MEDIATORS OF THE WATER ECONOMY

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