Permanent groundwater storage in basaltic dyke fractures and termite mound viability

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ABSTRACT

Many basaltic dykes of the Ethiopian flood basalt province are observed in the northwestern Ethiopian lowlands. In this area, the termites preferentially build their epigeous mounds on the top of dolerite dykes. The relationship between termite mounds and dykes is investigated from the analysis of their distribution along one of these dykes, of thickness 2–5 m, that we could follow over 2000 m. Termite mounds are periodically spaced (mean distance 63 m, $R^2 = 0.995$), and located exclusively where the topographic relief of the dyke is not more than 2 m above the surrounding area. From these observations and from the geological context, a hydrological circuit model is proposed in which (1) dykes are preferential conduits for groundwater drainage during the rainy season due to pervasive jointing, (2) during the dry season, the portion of the dyke forming a local topographic relief area dries up more quickly than the surroundings, the elevation difference between the dyke summit and the surroundings being a factor restricting termite mound development. For dyke topographic relief >2 m, drying is an obstacle for maintaining the appropriate humidity for the termite colony life. Periodic termite mound spacing is unlikely to be related to dyke or other geological properties. It is more likely related to termite population behaviour, perhaps to clay shortage, which restricts termite population growth by limiting the quantity of building material available for mound extension, and triggers exploration for a new colonization site that will be located along the dyke at a distance from the former colony that may be controlled by the extent of the zone covered by its trail pheromones. This work brings out the importance of dykes in channelling and storing groundwater in semiarid regions, and shows that dykes can store groundwater permanently in such settings even though the dry season is half the year long. It contributes also to shedding light on water supply conditions tolerated by termite populations, and factors governing termite mound distribution.

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1. Introduction

After several years of work in the Ethio-Sudanese plain of northwestern Ethiopia, where the largest dyke swarms of the Ethiopian volcanic province are observed, it has become obvious that relationships exist between the distribution of these dykes and the distribution of termite mounds. The dykes are dominantly doleritic (Mège and Korme, 2004a,b) and the host rock is made of the corresponding lava flows. During field work in January 2008 we investigated the relationships between basaltic dykes and termite mounds in the Ethio-Sudanese plain in the Qwara district of Ethiopia in more detail. We report on the results of this work in this paper.

Termites play a significant role in a variety of ecosystems, in which they increase or contribute to maintain biodiversity (e.g., Glover, 1967; Braack and Kryger, 2003). They are also amazing soil ecosystem engineers and soil processors (Bignell, 2006). How they modify the soil properties has been a subject of intense research due to their influence on many pedogenetic processes (Boyer, 1973; 1975a,b), especially soil porosity, water infiltration, and run-off (Yakushev, 1968; Garnier-Sillam et al., 1991; Ouedraogo and Lepage, 1998; Léonard and Rajot, 2001), and soil pH rise (Donovan et al., 2001); on soil textural changes, including transportation of deep clay particles to the surface (e.g., Grassé and Noirot, 1959; Mando and Miedema, 1997; Johnson et al., 2005) and organic matter transformation by termite gut microbiota (Brauman, 2000; Fall et al., 2007), all these factors having profound agricultural implications (Harris et al., 1994; Miller et al., 1994; Duboisset, 2003). In contrast, the detailed relationships maintained between geology (pedology excluded) and termite colony settlement have been scarcely investigated, usually attracting attention on the accumulation of Ag, Au, Cr, Cu, Mn, Mo, Ni, Pb, and Zn in termite mounds (West, 1965, 1970; D'Orey, 1975; Watson, 1970, 1972; Wild, 1975;

Brooks, 1983; Prasad et al., 1987; Kebede, 2004; Melchiorre et al., 2006) by displacement of small soil particles by termites from deep soil levels to the surface. These works have been partly inspired by an account given by Herodotus (Ìστορίαι III, 102–105) relating exploitation of auriferous sands accumulated by ants in a dry location of northern India or Pakistan, supported by other accounts of "ant-gold" occurrence in the Mahābhārata (II, 52) and in ancient Mongolian (Laufer, 1908) and Tibetan (Ball, 1881, pp. 124–128; Francke, 1924; Burnay, 1931) texts and oral stories. Most scientific investigations demonstrate the role of termites in rising metals from underground (some of which will be discussed later in this article), and the Mahābhārata probably testifies to the Indian knowledge of gold-bearing sand digging by termites. However, the issue is complex (a detailed discussion can be found in Dube, 1993); some of the accounts, especially by Herodotus, may refer to exploitation by the Tibetan Minaro people of auriferous soil excavated by the long-tailed marmot, *Marmota caudata* (Peissel, 1984; Simons, 1996), instead of auriferous sand digging by termites, an interpretation that Laufer (1908) and Francke (1924) favoured in spite of their knowledge of the mammal interpretation.

Termite colonies are widespread in Ethiopia like in many other African countries. Along a few roads of southern and eastern Ethiopia an inventory of termite populations has been done and published (Cowie et al., 1990). Nevertheless, putting aside the environmental damage caused by termites in southern Ethiopia (Wood, 1991, and reports referenced therein) and the potential control methods (Abdurahman, 1990; Abebe, 2002), overall little information is available about the biology, ecology, and ethology of these termites (Grassé, 1937; Kevan, 1953; Barnett et al., 1988; Cowie and Wood, 1989; Cowie et al., 1990), and none appears to be available in the Ethio-Sudanese plain west of lake Tana, where the study area is located (Fig. 1b).

Wild (1975) studied the soil brought to the surface by two termite species on serpentines from the Great Dyke of Zimbabwe, but neither its scale (several kilometres over more than 500 km) nor emplacement (as a layered intrusion, not a true dyke, Wilson and Prendergast, 1989) can be compared to those of the Farshewa dyke. Termite mounds have been reported on another volcanic setting in the northern Kruger National Park (Meyer et al., 1999), the Lebombo basalts and dolerites from the Karoo events in South Africa (Klausen, 2009). Interestingly, mound abundance has been found to be lower on basalts and associated dolerites than on other rocks such as rhyolite, granite, gneiss, and gabbro, although basaltic soils contain the same nutrients as gabbroic soils in comparable abundance. It is probable that the lower than average abundance of termite mounds in this volcanic formation is due to its location
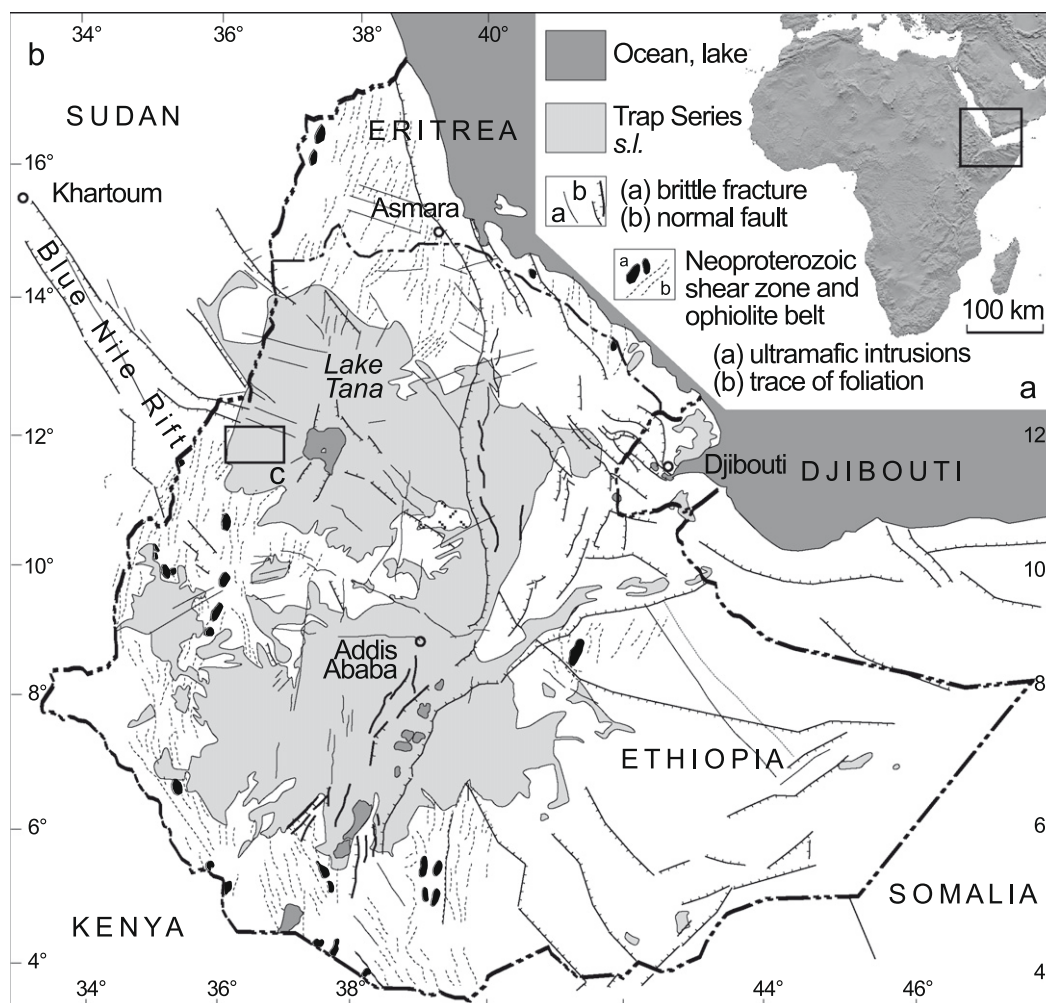
Fig. 1. Location maps: (b) is from interpretation of Landsat Geocover 1990 mosaic; (c) is an interpretative map of the study area partly based on Landsat Geocover 1990 and 2000 mosaics, ASTER imagery (15 m/pixel), Spot panchromatic imagery (2.5 m/pixel, not available in the western third of the map), results presented in Mège and Korme (2004a), field observations, and GPS measurements. The undated sandstone is probably Mesozoic (Seyid, 2002). Its eastward extent is unknown, the trap series unconformably overlies the Precambrian basement south of the study area (Mège and Korme, 2004a). In mountainous areas the fractures are observed to be vertical or near vertical.

Fig. 1 (*continued*)
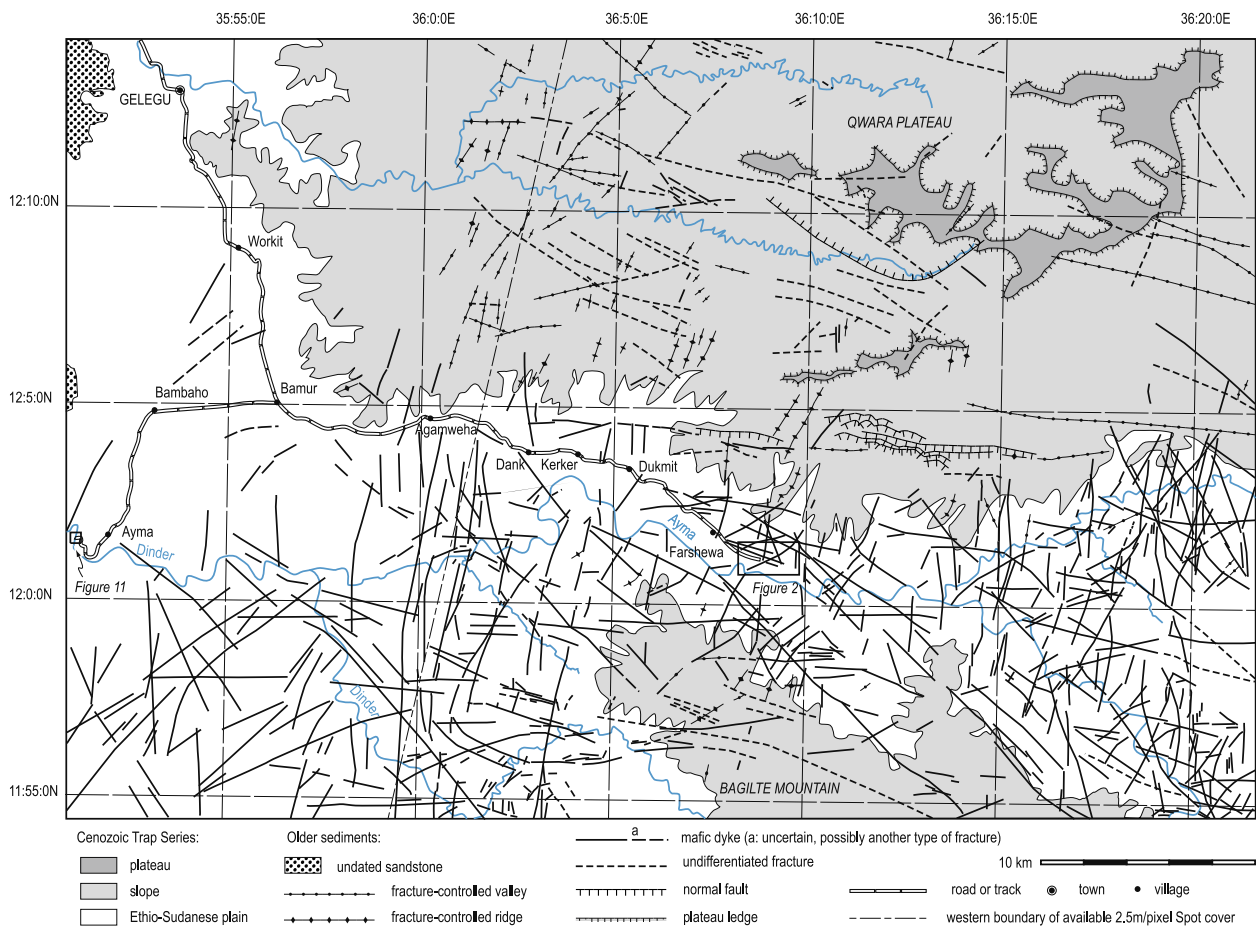
in a flood plain. Unfortunately though, the proportion of mounds on the dolerite dykes compared to the basalts has not been studied.

Termite colony sites offer a compromise between access to water and avoidance of periodic inundations indeed (e.g., Miller et al., 1994). Survival conditions include relative humidity in the order of 90–98% (Grassé, 1984, pp. 589–593) because of the permeable termite tegument. For this reason, it is likely that the correlation observed in the Ethio-Sudanese plain between dykes and termite mounds is related to wetter subterranean conditions in dykes than in the surrounding lava flows. Many dykes are observed to display field evidence for aqueous alteration. In northern Ethiopia, the basaltic dykes and stocks intruding the Antalo limestone play a key role in groundwater storage and potable water supply to the city of Mekele (Ferriz and Bizuneh, 2002, see additional references in Ayenew et al., 2008). In the Red Sea Hills of Sudan, ponds on dykes show that they are preferential conduits for groundwater flow (Babiker and Gudmundsson, 2004). Similar to the Mekele area and the Red Sea Hills, channelling along dykes is an efficient mechanism for underground water transportation in the Ethio-Sudanese plain, and reveals the potential of these dykes for drinkable water pumping and irrigation of this poorly developed area.

2. Study area

2.1. Geology

The studied dyke is located on the Ethiopian side of the Ethio-Sudanese plain, at the basal level of the Oligocene trap series from which the Abyssinian plateau has built. It lies at the base of the Qwara volcanic plateau, a remnant of the Abyssinian plateau, and is located a few kilometres east of Farshewa, a village from the Qwara district (Fig. 1a and b). We call it the Farshewa dyke (Fig. 2). It can be accessed from the Abyssinian plateau by following the Metema road up to Shehedi, then the road to Gelegu and Bamur, and a track from Bamur to Farshewa (Fig. 1c). The Ethio-Sudanese plain displays a tremendous quantity of dykes which contributed to feed the trap series, part of which has been studied (Jepsen and Athearn, 1963; Chorowicz et al., 1998; Mège and Korme, 2004a,b; Schultz et al., 2008). From comparison with field work data obtained in other zones within the Ethio-Sudanese plain and other areas in the trap series (e.g., Mohr, 1963; Mohr and Zanettin, 1988; Mège and Korme, 2004a), the thickness of the lava pile is expected to be a few tens of metres below the base level, at the Ayma river (Fig. 1c). Horizontal basaltic flows probably make most of the pile, with perhaps intercalations of basaltic tuff levels. The thickest and highest relief dykes in the Ethio-Sudanese plain are silicic, but most of the dykes are of basaltic composition. The strike of some of the basaltic dykes can be followed over more than 10 km, and their relief above the surrounding plain, which increases with thickness, is usually between 0 and 5 m (Mège and Korme, 2004b).

The Farshewa area contains many basaltic dykes, none of which had been studied in the field prior to the present work. The Farshewa dyke (Fig. 2) can be followed easily not only on very high-resolution satellite imagery (Spot, 2.5 m/pixel), but also on the much coarser imagery (ASTER, 15 m/pixel) from the shading of its debris slopes and its association with higher vegetation density (Mège and Korme, 2004b).
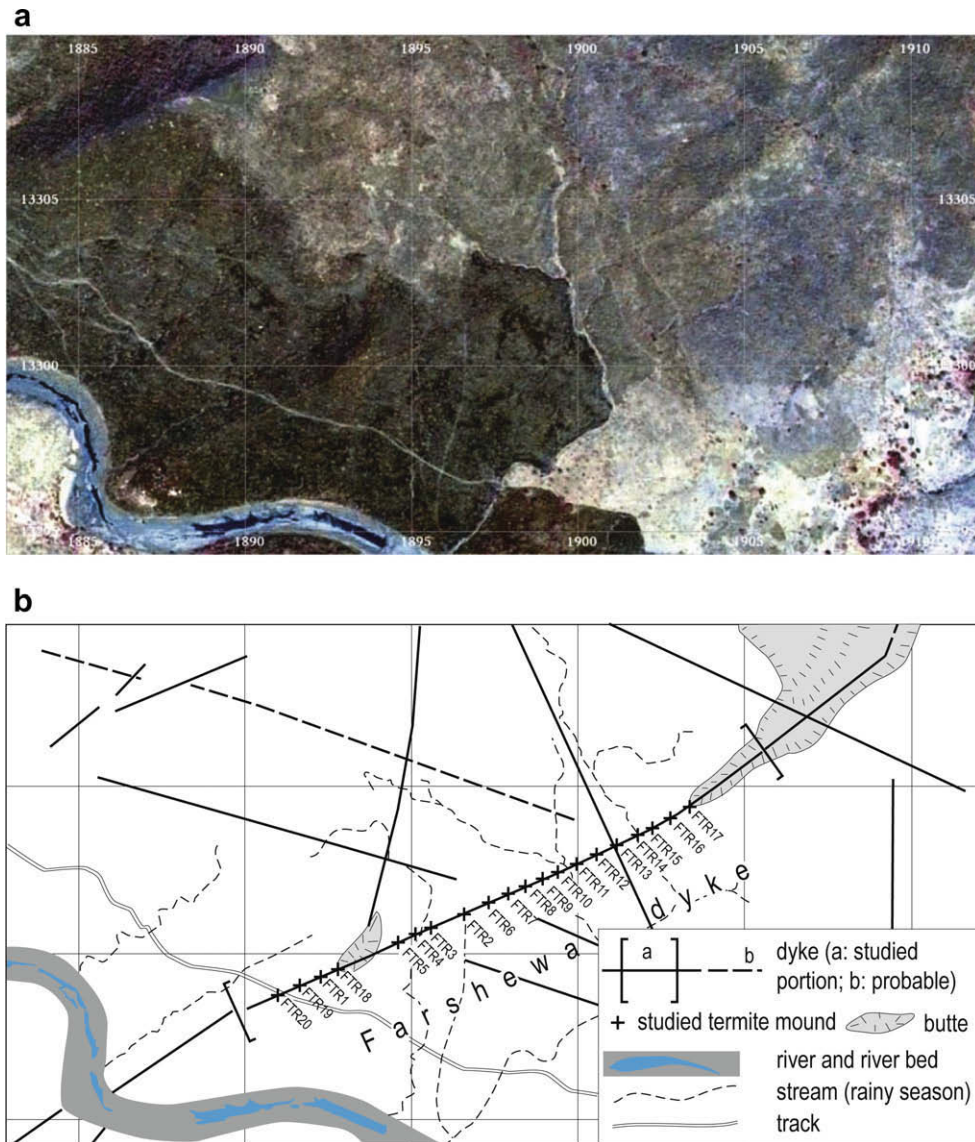
Fig. 2. The Farshewa dyke. (a) Brovey transform image of the study area, using a Spot 5 panchromatic image (2.5 m/pixel) and an ASTER multispectral image (15 m/pixel, RGB-coded channels 3N, 2, 1), both acquired during the dry season (ASTER: January 30, 2002; Spot: February 4, 2004). The Farshewa dyke is apparent but the termite mound horizontal dimensions are two small to be distinguished. The satellite and field images reproduced in grey levels in the print version of this article are available in colour in the electronic file. (b) Interpreted map displaying the GPS location of the termite mounds (FTR01–FTR20). North is to the top, grid cell width is 500 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Topography

The available topography sources include (1) the local topographic map (EMA, 2001), established from 10 m-Spot stereoscopy, displaying 20 m spaced contours. Its vertical accuracy is thought to be grossly similar to that of the SRTM elevation dataset. Although horizontal resolution is better in theory, the poor computer interpolation of contours makes this dataset uneasy to handle; (2) SRTM-3 data (Farr et al., 2007), with a cell size of ~86 m (Fig. 4a). By examining the maximum height and depth of the erroneous peaks and hollows along the Ayma river topographic profile south of the Farshewa dyke, the vertical accuracy in the study area is estimated to be ±~9 m (Fig. 4b), in agreement with the theoretical vertical error expected in this region (Farr et al., 2007). The SRTM digital elevation model (DEM) has been used in this study for evaluating mean topographic slopes at the scale of windows of 4 by 4 pixels or more; (3) relative elevation differences mea-

sured in the field for dykes having a topographic relief lower than a few metres using a measuring tape, with a vertical accuracy estimated to be ±0.3 m. Levelling instruments, which could have provided more accurate measurements, were not available; (4) GPS altimetry was recorded at every termite mound and in several other sites together with the geographic coordinates, but its accuracy is thought to be much lower than the other available topography data, and this dataset was not considered.

The mean elevation of the Farshewa dyke is 730 m. The present topography of the study area has been carved by the drainage system of the Ayma river, a tributary of the Blue Nile river flowing at an elevation of ~700 m that crosses the Farshewa dyke (Fig. 3). This elevation gives an idea of the depth of the water table in the studied area. At a mean elevation of 740 m, the village of Farshewa has a water well. The villagers of Farshewa say that it is empty during the dry season. All the water used by the villagers during the dry season needs to be transported from the Ayma river.
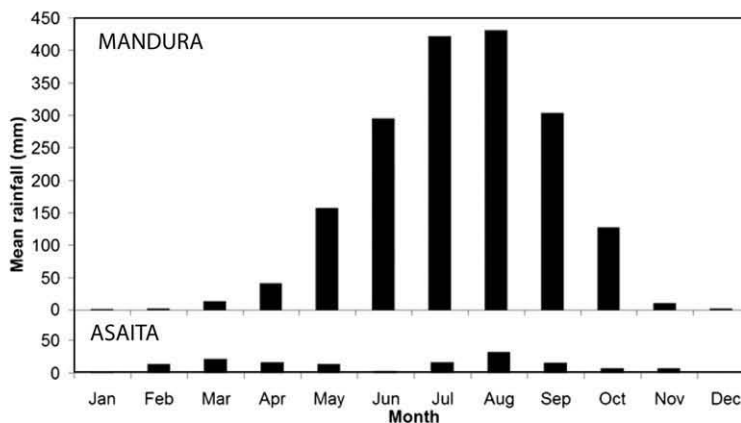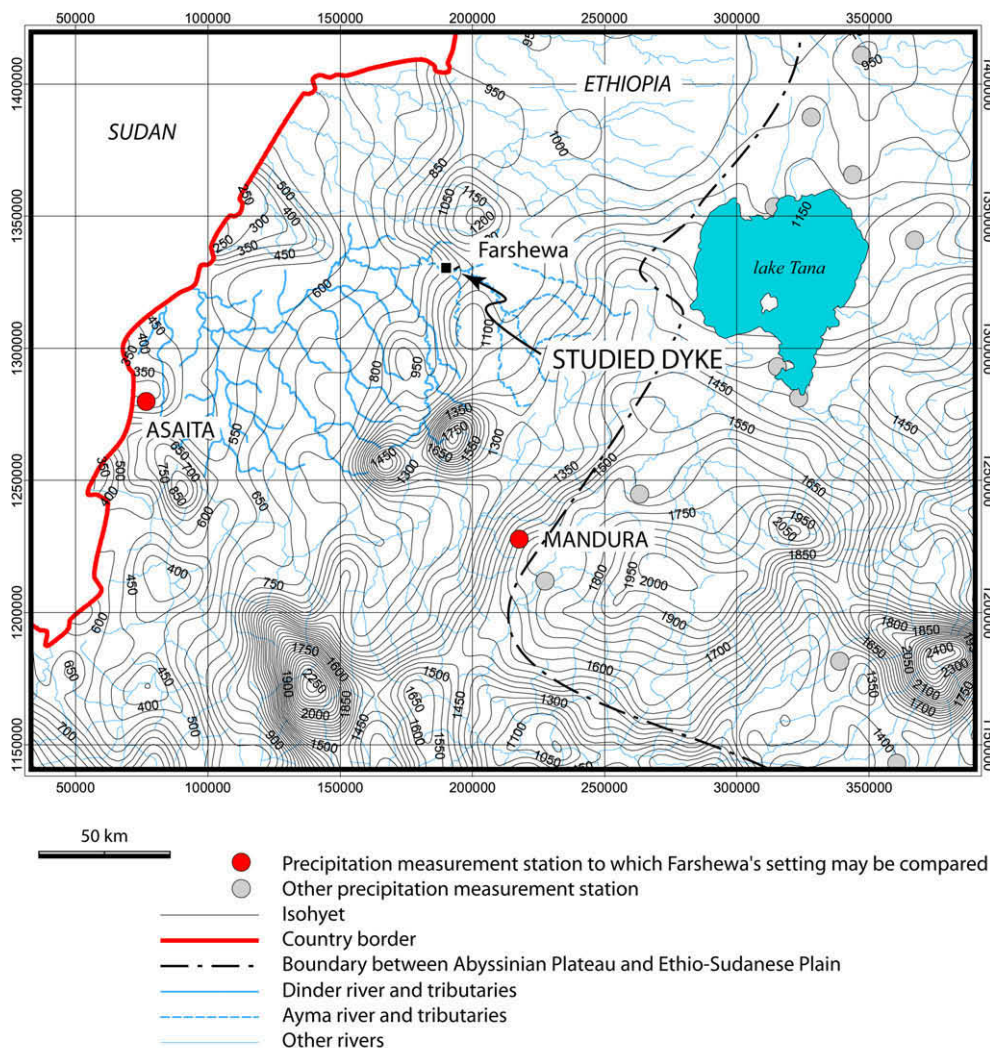
Fig. 3. Isohyets in the Ethio-Sudanese plain in Ethiopia, and rainfall patterns at Mandura (averaged over 19 years) and Asaita (15 years). Farshewa is probably between these two types, closer to the Mandura-type. The Ayma and Dinder rivers and their tributaries are located. Source: EthioGIS project (Kohler and Krauer, 1996).

2.3. Topography

2.3.1. Vegetation and climate

The vegetation in the dyke area is mainly deciduous wood-land, with scattered trees among which frankincense and acacia trees are common species. There is a rainy season and a dry sea-son, the dry season being from November to April. The rainfall pattern is expected to be a mixture of the patterns recorded in nearby settings at Mandura and Asaita (Fig. 3). It is likely, from its topographic setting close to the Trapean plateau edge, that rainfall in the study area is more similar to the Mandura-type pattern.
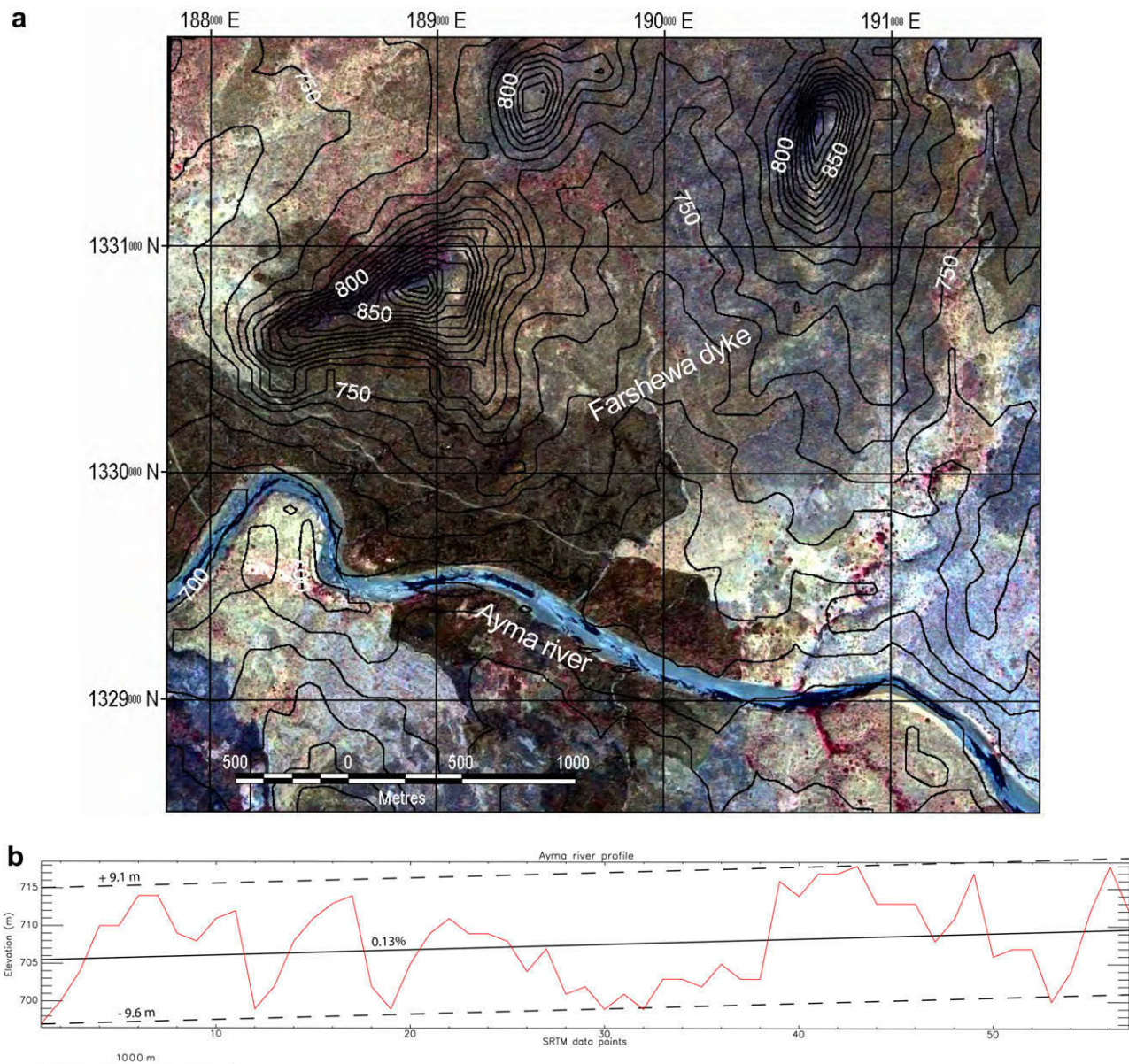
Fig. 4. (a) Contour interpolation of SRTM-3 DEM of the Farshewa area; (b) Estimation of vertical accuracy from relative elevation error along the portion of the Ayma river profile displayed on (a). Error on SRTM data (dashed lines) is estimated by comparing the SRTM profile to a mean theoretical linear river profile (solid line). Its slope, 0.13%, is close to the linear/meandering river transition reported by Schumm et al. (2002), in agreement with the observed river geometry.

3. Observations

3.1. Farshewa dyke

The Farshewa dyke (Fig. 5), of direction NE-SW, could be followed over a distance of ~2000 m. The dyke is vertical; its thickness could be estimated in several locations where either chilled margins or the contact with the basaltic host rock could be observed. Dyke thickness usually varies from 2 to 3 m, but in its highest part it was found to be at least 5 m. Thus a correlation appears to exist between dyke thickness and topographic relief. This correlation is explained by the dependence of cooling rate on dyke thickness, a slow cooling rate resulting in a lower density of retraction joints, hence a lower alteration rate, and a higher dyke strength (e.g., Hoek et al., 1997) and topographic relief. Retraction joints (e.g., Jaeger, 1968) cut the Farshewa dyke into decimetre-scale horizontal prismatic blocks, as illustrated on Fig. 5b; in con-

trast, jointing in the surrounding basaltic flows, as well as in many other areas in the Ethio-Sudanese plain, is significantly less dense (Fig. 6). This major difference in fracture density suggests that the dykes in the study area play an important role in collecting runoff water (e.g., Babiker and Gudmundsson, 2004). This is confirmed by analysis of ASTER multispectral imagery, on which the Farshewa dyke as well as many other nearby dykes are highlighted by a vegetation that is denser than in the surroundings, including many river banks (Fig. 7a). The meandering geometry of the Ayma river and some of its tributaries is also observed to be influenced by the azimuth of dykes, as illustrated on Fig. 1c.

The topography of the Ayma drainage basin around the Farshewa dyke is gently undulating. The Ayma river has a few tributaries, the two largest ones crossing the dyke between termite mounds FTR11 and FTR12 and mounds FTR14 and FTR15 (Fig. 2b). The typical topography associated to the Farshewa dyke is an elongated ridge, consisting of the dyke at the centre and a
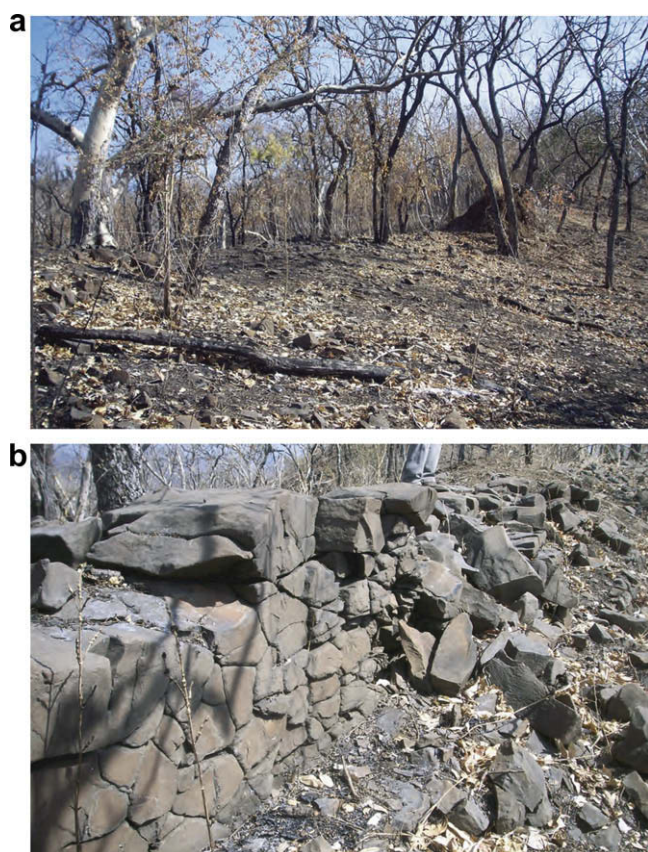
Fig. 5. Field photographs of the Farshewa dyke (views to the NNE). (a) Typical low-relief (~1 m) dyke outcrop. Note the termite mound (FTR01 on Fig. 2b) located on the dyke on the right. (b) Typical high-relief (~20 m) dyke outcrop (between mounds FTR5 and FTR 18 on Fig. 2b). Note the densely jointed fracture network, mostly retraction joints formed during magma cooling. The fractures collect and store water during the rainy season.

Fig. 6. The dry bed of the stream cutting across the Farshewa dyke between termite mounds FTR11 and FTR12. Note the difference in dyke (left) and host rock (right) fracture density. During the rainy season, some of the water can directly seep into the dyke through its pervasive fracture network, mainly parallel and perpendicular to the dyke strike. View is to the West.

debris slope around it. Ridge relief relative to the surrounding slope (Fig. 8) is usually lower than or equal to 2 m, except near the southwestern portion of the study area and at its northeastern end, where both field and SRTM data show that it attains as much as ~20 m (Fig. 7c).

3.2. Termite mounds

Twenty termite mounds (Fig. 2b, view example on Fig. 5a) have been observed over a distance of 1460 m along dyke strike, all of them located along the dyke. Other mounds have been identified along nearby dykes. Along the track from Bamur to Farshewa (on Fig. 1c), where dykes are abundant, almost no mound has been observed to have been built on lava flows. Termite mound location could even be used as a convenient tool for quick dyke identification in the field.

The termite mound displayed on Fig. 5a is representative of the mounds observed on the Farshewa dyke. The photographed area is also typical of the forested landscape of the volcanic portion of the Ethio-Sudanese plain. The mounds are dome-shaped, and have height usually in the range 1.5–2 m. There is no appreciable change in mound height (and size) with dyke topographic relief. In northern Kruger National Park, South Africa, Meyer et al. (2000) quantified the correlation between mound size and termite population; they showed that *Macrotermes natalensis* mound height is related to termite population size following the equation ln(population) = height * 1.093 + 7.893, with a coefficient of correlation $r = 0.92$. This relation may not be reliable for estimating the size of the termite population inhabiting the Farshewa dyke, for which the genus and species have not been identified yet; however, it gives a number of inhabitants in the range 14,000–24,000 per mound, a small population given that populations of several hundreds of thousand inhabitants per mound, sometimes more, are encountered worldwide (e.g., Grassé, 1984, pp. 150–155). This range suggests that the colonies in the Farshewa dyke are probably at the lower end of the existing colony size distribution.

Field observations and SRTM data have shown that dyke topographic relief above the surrounding host rock is between 0 and ~20 m; however, the termite mounds were built only where it is not higher than 2 m (Fig. 8). Another surprising observation is that the termite mounds display constant spacing (Fig. 9).

4. Discussion

4.1. Dyke-related factors influencing termite mound distribution

It is likely, as argued above, that the termite mounds are located along the dyke because of easier access to moisture, good drainage provided by dyke-related fracturing, and location above the Ayma river flooding plain. The other reported examples of termite mound alignments also stress the essential dependence of mound location on surface water or groundwater distribution (photo 2 of De Bont, 1955; Prasad et al., 1987; Miller et al., 1994). Bodot (1967a) showed that *Bellicositermes natalensis* can drill wells down to the water table in soft sediments to find and transport the water required for the climatic regulation of their termitary, and groundwater drilling by *Amitermes excellens* to a level as deep as 70 m has been reported (Yakushev, 1968).

Other critical factors for termite population development in mounds do exist, however, and include CO_2 concentration, food, and temperature (e.g., Grassé, 1984, pp. 578–600; Korb, 2003; Korb and Lenz, 2004). Those factors are probably little involved in termite colony preference for dykes for the following reasons.

(1) Cooled dykes are not associated with any CO_2 emissions.
(2) Termite food includes either plant or plant-derived products (wood, leaves, grass, humus), or mineral nutrients from soil horizons (e.g., Grassé, 1986, p. 377; Brauman, 2000). Their role in Farshewa termite feeding cannot be clearly assessed because the termite species has (have) not been identified yet. In the case of termites feeding on plant material, despite
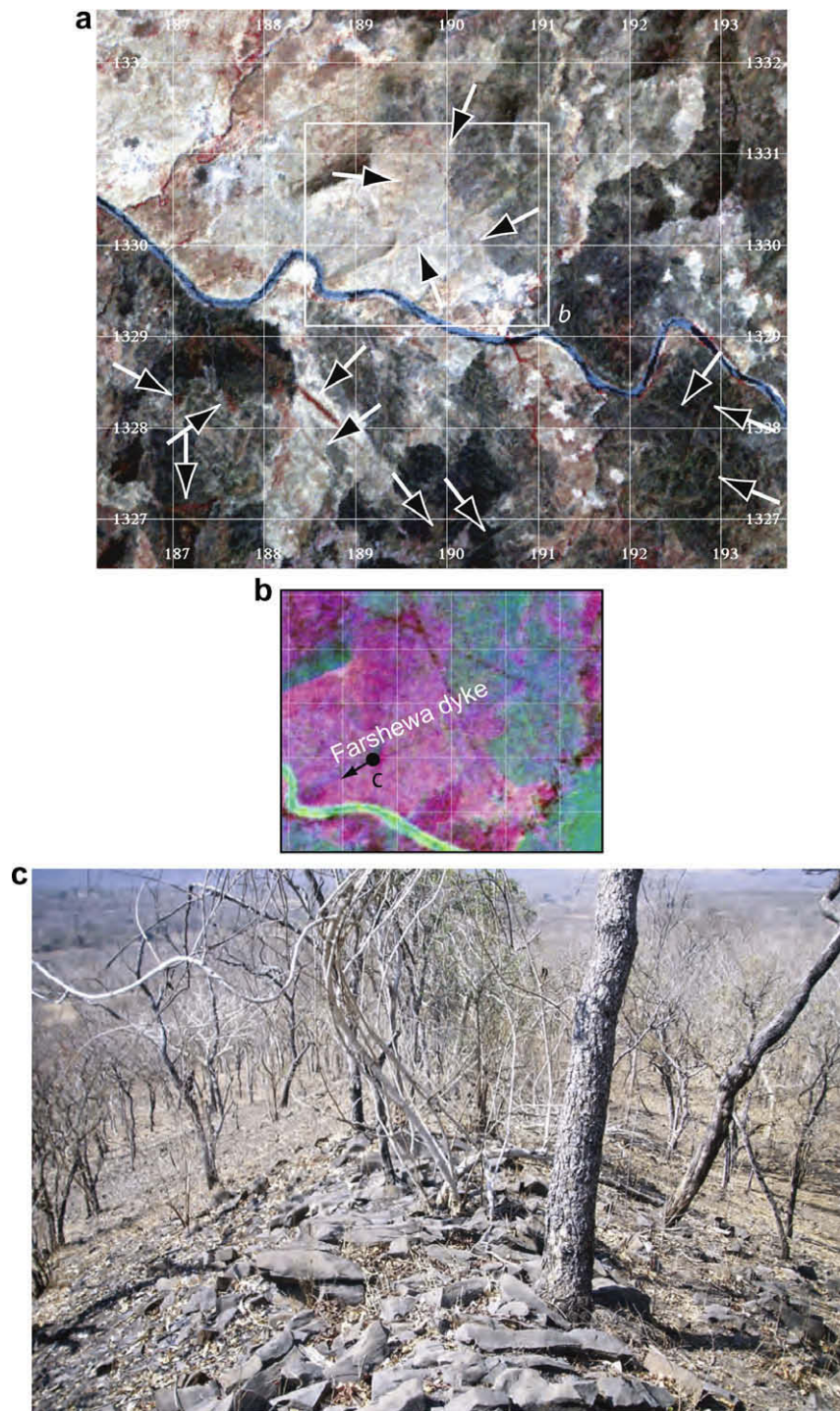
Fig. 7. (a) ASTER image of the study area (bands 3 N, 2, 1 as RGB, 15 m/pixel, obtained during the dry season on January 30, 2002) with the vegetation in red; note that the dykes are underlined by vegetation. The arrows point to (and are perpendicular to) basaltic dykes underlined by denser vegetation concentration than their host rock (always basaltic lava flows). Dyke vegetation is usually denser than on the Ayma river banks, and as much dense as along some of the Ayma tributary streams. (b) Principal component analysis of part of (a), in which dyke signature is strongly highlighted. (c) Field view of the Farshewa dyke illustrating that the trees are preferentially located on the dyke, in particular the largest trees (a common observation throughout the Ethio-Sudanese plain). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the relative concentration of trees along the dyke, it is unlikely that tree abundance has significantly contributed to determine termite settlement because trees are abundant in the whole study area. In the case of termites feeding on humus or mineral-derived nutrients, the nutrients may concentrate and accumulate within the dyke fractures during the rainy season. It is not sure, however, that connections between the nutrient-rich zones are good enough to make the dyke more attractive for food than the surrounding basaltic soil.

(3) Life in a termite mound requires mechanisms for mitigating temperature fluctuations; in this respect dyke influence is ambiguous. On the one hand, dyke thermal inertia is increased compared to the surrounding host basalt owing
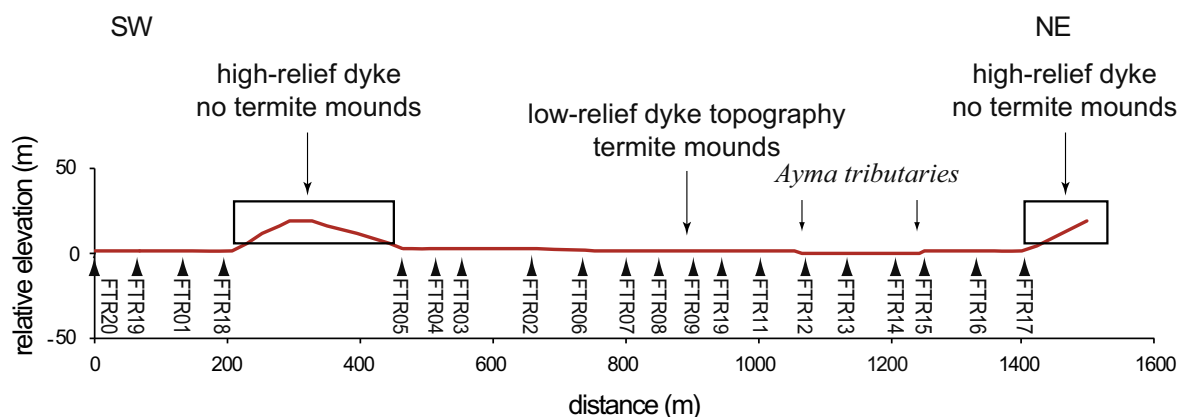
Fig. 8. Relative along-strike dyke topography above the surrounding areas from field measurements (low-relief portions) and SRTM DEM (high-relief portions), and location of the observed termite mounds from GPS measurements. Vertical scale exaggerated twice.
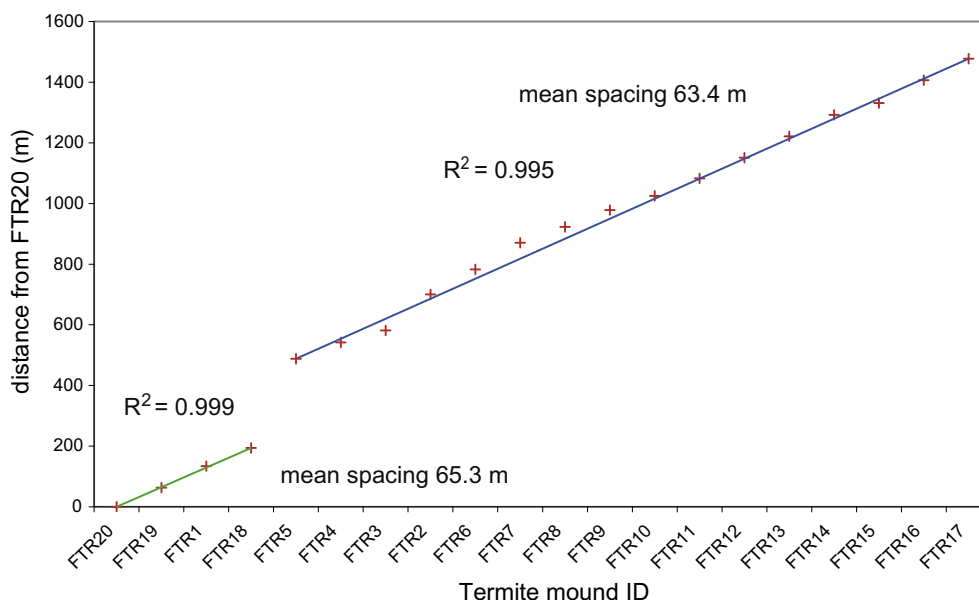

Fig. 9. Termite mound spacing plot as a function of the distance to FTR20, at the southwestern end of the Farshewa dyke. R^2 is the coefficient of determination.

to intrinsic coarser granulometry at grain scale, higher mechanical strength, and resistance to alteration. Heat accumulated during daytime is restituted at night more efficiently, which tends to regulate the diurnal temperature variations within the termite mound. On the other hand, dyke widespread fracturing tends to decrease its thermal inertia, which may counterbalance the high thermal inertia of the dyke blocks. Consequently, the role of dykes in terms of temperature regulation for the termite colonies remains unclear. The role of dolerite dykes as preferential sites for water drainage at surface and storage at depth appears to be the dominant factor for termite mound settlement.

4.2. Hydrological circuit

The water made available to the termites can follow three channel types, and can be stored in two reservoirs (Fig. 10). The channels include the Ayma river tributaries, two of which cut across the Farshewa dyke (between mounds FTR11–12 and FTR14–15, Fig. 8), the dyke fracture network (Winberg et al., 2003; Babiker and Gudmundsson, 2004), and the Ayma river. The two reservoirs are the main water table (Chernet, 1988), which outcrops at the

Ayma river, and the Farshewa dyke, as discussed below. West (1970) had proposed an interesting mechanism for *Macrotermes natalensis* access to water in Zimbabwe which is in part similar to the mechanism described here; we found it appropriate to reproduce it on Fig. 11. The water table is fed by the Abyssinian plateau on the East, the Qwara plateau on the North, and the Bagilte mountain on the South, all of which are drained by the Ayma river (Figs. 1c and 3). In the Farshewa dyke area, water comes from the Qwara plateau. During the rainy season, water infiltrates the dyke from the surface by runoff through Ayma river tributaries (Fig. 6), percolates downward along the dyke fractures, and forms an aquifer that feeds the Ayma water table. Water infiltrating the Qwara plateau slope above the dyke may also be trapped by the dyke conduit. The dyke is a bottleneck for water percolation toward the Ayma water table, water penetrating the dyke aquifer is temporarily stored within the dyke, which gradually fills up from the main water table upwards. After the rainy season, the water stored in the water table and the aquifer is gradually discharged through the Ayma river to the Dinder river and the Sudan lowlands (Fig. 3). Despite the large size of the Ayma river drainage basin, 2020 km² (data from Kohler and Krauer, 1996), its water table may dry almost completely, as suggested
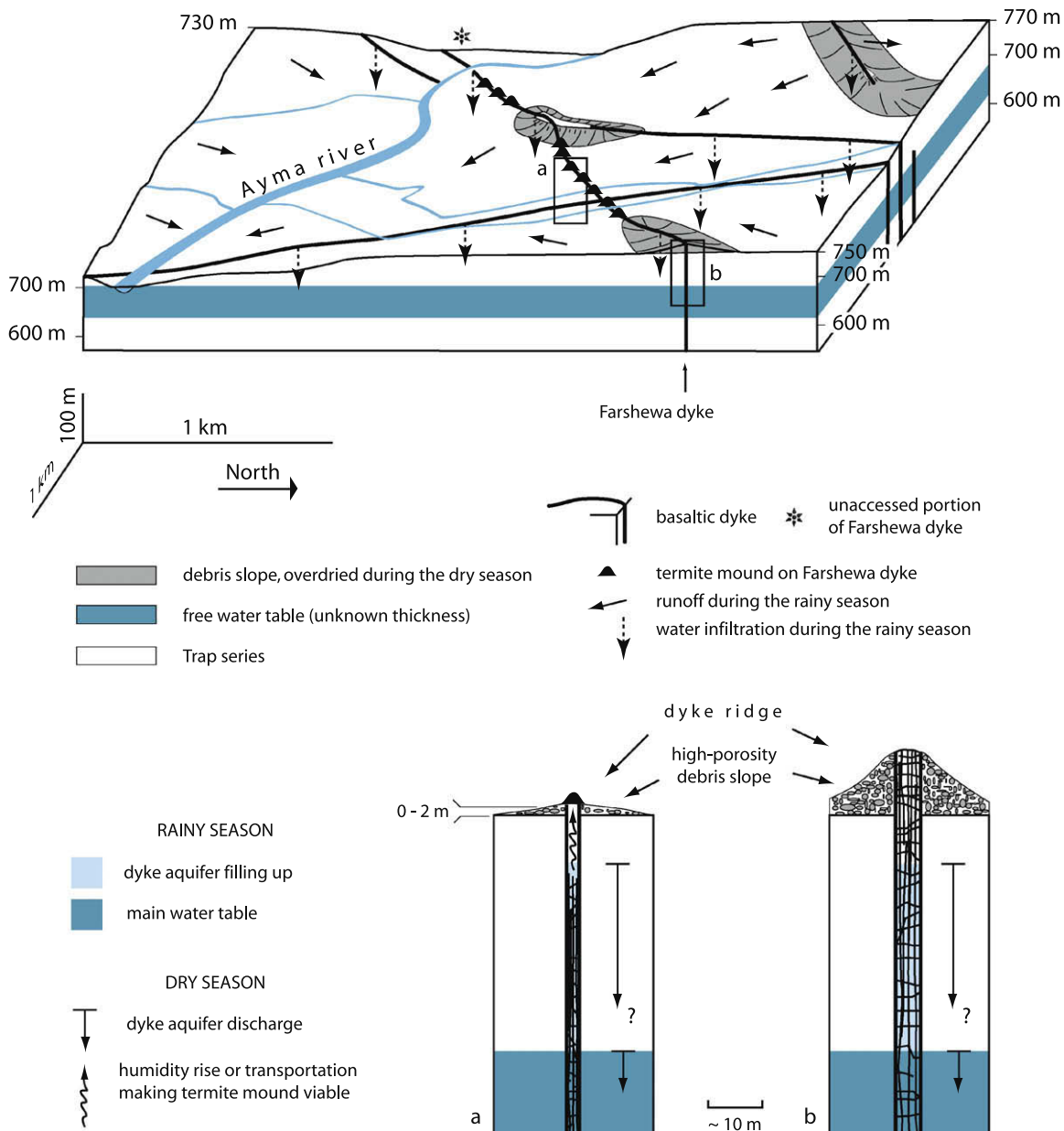
Fig. 10. Conceptual view of the hydrological system in the study area. The dykes other than the Farshewa dyke are from interpretation of satellite imagery. Termite mounds have also been observed along these dykes but their distribution could not be studied.

by our observations of a very low water level in various places along its course and the Dinder river course in January 2008 (Fig. 12). Settlement of termite colonies on the dykes of the Farshewa area demonstrates, however, that despite the length of the dry season, water availability in their aquifers remains higher than in any other geological setting. The Ayma river is located 20–30 m below the elevation of the Farshewa termite mounds (Fig. 4), which gives an idea of the vertical extent of the Farshewa aquifer thickness above the main water table. The role of the Farshewa dyke for termites may be compared to other examples of perched water tables filled in during the wet season and used by termites during the dry season in other regions of Africa (Boyer, 1975b; Turner, 2006).

4.3. Dependence of dyke ridge relief on termite mound distribution

Pomeroy (1977) reported dependence of termite mound distribution with ground elevation in Uganda, and ascribed this depen-

dency to the difference of atmospheric temperature. Here the elevation difference is not more than 20 m, which is not sufficient for a significant temperature dependence effect. It is suggested instead that the dyke ridge dries up more, and more rapidly than the surroundings because the debris slopes are much less consolidated than the host rock. Humidity within the dyke is therefore more rapidly evacuated through the debris slope, transforming the dyke ridge into a dry barrier between the ridge base and potential termite mounds.

For a dyke ridge relief up to 2 m, during the rainy season, colony survival is made possible in a mound located at the dyke top, at a short distance from the aquifer. Most termite species do not offer any resistance to desiccation below a relative humidity of ~90% (Grassé, 1984, pp. 589–593). During the dry season, colony survival requires a strategy to mitigate desiccation. Grassé and Noirot (1948) showed that *Psammotermes*, in Sahara, carry water upward from a water table located several metres below sand dunes, and a reliable depth of 23 m has been reported in Zimbabwe for
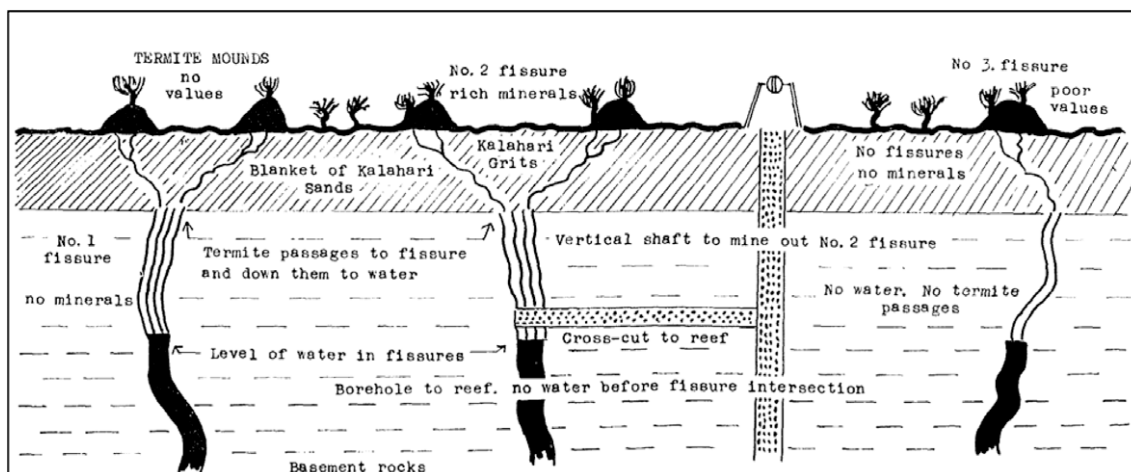
Fig. 11. Termite passages to water and gold in the area of the former Leopard gold mine (now part of the Jena Mines), near the village of Silobela, Zimbabwe, after West (1970). The dotted area is a gold-bearing quartz reef, the depth of its horizontal portion is 23 m (according to Watson, 1972). Main water table depth has been estimated to be 60–90 m (West, 1970). The basement rock below the Kalahari sands, of variable thickness, is fractured ("fissures" on the figure). These fractures are connected to the main water table at depth, they fill in during the rainy periods and withdraw during the dry periods. The depth of the top of this perched aquifer was at 27 m while Watson was investigating. The termites forage the sands and follow the fractures to access moisture. On the way back they carry gold if the reef is located along their pathway (the two mounds at the centre of the figure, note that Watson, 1972 disagrees with West on that issue). The behaviour of these termites (*Macrotermes natalensis*) with respect to water may be similar to the behaviour of the Farshewa dyke termites, the dyke fractures replacing the basement fractures, resulting in termite mound alignment along the dyke.

Fig. 12. The Dinder river 15 km downstream from its junction with the Ayma river, one of its tributaries (N12°01′38″ E035°51′59″, location on Fig. 1c). View is to the SW. The image was taken on January 15 h, 2008, at the middle of the dry season. The Dinder river drains major topographic reliefs, including parts of the Abyssinian and Qwara plateau as well as the Bagilte mountain. Water level is only a few tens of centimetres at most, and a trail in the background indicates that it is commonly used by small trucks. The river is probably completely dry at the end of the dry season, the relief of the terraces suggests the top level of the water table may decrease by 2 m or more compared to the rainy season.

Odontotermes latericius (Watson, 1972). By analogy, the suggestion can be made that the Farshewa termite mounds are kept wet during the dry season by water or moist food ingestion close to the water table level and restitution to the mound (e.g., Grassé, 1984, pp. 595–597). Alternatively, the termites may leave their mound during the dry season and migrate downward along the dyke fractures in order to stay in a wet, though drained, environment, as reported for *Cubitermes* in northern Ivory Coast and eastern Republic of Guinea, and *Trinervitermes* in the Senegal savannas (Grassé and Noirot, 1948; Bouillon, 1970; Grassé, 1984, pp. 593–594). *Trinervitermes* have also been identified in Ethiopia south of the study area (Illubabor and Gamu-Gofa, Cowie et al., 1990). In addition to finding more appropriate microclimatic conditions, migration at depth would also protect the termites against the frequent forest fires. Other strategies for mitigating the effects of moisture shortage have been developed by some termite populations, and include seasonal reduction of termite body-water content at the cost of restriction of the termite reproduction period to the rainy season (van der Westhuizen et al., 1985), building small subterranean water bags for use during long dry seasons (Leprun, 1976), and symbiotic life with fungus cultivated within the mounds (e.g., Aanen and Eggleton, 2005). Mounds of *Microtermes aethiopicus*, a fungus-growing termites, have been described in southwestern Ethiopia 275 km away from the Farshewa area (Barnett et al., 1988).

For dyke ridge relief more than a few metres high, the vertical extent of the overdried rock is too large for any of these mechanisms to be efficient, which makes any potential termite mound not viable.

4.4. Hypotheses for colony migration along dyke and constant mound spacing

The portions of the Farshewa dykes displaying mounds are homogeneous in terms of lithology and fracturing, there is no clear intrinsic dyke property that would encourage periodic termite mound settlement along dyke strike. A detailed investigation of mound spacing has been carried out in relation to ridge relief height for heights ⩽2 m in order to determine if spacing is dependent on dyke topography variations, given that the lower the topography, the thinner the dry barrier during the dry season. The distance between a termite mound and its two adjacent mounds was measured and plotted against its own ridge relief (Fig. 13). There is no correlation observed, suggesting that termite mound spacing is not a function of dyke ridge relief. However, the number of data points is too small to demonstrate this result, which needs to be confirmed with more accurate height measurements.

It may be more likely that constant termite mound spacing is due to factors pertaining to the termite populations themselves. A new colony may develop when conditions that were suitable for a small colony become unsuitable for a larger one. Of crucial importance for a colony are maintaining constant atmospheric conditions (air composition, temperature, moisture) within the
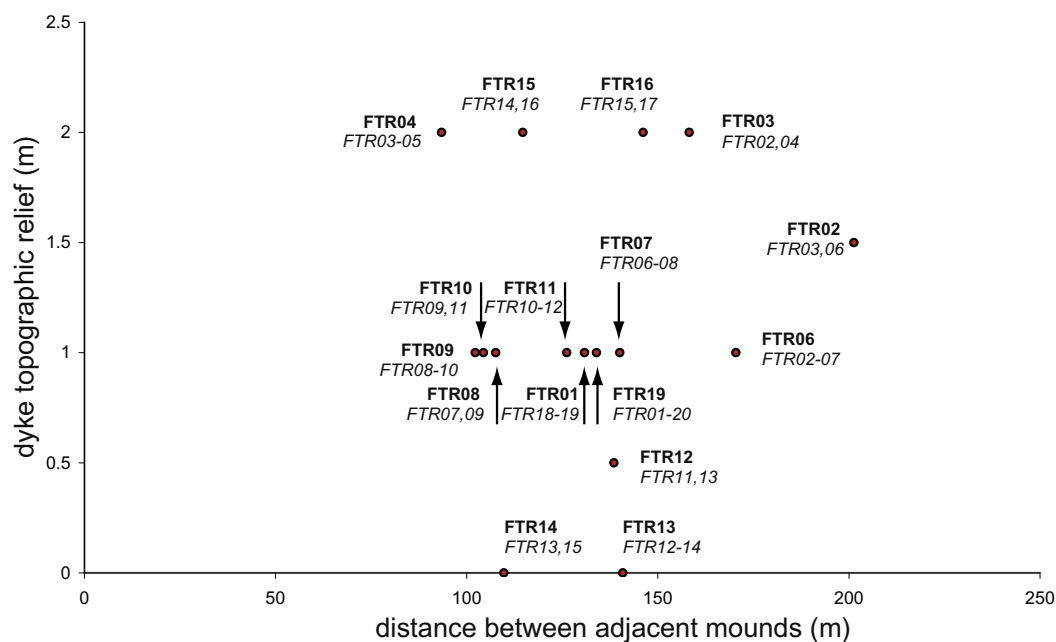
Fig. 13. For any given mound (in bold, e.g., FTR07), the spacing between the two adjacent mounds (in italic, e.g., FTR06 and FTR08) cannot be correlated with the topographic relief of the dyke (at FTR07). Error on distance and dyke topographic relief is ±5 m and ±0.3 m, respectively.

mound, ensuring that the quantity of food required for the growing population is available, as well as the mound building materials required for mound extension. If any of these conditions is no longer met the colony will spread to a new settlement site. Colony migration for inadequate temperature and moisture conditions, as well as food shortage, have been discussed by Basalingappa (1974), and for clay shortage by Meyer et al. (2000). Below is discussed how much these conditions are critical in the study area.

(1) The conditions for atmospheric regulation are very likely to be similar everywhere along the low-relief portions of the dyke, making the search for more appropriate conditions along the dyke to find more appropriate conditions pointless. Moreover, the variety of the described responses of termite colonies to periodic dryness, listed in the previous section, does not include horizontal migration. (2) Availability of food for the growing colony may be an issue if the renewal rate of food, e.g., leaves, is slower than the rate of population growth. The new colony would settle at a minimum distance from the first mound determined by the requirements for both the old and new colonies to feed. However, this solution would not be appropriate for more than a couple of mounds because practically, the mounds that are surrounded by two mounds or more would need to migrate over distances of hundreds of metres, much more than the migration distances reported in the literature (e.g., Noirot et al., 1986). (3) One of the key building materials for mound building is clay, which mixed with termite saliva, cements mound internal and external walls (Bodot, 1967a; Bachelier, 1977; Boyer, 1982) and contributes to maintaining appropriate termitary moisture (Lee and Wood, 1971, p. 62). Termite mound density on latosol was shown to be directly proportional to the abundance of clay in Congo (Sys, 1955). The proportion of clay in the habitacle of *Macrotermes*, one of the genera expected to be represented in the study area (Krishna, 1970; Cowie et al., 1990), is ca. 10% (Bouillon, 1970). These works show that the maximum size of a mound is governed by clay or soil availability in regions of thin soil cover (Grassé and Noirot, 1961; Meyer et al., 1999); a new mound needs to be founded elsewhere once this maximum size is attained. This is specifically the case in the study area, where soil is thin or absent, and the colonies are

found to be small. The morphoclimatic conditions for soil development are similar along the dyke, so that the available quantity of mound building material does not vary appreciably along-strike, a possible explanation for the observation that the mounds have all the same size. Therefore, we suggest that clay availability is the main reason for founding new colonies along the Farshewa dyke. Clay may be found at the surface, resulting from basaltic flow alteration, but may also result from alteration of dyke fractures down to several metres. *Macrotermes* were found to transport clay from a depth of 12 m in Central African Republic (Grassé, 1984, p. 210).

Termite mounds are frequently rather homogeneously distributed in the field (e.g., distribution of *Bellicositermes subhyalinus* in Central African Republic, see the aerial photograph displayed in Bouillon and Kidieri, 1964, either photograph 1 in Boyer, 1973 or figure 190 in Grassé, 1984; *Cubitermes fungifaber* in Grassé, 1984, p. 569; *Hamitermes vitiosus* on Fig. 8 of Ratcliffe et al., 1962; *Amitermes vitiosus* on Fig. 4 of Melchiorre et al., 2006). Although the density of mounds per hectare is sometimes given, spacing does not appear to have been studied in itself. For *Cubitermes fungifaber*, mean spacing between successively built mounds (i.e., independently of the general spatial distribution of mounds in the studied area) has been observed to be 3.2 m (Noirot et al., 1986), but scattering is high, ranging between 1 and 5 m. Migration distances for *Anoplotermes* were observed to be 10–15 m (Grassé and Noirot, 1951). Sattaur (1991) and Miller et al. (1994) have also reported parallel, 0.4 m (Miller et al.) to 2 m (Sattaur) high *Odontotermes* ridges several hundred metres long (from high-resolution satellite imagery made available by DigitalGlobe™ through Google Earth, 2009) in Botswana, displaying a regular spacing of ∼50 m. Ridge orientation is clearly influenced by the local hydrologic patterns. Similar to the Farshewa dyke mounds, these ridges are also associated with much higher vegetation density than the surroundings (Fig. 2 of Miller et al., 1994, and imagery provided by DigitalGlobe™).

If the factors governing mound distribution homogeneity or heterogeneity in these cases have not been clearly discussed, distribution of constant-spaced mounds along a single trend such as
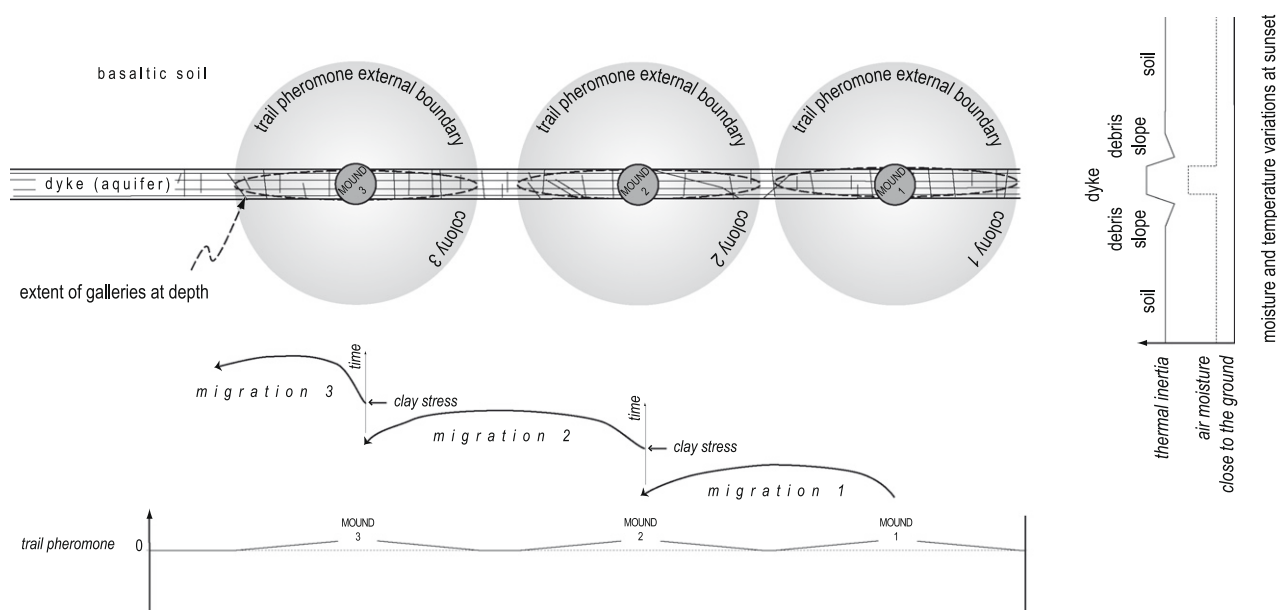
Fig. 14. Termite mound settlement and constant spacing may result from migration in response to clay shortage. The location of the mound of the migrant colony is determined from a range of possible factors, the most important of which include dyke trend, geographical extent of trail pheromone of the termite colony left behind (by either swarming, sociotomy, or following dyke fractures), thermal inertia contrast, and difference in moisture conditions between dyke and surrounding basaltic soil. The extent of the trail pheromone zones is restricted by the dyke margins at depth, but can spread in every direction at surface.

in the Farshewa dyke case had never been described. We suggest that constant spacing of the Farshewa mounds may result from a combination of two factors. One of the strongest constraints for a termite population to find a new settlement site is related to the pheromone emission of the colony, especially the trail pheromone (e.g., Noirot, 1969; Tschinkel and Close, 1973) used by most termite genera for finding their way back to their termitary. A new colony can be founded only at a distance from the parent colony beyond which there is no pheromone (Fig. 14). On the ground, this distance can be estimated to tens of metres. *Longipeditermes longipes* in Borneo have been found marching along open-air trails for distances as long as 14.5 m (Hoare and Jones, 1998), 39 m (Gray and Dhanarajan, 1974) from their nest to feeding sites. Remarkably, trails commonly 100 m long, exceptionally more than 300 m long, were measured for *Hospitalitermes sharpi* (Jander and Daumer, 1974). Trail pheromone fade-out time is highly variable and depends on circumstances, from hours to 1 year or more in experimental conditions (Traniello, 1982; Runcie, 1987). On the ground, this time may be shortened because of permanent surface reworking by rain, wind, and other agents. However, at depth these pheromones, whose network must follow the foraging gallery network, are expected to be much more persistent. The shape and dimensions of the gallery network may therefore constrain the minimum distance between mounds of different colonies more safely than the termite pathways above ground. The radial distance from the central nest over which subterranean galleries built by *Baucaliotermes hainesi* in Namibia have been observed in 15 m (Tschinkel, in press). Ratcliffe and Greaves (1940) have studied a gallery system radiating from a *Coptotermes lacteus* mound until a distance of 30 m, a distance that would give 60 m as the minimum distance for a new independent colony to settle (see Lee and Wood, 1971, for a review of gallery systems). This distance is close to the mean spacing, 63 m, measured or the Farshewa mounds.

Another constraint may be the maximum distance at which new colony can be founded. Foundation of a new colony may be achieved either by swarming (e.g., Basalingappa, 1974) although the primary objective of swarming is nuptial (Grassé, 1942, 1984,

pp. 65–132), by sociotomy (colony fragmentation by migration on the ground of termite groups in which all the casts are represented and aiming at founding a new settlement site; Grassé and Noirot, 1951; Basalingappa, 1976; Grassé, 1984, p. 135–138), or by underground migration along galleries (Noirot et al., 1986). In case of swarming, the maximum distance alate can fly ranges between a few tens of metres (Bodot, 1967b) and kilometres (Nutting, 1969) or more, depending on both species and wind conditions (Ratcliffe et al., 1962, p. 22). The measured mean mound separation distance of 63 m along the Farshewa dyke is consistent with this range, which is obviously not much constraining. In case of sociotomy, migration direction along the Farshewa dyke would be explained by the difference in surface moisture between the dyke and the surrounding flow, a difference that alates are sensitive to during swarming (Grassé, 1942), in air moisture above the dyke and the flow, and in thermal inertia, the contrast between dyke and flow being enhanced by the end of the day, a period of preferred swarming for a number of termite species (Nutting, 1969). In case of underground migration of a termite group, the termites would naturally follow the dyke fractures, but little information is available as to the maximum distance they would travel. The underground *Cubitermes fungifaber* migrants studied by Noirot et al. (1986) have migrated a few metres only.

Mound spacing may therefore be a trade-off between the minimum distance required to escape the pheromone emissions of the older colony, and the maximum distance a termite migrating group can cover, either by the air (alates), on the ground, or underground.

The trail pheromone constraint on mound spacing is considered to be strong because it is well documented, the maximum migration distance constraint being more hypothetical. Fig. 14 illustrates and synthesizes the parameters that are thought to play a possible role in termite mound spacing along the Farshewa dyke.

4.5. Additional remarks

The observed mounds are dome-shaped (Fig. 5a). Termite mound morphology depends on environmental conditions more

than termite genus. Dome-shaped mounds are more frequently observed where the external temperature is cool and rather equable, such as in a dense forest, than in warmer shrub savanna, where diurnal as well as seasonal temperatures are more fluctuating, resulting in cathedral-type mounds displaying ridges and turrets (Korb and Linsenmair, 2004). The Farshewa dyke environment is made of woodland with scattered trees (see Figs. 5a and 7c), which is an intermediate situation. Although we have not visited the dyke during the rainy season and could not evaluate the vegetation cover at that time of the year, the observed dome shape may reflect the intense termite activity during the rainy season, during which temperatures are lower and more equable than during the dry season. During the dry season, the architecture of the termite mounds would not evolve because of the reduced activity induced by the hydric stress or by migration of the population at depth.

The dyke setting of the Farshewa mounds differs significantly from most termite mound building contexts previously described, in that soil is absent below the mounds, which are build on hard rock, preventing the termites from digging galleries. The termite population totally relies on the dyke fracture network for access to moisture. Due to the absence of a well-developed soil, and to dyke mechanical strength, termites are unable to tunnel like they would do in e.g., clays, and it is likely that dyke fracture network controls subterranean gallery geometry, resulting in a gallery network optimisation that is different from theoretical models that consider a homogeneous substrate (Perna et al., 2008).

5. Conclusion

Closely-spaced (63 m) termite mounds have been built on a dyke at a topographic level tens of metres higher than the regional water table surface. Because of the half-year long dry season, this suggests that the dyke may be a permanent aquifer. Other basaltic dykes nearby (Fig. 7) are in a similar setting and those that we could observe in the field do also focus the termite mounds. The Ethio-Sudanese plain in Ethiopia displays thousands of basaltic dykes. Many remote villages do not have access to potable water, which could justify that more detailed studies of relationships between dykes, groundwater, and termite mounds be undertaken.

The relative dyke ridge relief above the surrounding area is between 0 and ∼20 m, but the termite mounds are built where it is not more than 2 m. This suggests that during the dry season, desiccation of the dyke ridge when it is higher than a few metres generates a dry barrier that discourages termite colonization. Dyke ridge drying is increased by the higher dyke debris slope porosity compared to the porosity of the host rock. For low dyke ridge relief, possible mechanisms for water collection in the termite mound include water transportation by the termites, and the possibility for the termites to endure limited seasonal desiccation or mitigate desiccation by growing fungus. Alternatively, the termite populations may migrate at depth within the dyke to get closer to the dyke aquifer.

Mound spacing along the Farshewa dyke is remarkably regular. Colony migration is likely not related to along-strike variations of dyke properties, rather it may be related to intrinsic termite population behaviour, such as the need to space out from the former colony when the colony size becomes critical on mound building material supply. Constant spacing is thought to result from the requirement to migrate along the dyke at a distance that is long enough to be liberated from the pheromone emissions of the older colony, and short enough to be easily reached by the migrants.

Future field work aiming at identifying termite genus and refine the interpretations presented in this paper is being considered.

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