RESEARCH ARTICLE

Relation between termite numbers and the size of their mounds

G. Josens · K. Soki

Abstract This article provides a meta-analysis of quantitative data available in literature regarding the relation between termite numbers and the volume of their mounds for 24 species belonging to 13 genera. The leading question behind this analysis is: "how do the respiratory gas exchanges regulate the size of termite mounds?" This question is answered through the analysis of the log–log regression between the volume of the mound and the number of inhabitants. The most confident data support the hypothesis of a respiratory regulation that can be achieved through a relation between the termite numbers and (1) the volume of their mounds (slope of the regression near 1, *Noditermes*), (2) the surface of the outer walls of their mounds (slope of the regression near 0.67, Termitinae and *Nasutitermes*) or (3) a compromise between the surface of the outer walls of their mounds and some linear structures of their nests (slope of the regression between 0.67 and 0.33, *Trinervitermes* and *Macrotermes*). The way this is achieved is linked with the architecture of the mound. A confident relation was found between the number of individuals and the epigeal volume of their mounds for 18 species for which the most reliable data were provided. Three more accurate models are proposed for estimating the termite population based on the nest material and architecture and on the size of the termites.

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Introduction

The populations of mound-building termites have been estimated for various purposes, mainly in studies of nest size regulation and of the quantitative role of these insects in ecosystem functioning (Wood and Sands, 1978). Porter and Hawkins (2001) failed to find an influence of latitude and annual evapotranspiration on termite nest size. Wiegert and Coleman (1970) found a significant linear relation between the number of individuals in *Nasutitermes corniger* colonies (reported as *N. costalis*: see Scheffrahn et al., 2005) and the surface of their nests, suggesting that respiration was a regulatory parameter of their nest size. Since this study, other works have either confirmed or invalidated this point of view (Josens, 1972, 1983; Han and Lepage, 1991; Soki, 1994).

The nests built by several *Macrotermes* spp. deserve more attention and several mechanisms have been proposed for explaining the function of their large, impressive mounds. The sensitivity of their symbiotic fungi to temperature suggests a thermoregulatory function with some constraints imposed by the necessity of gas exchanges, resulting in different architectures in savanna and forest environments (Korb and Linsenmair, 1999). However, the way these gas exchanges occur, and whether they are internally or externally induced, is still a matter of dispute (see Korb, 2003).

Amongst the various functions of the epigeal termite mounds, their size is regulated in some way by the necessity of sufficient respiratory gas exchanges and by the limiting factor of these exchanges (Noirot and Darlington,

2000). Such gas exchanges can actually be achieved by two mechanisms: molecular diffusion and gas convection. It is obvious that both of them can be influenced by differences in pressure induced by wind (Turner, 2001), but the mounds should be able to fulfil their respiratory function even when there is no wind.

If the necessity of gas exchanges is combined with the architecture of the mounds, three diagrams of regulation between the size of the nests and their populations can be expected: (1) *volume-regulated mounds* if gas exchanges are minor constraints, (2) *surface-regulated mounds* if the limiting parameter is a molecular diffusion, mainly through the outside wall, and (3) *line-regulated mounds* if the limiting parameter is gas convection.

This paper provides a meta-analysis of scattered data and tries to check which of the diagrams above are most appropriate to the mound-building termites.

Materials and methods

Since most of the publications provide information about population size and mound volume (rarely mound surface, but see Korb and Linsenmair, 1998, for a simple and clever way of measuring the true surface of a complex mound), we used those data and log–log regressions were computed with "the number of sterile individuals (larvae included)" as dependent variable and "the volume of the epigeal part of their nest" as predictor variable. Assuming that all mounds of a given species or genus have the same general shape, the slope of the linear regression should provide a clue to the relation between both factors. The closer to 1.00, the better the termite number should fit the volume, suggesting possible regulation by the number of individuals (and not by gas exchanges). The closer to 0.67, the better the termite number should fit the outer surface of the nest, suggesting a role played by a diffusion process through a surface (as respiratory gas exchanges), and a slope of 0.33 would suggest a possible relation between the number of termites and some linear dimension of their nests and a process, as gas convection, linked to it.

All the data used depend on two sensitive assessments: (1) sampling of the total population, and (2) calculation of the volume of the mound.

Population assessment

The sampling methods reported in literature vary chiefly depending on the size and the location of the mounds. All arboreal nests and small terrestrial mounds ($<20 \ dm^3$) are generally removed completely (including their subterranean part) in one go and the termites are hand-sorted and their number counted. Larger terrestrial mounds (between about 20 and 200 dm^3) are generally surrounded by a circular trench and subsequently lifted and broken to pieces. The termites are then either hand-sorted or extracted by a flotation method and the number of termites is generally assessed by sub-sampling. The largest mounds ($>200 \ dm^3$) are opened to remove the central structure through a perpendicular trench, sometimes after having surrounded the mound with a ring-shaped trench; however, the time required for digging these trenches is critical since such mounds generally have broad subterranean galleries allowing the termites to run away from their mounds. Digging the ring-shaped trench took 1–3 days in the study by Meyer et al. (2000). Darlington (1984) estimated that 50–90% of the termites could escape the sampling by this evacuation behaviour, leading to an underestimation up to an order of magnitude. Therefore, the large-mound termites have to be immobilized before digging into the nest. Darlington (1984 and subsequent papers) achieved this by fumigation procedures adapted to the inner architecture of the mounds.

Volume assessment

The volume assessment methods reported in literature depend chiefly on the species and the shape of their nests. Some arboreal or semi-arboreal nests have been considered as ellipsoids (*Nasutitermes*, Thorne, 1982; *Acidnotermes praus* and *Astalotermes quietus*, Soki, 1994) or hemiellipsoids (*Constrictotermes*, Vasconcellos et al., 2007) and small terrestrial mounds as cylinders (*Thoracotermes*, Soki, 1994; some *Cubitermes*, Han and Lepage, 1991) or as stacks of geometrical volumes (*Cubitermes*, Soki and Josens, 1996: *Trinervitermes*, Josens, 1972). Large nests have been considered as cylinders or cones (*Odontotermes*, Singh and Singh, 1981; *Macrotermes*, Collins, 1981), paraboloids of revolution, cones or concavely tapered cones (Meyer et al., 2000).

In several cases, literature does not mention the volume of the terrestrial mounds, but provides some measurements [height and circumference or diameter(s) at the base] from which a volume can be assessed. After various trials, we used preferentially a truncated cone capped with a smaller cone, provided that a sketch of the mound was available (Fig. 1). The volume estimated in this way is often close to that computed with the formula of a paraboloid of revolution, but offers more flexibility. The volume assessment using a truncated cone capped with a smaller cone was applied to the nests of *Nasutitermes exitiosus* (Holdaway et al., 1935; Gay and Wetherley, 1970), *Odontotermes obesus* (Gupta, 1953), *Macrotermes ukuzii* (on the average data from six nests, Rohrmann, 1977), *Macrotermes michaelseni* (Darlington, 1986; Darlington and Dransfield, 1987; Darlington, unpubl. data), *Macrotermes subhyalinus*
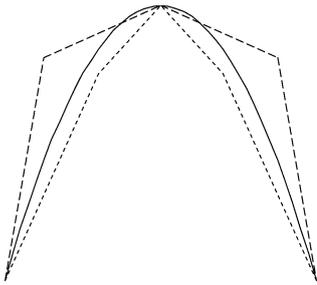
Fig. 1 Once the basal diameter and the height are known, only one paraboloid of revolution can be drawn (*solid line*); however, several truncated cones capped with smaller cones can be drawn (two examples in *dotted lines*)

(Darlington, 1990) and *Macrotermes jeanneli* for the basal hump alone, the pillar being neglected (Darlington et al., 1992).

Generally, the section at the base of the mound is more or less oval shaped, and several authors express it in terms of the larger and smaller diameters (but sometimes only as a circumference). A rigorous calculation of the mound volume should take both diameters into account; however, a mean value between both diameters generally does not induce a large error. If the ratio of larger/smaller diameter is smaller than 1.5, then the error in replacing ellipses by circles is negligible (<5% on the surface of the base and hence on the volume of the mound). However, for higher ratios, ellipses should be computed for the base instead of circles.

In some other cases, literature gives the weight of the mounds, from which a volume can be deduced provided that a specific mass is available. For *Cubitermes sankurensis* (Bouillon and Lekie, 1964), the termite numbers were related to their mound weights, including the basements. To convert them into epigeal volumes, 1/4 of the mass was deducted, corresponding to the basements of the mounds, and 1/10 of the remaining mass was deducted to allow for the water content (Bouillon, pers. comm.). The remaining mass was converted into volume using a specific dry mass of 1.23 kg/dm^3, inferred from the measurements of some *C. sankurensis* nests of the collection of the Royal Museum of Central Africa, Tervuren, Belgium. For *Anoplotermes banksi*, the nest fresh weights of which are figured in Martius and Ribeiro (1996), a specific mass of 1.20 kg/dm^3 was measured from a fresh nest collected in French Guiana by Y. Roisin. For the *Dicuspiditermes nemorosus* type A (pillar-shaped) nests, a specific mass of 1.25 kg/dm^3 could be inferred from the average nest measurements (Matsumoto, 1976) and the same specific mass was applied to the type B nests. For the *Homallotermes foraminifer* carton nests, a specific mass of 0.95 kg/dm^3 could be inferred from the average nest measurements (Matsumoto, 1976).

In this study, we used the total sterile populations (unless quoted) and the epigeal volumes of their nests; the hypogeal volumes were thus ignored considering that gas exchanges occur mainly through the epigeal structures. Some data were discarded if they appeared to relate to outliers (small populations in large, possibly senile nests).

Statistical analyses

The regressions between populations and nest volumes were computed on log_{10}-transformed data. The strength of the regression was assessed by the determination coefficient, which was used as a dispersion indicator and as a clue for the presence of outliers (and not for assessing the confidence of the sampling).

The comparison of the regression slopes with theoretical slopes (0, 0.33, 0.67 and 1) was performed with a Student's *t* test. The slopes and elevations of regression lines were also compared with Student's *t* tests (Zar, 1999). When ranges are quoted, 10–90 percentile ranges are used instead of the full ranges to avoid extreme values. In the figures, 90% concentration ellipses were generated with Statistica® 8.

Results

The log–log relations between the total sterile populations and the epigeal volumes of their nests for 24 mound-building species, belonging to 13 genera, are listed in Table 1.

Termitinae

The slope ($b = 1.01$) for *Noditermes cristifrons* (Wasmann) is the closest to 1 but with a moderate confidence ($r^2 = 0.49$). Actually, the slope cannot be distinguished either from 1 or from 0.67 (Soki, 1994: Table 5.27).

The slopes for three species of *Cubitermes* are closer to 0.67 and actually are significantly different from 0, 0.33 and 1, but not from 0.67. This state is achieved with the highest confidence ($b = 0.66$, $r^2 = 0.89$) regarding *Cubitermes fungifaber* (Sjöstedt) (Han and Lepage, 1991: Table 1). In *Cubitermes speciosus* Sjöstedt, the slope ($b = 0.79$) is somewhat steeper, but with a moderate confidence ($r^2 = 0.59$) (Soki and Josens, 1996: Table 1). In *Cubitermes sankurensis* Wasmann, the slope ($b = 0.59$) is somewhat gentler, but with a low confidence ($r^2 = 0.26$) (Bouillon and Lekie, 1964: Tables 1, 3, 5); from the total series of 58 data for this species, two obvious outliers (very small numbers of individuals, possible senile societies) were discarded.

Table 1 Relations between termite numbers and mound volumes: log–log linear regressions, determination coefficients and t tests against theoretical slopes

Species	n	Regression[a]	r^2	Test slope $= 0.00$[b]	Test slope $= 0.33$[b]	Test slope $= 0.67$[b]	Test slope $= 1.00$[b]	Comment	Reference
Termitinae									
Noditermes cristifrons	24	Log N = 3.33 + **1.01** log V	**0.49**	***	**	NS	NS		Soki, 1994
Cubitermes fungifaber	40	Log N = 3.81 + **0.66** log V	**0.89**	***	***	NS	***		Han and Lepage, 1991
Cubitermes sankurensis	56	Log N = 3.71 + **0.59** log V	**0.26**	***	*	NS	**	Two nests discarded	Bouillon and Lekie, 1964
Cubitermes speciosus	49	Log N = 3.36 + **0.79** log V	**0.59**	***	***	NS	*		Soki, 1994; Soki and Josens, 1996
Dicuspiditermes nemorosus	23	Log N = 4.46 + **0.55** log V	**0.62**	***	*	NS	***	One nest discarded	Matsumoto, 1976
Homallotermes foraminifer	11	Log N = 4.02 + **0.66** log V	**0.67**	**	NS	NS	NS		Matsumoto, 1976
Thoracotermes macrothorax	15	Log N = 4.46 + **0.25** log V	**0.21**	NS	NS	**	***	Lack of small nests in the series	Soki, 1994
Nasutitermitinae									
Trinervitermes geminatus	12	Log N = 3.87 + **0.51** log V	**0.92**	***	***	***	***		Josens, 1972
+ *T. togoensis*	+2								+ Josens, 1972
+ *T. trinervius*	+7								+ Lepage, 1974
+ *T. rhodesiensis*	+2								+ Ferrar, 1982
Constrictotermes cyphergaster	12	Log N = 3.76 + **0.60** log V	**0.29**	NS	NS	NS	NS	Larvae excluded from the population count	Vasconcellos et al., 2007
Nasutitermes exitiosus	4	Log N = 4.95 + **0.46** log V	**0.42**	NS	NS	NS	NS		Holdaway et al., 1935
	+1								+ Gay and Wetherley, 1970
Nasutitermes corniger	12	Log N = 4.55 + **0.80** log V	**0.74**	***	*	NS	NS		Thorne, 1982
Apicotermitinae									
Astalotermes quietus	7	Log N = 3.27 − **0.63** log V	**0.15**	NS	NS	NS	NS	Paradoxical negative regression	Soki, 1994
Acidnotermes praus	3	Log N = 3.19 − **0.64** log V	**0.59**	NS	NS	NS	NS	Paradoxical negative regression	Soki, 1994
Anoplotermes banksi	5	Log N = 4.73 + **0.67** log V	**0.78**	*	NS	NS	NS	Two nests discarded	Martius and Ribeiro, 1996
Macrotermitinae									
Macrotermes michaelseni	35	Log N = 5.09 + **0.45** log V	**0.84**	***	**	***	***	Nest fumigated; Two nests discarded	Darlington, 1986; Darlington and Dransfield, 1987; Darlington, unpublished data
Macrotermes jeanneli	7	Log N = 4.87 + **0.44** log V	**0.95**	***	NS	**	***	Nest fumigated	Darlington et al., 1992
Macrotermes subhyalinus	13	Log N = 4.45 + **0.52** log V	**0.91**	***	**	*	***	Nest fumigated	Darlington, 1990
Macrotermes bellicosus	5	Log N = 4.29 + **0.40** log V	**0.67**	***	NS	NS	***	Populations possibly underestimated; One nest discarded	Lepage, 1974; + Collins, 1981
	+18								

Table 1 continued

Species	n	Regression[a]	r^2	Test slope = 0.00[b]	Test slope = 0.33[b]	Test slope = 0.67[b]	Test slope = 1.00[b]	Comment	Reference
Macrotermes natalensis	7	Log N = 1.52 + **0.96** log V	**0.85**	**	*	NS	NS	Populations underestimated	Meyer et al., 2000
Odontotermes obesus + O. redemanni	12	Log N = 2.57 + **0.68** log V	**0.97**	***	***	NS	NS	Populations underestimated	Singh and Singh, 1981
Odontotermes obesus	7	Log N = 3.39 + **0.62** log V	**0.57**	*	NS	NS	NS	Populations possibly underestimated	Gupta, 1953

[a] Logarithm base 10, N = number of individuals, V = epigeal volume in dm^3

[b] *NS* not significantly different from the slope tested ($P > 0.05$), * significantly different ($P < 0.05$), ** very significantly different ($P < 0.01$), *** highly significantly different ($P < 0.001$)

In *Thoracotermes macrothorax* (Sjöstedt), the slope was significantly different from 0.67 and 1, but not from 0.33 or 0 (i.e. absence of a significant correlation), with a very low confidence ($r^2 = 0.21$) (Soki, 1994: Table 5.40).

Dicuspiditermes nemorosus (Haviland) occurs in two morphologically different nests (types A and B), the regression lines of which were compared (slopes and elevations) and did not differ significantly from each other. All the nests were thus pooled. The slope of the resulting regression ($b = 0.55$) is significantly different from 0, 0.33 and 1, but not from 0.67, with a fairly high confidence ($r^2 = 0.62$) (Matsumoto, 1976: Table 4). From the total series of 24 data, one was discarded because the number of larvae was not mentioned and thus the total number of individuals could not be computed.

In *Homallotermes foraminifer* (Haviland), there is a fairly high confidence ($r^2 = 0.67$); however, with only 9 df the slope ($b = 0.66$) is significantly different from 0, but not from 0.33, 0.67 or 1 (Matsumoto, 1976 Table 4).

Apicotermitinae

The three soldierless species show paradoxically consistently negative slopes. In each of the three species, the largest nests contain proportionally few termites; however, the correlation is not significant for any of them. To remove negative correlations, at least 30% of the points of each species should be considered as outliers. This was done for one of the three species.

In *Anoplotermes banksi* Emerson, the negative correlation is due to the two heaviest nests, which could have been in decline despite their high percentage (>50%) of larvae (Martius and Ribeiro, 1996: Tables 1, 2). If those two mounds (out of seven) are discarded, the regression becomes significant and positive ($b = 0.68$), with a high confidence ($r^2 = 0.78$).

Nasutitermitinae

The nests of most *Trinervitermes* species display similar shapes and architectures; thus 12 mounds of *T. geminatus* (Wasmann) and 2 of *T. togoensis* (Sjöstedt) (Josens, 1972: Table 44), 7 of *T. trinervius* (Rambur) (Lepage, 1974: Table 41) and 2 of *T. rhodesiensis* (Sjöstedt) (Ferrar, 1982: Tables 4, 5) were pooled and produced a resulting slope of 0.51 with a very high confidence ($r^2 = 0.92$). This slope is significantly different from the four theoretical slopes tested and is situated between 0.33 and 0.67.

The regression for *Constrictotermes cyphergaster* (Silvestri) is based on the adult sterile population (the larvae that might have been confused with those of the inquilines genus, *Inquilinitermes*, have not been figured) and has a low confidence ($r^2 = 0.29$) with a slope ($b = 0.60$) that

cannot be distinguished from any of the four theoretical slopes tested (no significant correlation) (Vasconcellos et al., 2007: Table 1).

In *Nasutitermes exitiosus*, four items of data come from nests of almost the same sizes with rough estimates of the populations (Holdaway et al., 1935: Tables 1, 3) and from one exceptionally large mound (Gay and Wetherley, 1970: Table 1). All these mounds were sampled in rather cold conditions when the termites were said to be concentrated in their nests and had very little mobility. However, the slope ($b = 0.46$) of such a sample (absence of small nests), with only three df, does not differ significantly from any of the four theoretical slopes tested (i.e. absence of significant correlation), and the regression has a rather low confidence ($r^2 = 0.42$).

In *Nasutitermes corniger* (Motschulsky), the slope of the regression ($b = 0.80$) is significantly different from 0 and 0.33, but not from 0.67 or 1, with a fairly high confidence ($r^2 = 0.74$); (Thorne, 1982: Table 1).

Macrotermitinae

The epigeal mounds of the Macrotermitinae can be very large, and hence are difficult to sample accurately. Three species were sampled after fumigation and will be taken as references. These three species, *Macrotermes michaelseni* (Sjöstedt), *M. jeanneli* (Grassé) and *M. subhyalinus* (Rambur), show consistently very gentle slopes located between 0.33 and 0.67, with high or very high confidences, and are significantly different from the four theoretical slopes tested (with one exception).

The data for *M. michaelseni* ($b = 0.45$, $r^2 = 0.84$) come from Darlington (1986: Tables 3, 4), Darlington and Dransfield (1987: Tables 1, 2), and for the mound dimensions, from Darlington, personal communication. From the so-called "short data set" (Darlington and Dransfield, 1987), two nests were discarded: one of them because it was totally hypogeal and the second because it was a very young society established in an old, large nest. In *M. jeanneli* (Grassé), the volume of the chimney, which was not inhabited, was not counted in the volume of the mound. The slope ($b = 0.44$, $r^2 = 0.95$) is not significantly different from 0.33 (Darlington et al., 1992: Tables 1, 2, 3). The data for *M. subhyalinus* (Rambur) ($b = 0.52$, $r^2 = 0.91$) come from Darlington (1990: Tables 1, 2, 3). The regression slopes of these three species, the nests of which were fumigated do not differ significantly from each other, but their elevations are significantly different (*t* test, $P < 0.01$) in the order: *M. michaelseni* > *M. jeanneli* > *M. subhyalinus*.

In *Macrotermes bellicosus* (Smeathman) savannah nests from Nigeria, the relation is equally gentle and is described with confidence ($b = 0.48$, $r^2 = 0.73$) (Collins, 1981:

Table 3); the youngest nest, without any epigeal structures, was discarded. Five large mounds of *M. bellicosus* were sampled in Senegal, but the correlation between nest volume and population is not significant probably because of the absence of small mounds in the sample (Lepage, 1974: Table 29, quoted in Grassé, 1984). The populations estimated by Lepage and Collins (for the largest mounds) are similar and have thus been pooled. The resulting relation has a gentle slope ($b = 0.39$) that is significantly different from 0, 0.67 and 1, but not from 0.33, with a fairly high confidence ($r^2 = 0.67$).

A single average value of mound volume and population could be deduced for *Macrotermes ukuzii* Fuller from Rohrmann (1977). This average point seems to fit well into the series of *M. bellicosus*.

In *Macrotermes natalensis* (Haviland) (Meyer et al., 2000: Table 1), the slope ($b = 0.96$, $r^2 = 0.85$) conflicts with those of all other *Macrotermes* species. Several indices suggest that the populations are underestimated.

Two *Odontotermes* species, *O. obesus* (Rambur) and *O. redemanni* Wasmann, build large mounds and show very similar results in the study by Singh and Singh (1981: Table 1). Thus, they have been pooled. In comparison with the *Macrotermes* mounds sampled after fumigation, they show a steep slope with a very high confidence ($b = 0.68$, $r^2 = 0.97$) but very low population densities (Table 2). By contrast, the mounds of *O. obesus* in an older study (Gupta, 1953: Tables 1, 2, 3) housed much larger populations (almost of an order of magnitude) with many more larvae (about 35%) and with a rather similar slope but a lesser confidence ($b = 0.62$, $r^2 = 0.57$).

Discussion

The discussion will be conducted at the level of the subfamilies since the inner architectures of their nests are different and are one of the parameters influencing the gas exchanges (and hence the size of the populations).

Termitinae

The inner architecture of most Termitinae mounds is alveolar and compartmentalized in chambers communicating with each other through narrow corridors. This structure meets the requirements of a static warfare defence based on a low number of soldiers (Deligne et al., 1981, Deligne and Pasteels, 1982), but nevertheless provides efficient connectivity (Perna et al., 2008). This architecture does not allow gas convection. In such nests, we expect gases to diffuse relatively rapidly through the chambers, but more slowly through the corridors because they can be obstructed by single individuals. They probably pass still

Table 2 Ratios that can be used as indices of sampling quality

Species	n	Density (# ind/cm³) P 10–90 range	Percentage of larvae P 10–90 range	# ind/mg FM queen P 10–90 range	# ind/g DM fungus comb P 10–90 range	Reference
Termitinae						
Noditermes cristifrons	24	0.9–6.1	14–52		/	Soki, 1994
Cubitermes fungifaber	40	3.1–15	25–61	51–153	/	Han and Lepage, 1991
Cubitermes sankurensis	56	1.2–5.7	12–40	132–402 (n = 30)	/	Bouillon and Lekie, 1964
Cubitermes speciosus	49	0.6–1.8	19–40		/	Soki and Josens, 1996
Thoracotermes macrothorax	15	1.1–2.9	29–57		/	Soki, 1994
Dicuspiditermes nemorosus	23	14–52	31–68		/	Matsumoto, 1976
Homallotermes foraminifer	11	5.3–14	6.7–27		/	Matsumoto, 1976
Nasutitermitinae						
Nasutitermes corniger	12	14–45		45–329	/	Thorne, 1982
Nasutitermes exitiosus	4	3.1–8.3	2.4 (average)		/	Holdaway et al., 1935
Constrictotermes cyphergaster	12	0.5–6.1 (larvae excluded)			/	Vasconcellos et al., 2007
Trinervitermes geminatus	12	0.5–8.9	7 (average for T.g.)		/	Josens, 1972
+ *T. togoensis*	+2					+ Josens, 1972
+ *T. trinervius*	+7					+ Lepage, 1974
+ *T. rhodesiensis*	+2					+ Ferrar, 1982
Apicotermitinae						
Acidnotermes praus	3	28–75	37–46		/	Soki, 1994
Anoplotermes banksi	5	59–148	25–54		/	Martius and Ribeiro, 1996
Astalotermes quietus	7	6.3–24	9.7–49		/	Soki, 1994
Macrotermitinae						
Macrotermes bellicosus	18	0.06–2.2	35–77			Collins, 1981
Macrotermes natalensis	7	0.01–0.05	0.7–14			Meyer et al., 2000
Macrotermes jeanneli	7	1.7–38	28–79	56–121 (n = 5)	73–336	Darlington et al., 1992
Macrotermes michaelseni	35	2.2–22	36–56	82–150 (n = 32)	132–263	Darlington, 1986; Darlington and Dransfield, 1987; Darlington, unpublished data
Macrotermes subhyalinus	13	0.5–6.0	19–79	46–120	71–173	Darlington, 1990
Macrotermes ukuzii	8	0.34 (average)	47–86	14–62	20–80	Rohrmann, 1977
Odontotermes obesus	6	0.02–0.08	6 (O. o.)			Singh and Singh, 1981
+ *O. redemanni*	+6		9 (O. r.)			
Odontotermes obesus	7	0.16–1.2	19–49			Gupta, 1953

more slowly through the external nest wall, the latter thus being the limiting factor of the respiratory gas exchanges.

Only one species, *Noditermes cristifrons*, convincingly supports a linear relationship between termite number and mound volume, but a relation with the surface of the mound is equally likely since the slope is not significantly different from 0.67. Most of those mounds are built up against the base of a tree; thus, small mounds are small half cylinders and larger ones are taller but only slightly thicker half cylinders, entailing vertical growth. Therefore, the relation between the volume and the surface should be almost linear and the relations between the population and either the mound volume or the mound surface can also be linear.

The data concerning the three species of *Cubitermes* (slope of the regressions close to and not significantly different from 0.67) are consistent with a size regulation supporting the hypothesis of the respiratory function of the termite mounds by diffusion. The caps of these nests would act as water-shedding devices protecting the walls from becoming wet, which would substantially decrease the speed of gas diffusion through the walls (Ruelle, 1964;

Korb and Linsenmair, 1999). They would also increase the ratio surface/volume.

Amongst at least two of the three species of *Cubitermes*, the level of confidence of the observed relation can be related to the dynamics of mound building in a growing society. A growing society of *C. fungifaber* either builds additional structures or abandons its mound to build a new and larger one (Han and Lepage, 1991). Therefore, the match between the population density and the nest size can be expected to be fairly close (and actually the level of confidence is high: $r^2 = 0.89$). Indeed, Han and Lepage (1991) quoted very significant correlations between the population and several dimensions of the nests of *C. fungifaber*. In *C. speciosus*, the mound is either initially small and subsequently enlarged or rapidly built and never enlarged afterwards (Soki et al., 1996). The latter case must obviously lead to a lesser correlation between the size of the mound and the population ($r^2 = 0.59$). The dynamics of mound building by *C. sankurensis* is still unknown; the weak correlation between its population and its mound weight ($r^2 = 0.26$) has already been established by Bouillon and Lekie (1964). Besides the unknown dynamics of mound building, the scattering of the points could be partly due to the crude assessment of the mound volumes, since this species obstructs the peripheral chambers of its nests when the society becomes old (G.J., pers. obs.), hindering the conversion of weight into volume, the specific mass being no longer a constant.

In *Thoracotermes*, there is no significant correlation between termite numbers and mound volume and the confidence level is very low, probably because no small mound was sampled, obscuring the relationship for this species. Therefore, the slope, which is even lower than 0.33, in contradiction with the inner architecture that does not allow any gas convection, is probably meaningless. The *T. macrothorax* points superimpose on those of the larger nests of *C. speciosus* and will therefore be handled with *Cubitermes* spp.

The nests built by *Dicuspiditermes nemorosus* and *Homallotermes foraminifer* seem to conform to a surface regulation and house significantly more individuals per volume unit than those of *Cubitermes* and *Thoracotermes*. This is probably due to the small size of these species (<2 mg FM per individual), in comparison with *Cubitermes* spp. and *T. macrothorax* (>4 mg FM per individual).

In conclusion, all the Termitinae (except possibly *T. macrothorax*) fit into the surface regulation pattern. However, they can eventually be distinguished into three groups (Fig. 2): (1) *N. cristifrons* that shows a slope near 1, (2) the three *Cubitermes* spp. (plus *T. macrothorax*) that show a slope near 0.67 and are large species (most nests house 0.6–15 individuals/cm^3), and (3) *H. foraminifer* and *D. nemorosus* that also show a slope near 0.67 but are smaller species with higher densities (5–52 individuals/cm^3).
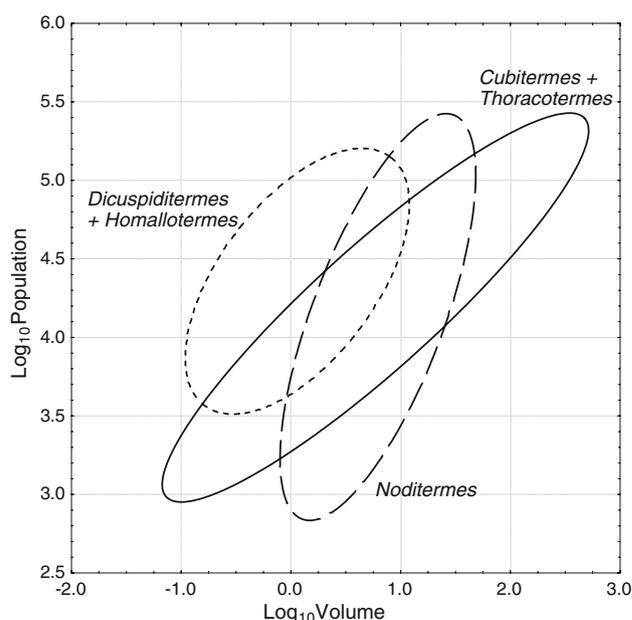
Fig. 2 Log–log relationship between the termite population and their mound volume (dm^3) computed for seven Termitinae species (five genera), showing the 90% concentration ellipses for three groups: (a) *Noditermes*, (volume-regulated mounds), (b) *Cubitermes + Thoracotermes* (surface-regulated mounds with large individuals) and (c) *Dicuspiditermes + Homallotermes* (surface-regulated mounds with small individuals)

Apicotermitinae

The negative correlation in *Astalotermes quietus* Silvestri might be linked with the temporary nature of its small nests, called "pseudoécies" by Grassé (1938). Actually in the Ivory Coast, most of these tiny structures were empty (Josens, 1972). In the Democratic Republic of Congo, *A. quietus* built larger nests, 70% of them containing variable numbers of workers, and a royal pair was found in one out of seven such "pseudoécies". However, the very variable percentages of larvae (27.2 ± 21.5%) also suggest a temporary function in this case (Soki, 1994: Table 4.6). The negative correlation for *Acidnotermes praus* Sands (Soki, 1994: Table 4.5) may be fortuitous since only three nests were sampled.

The nests of *Anoplotermes banksi* Emerson are not temporary structures, since a royal pair was present in each of the seven mounds sampled. When the two heaviest mounds are discarded, the regression becomes significant (Martius and Ribeiro, 1996) and is consistent with a surface regulation. The high elevation of the regression line ($a > 4$) seems to be linked with the small size of this species (<1 mg/individual).

Nasutitermitinae

The inner architecture of many Nasutitermitinae mounds is made of labyrinthine irregular spaces with relatively large

passages, allowing a mobile warfare defence and requiring a high number of soldiers (Deligne et al., 1981, Deligne and Pasteels, 1982, Noirot and Darlington, 2000). This architecture promotes gas diffusion and, if the spaces are sufficiently broad (as in the *Trinervitermes* mounds), might allow some gas convection as far as the external nest wall, which must be a limiting factor for respiratory gas exchanges.

Regarding *Trinervitermes* spp., the slope lies significantly between 0.67 and 0.33. Their nests do not include any vertical galleries and no driven ventilation has yet been described for this genus. However, their inner, open architecture does not preclude either vertical or horizontal gas convections and their location in savannas (exposure to direct sunshine and winds) might regularly induce gas movements. This would explain a slope, which is halfway between a surface and a linear regulation (see further discussion about *Macrotermes*). Their mounds are devoid of any water-shedding device and in the case of long-lasting rain, holes are opened at the base of the nests near the soil level and are guarded by a cohort of small soldiers. These holes are closed when the nest eventually dries off (Josens, 1983), which again allows efficient gas diffusion through the outer wall.

The data points of *Constrictotermes cyphergaster* are very scattered: 3 out of the 12 points might be outliers for several reasons (see Vasconcellos et al., 2007), but they were not discarded. Their mounds have an external earth wall and their points superimpose on those of *Trinervitermes* spp., so they were joined.

Nasutitermes corniger seems to be halfway between a volume and a surface regulation; however, 2 of the 12 mounds housed small populations and might have been outliers. Their removal hardly influences the slope and the regression then points to a surface regulation. Another population of this species, reported as *N. costalis,* supports a surface regulation (Wiegert and Coleman, 1970). Unfortunately, the raw data of this study are not available. *N. corniger* house many more individuals in their nests than *Trinervitermes* spp.

In conclusion, the Nasutitermitinae species are distinguished into two groups: (1) *Trinervitermes* spp. and *C. cyphergaster* with a gentle slope ($0.33 < b < 0.67$, to be confirmed for *C. cyphergaster*) (trade-off between a surface and a linear regulation) and with low population densities, ranging between 0.5 and 9 individuals/cm^3, and (2) *N. corniger* with a slope near 0.67 (surface regulation) and with significantly higher population densities (ranging between 14 and 45 individuals/cm^3). It is hypothesized that the external carton wall of the *N. corniger* nests, which is sprinkled with small apertures (Thorne, 1980), allows higher gas exchanges and thus higher population densities (Fig. 3). *N. exitiosus* is at present left aside because its
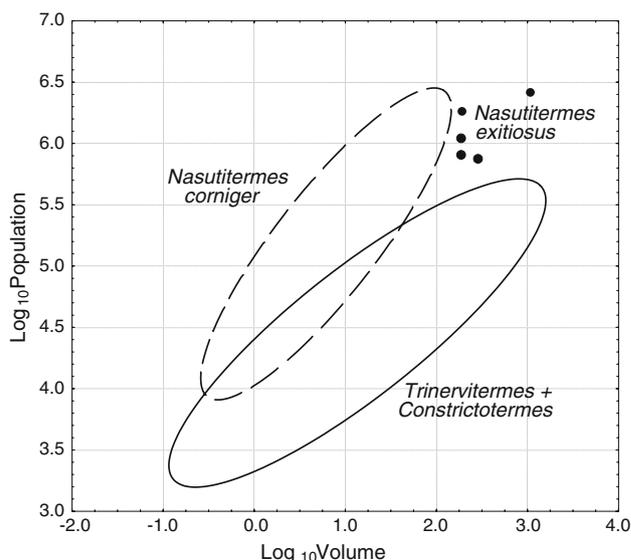
Fig. 3 Log–log relationship between the termite population and their mound volume (dm^3) computed for seven Nasutitermitinae species (three genera), showing the 90% concentration ellipses for (a) *Trinervitermes + Constrictotermes* (line surface-regulated mounds) and (b) *Nasutitermes corniger* (surface-regulated mounds); *N. exitiosus* is not joined, its populations being possibly underestimated

sample was not representative (due to a lack of small mounds in the sample) and it does not seem to fit into the *N. corniger* pattern.

Macrotermitinae

The fungus-growing termites have high respiratory needs because their symbiotic fungus gardens consume more oxygen and generate more carbon dioxide than the termites themselves (Konaté et al., 2003; Noirot and Darlington, 2000). The architecture of the *Macrotermes* mounds is much more complex than those of other termites; a part of it allows efficient gas movements, but gas diffusion is eventually necessary in most cases through a wall separating the internal from the external atmospheres, with one exception for *M. jeanneli* (Noirot and Darlington, 2000). Gas convections result from differences in temperature and/or pressure and can be driven internally by metabolic heat (thermosiphon of Lüscher, 1956, 1961) or externally by exposure to sunshine (Korb and Linsenmair, 2000) or by temporal variation in wind speed and direction (Turner, 2001). Whatever the mechanisms (which are not mutually exclusive), either gas convection or gas diffusion could be limiting at one time or another. Indeed, gas convection can vary in time (Loos, 1964), being slower at night or during the wet season (Korb and Linsenmair, 1999) and may sometimes be more limiting than diffusion through the outer wall.

The three *Macrotermes* species that were sampled after fumigation (*M. michaelseni*, *M. subhyalinus* and *M. jeanneli*) show slopes that are confidently between 0.67 and 0.33 and consistent with a trade-off between both limiting factors (diffusion and convection). Darlington and Dransfield (1987) had already noticed the equally high coefficients of correlation between the termite populations of *M. michaelseni* and either single mound parameters or combined parameters. The fact that the slope of *M. jeanneli* is the closest to 0.33 is consistent with the spectacular architecture of its nest and its prominent chimney, which is indeed a linear structure expelling the metabolic gases of the society; in this case, gas diffusion precedes convection (Darlington et al., 1992).

Since the regression lines of these three species are almost parallel, the significantly different elevations mean that different termite numbers can inhabit the nests; for example, a mound of 1 m^3 should house 1.02, 1.55 and 2.75 millions of individuals in *M. subhyalinus*, *M. jeanneli* and. *M. michaelseni*, respectively (Fig. 4). As these species have similar sizes, this also suggests that gas exchanges must be achieved with more efficiency by *M. michaelseni*, despite its closed ventilation system, than in the two other species that have open ventilation systems. It may be worth remembering that the inner side of the wall of the nests of *M. subhyalinus* is scattered with deep pockets or pits increasing gas diffusion (Noirot and Darlington, 2000), a

structure that was also mentioned for *Odontotermes obesus* (Roonwal, 1960).

Collins (1981) considered that the termite populations of *M. bellicosus* reached their maximum (about 800,000 sterile individuals) in 6-year-old colonies (within mounds of about 560 dm^3), and that the colony resources were subsequently channelled into the production of alates (despite the fact that the mound could subsequently be enlarged to more than 10,000 dm^3 with a remaining fairly high percentage of larvae). An alternative explanation is that the populations were underestimated, which is possible for a species that has evolved evacuation behaviour as a defence strategy against doryline ant attacks (Darlington, 1984; Darlington and Dransfield, 1987). Indeed, the populations of this species are very significantly lower than those of the species that were sampled after fumigation (*t* test on the elevations, $P < 0.001$; *t* test on the slopes, $P > 0.2$, Fig. 5) and show low densities within their mounds (Table 2). Actually, the regression that was computed is open to criticism since the populations in nests over 560 dm^3 remain roughly constant; an asymptotic regression should have been computed instead of a linear one. If only the smaller nests are taken into consideration, a true linear regression can be used. This gets closer to the regression for *M. subhyalinus*, but stays significantly below it (the elevation of the regression is lower for *M. bellicosus*; $P < 0.01$).
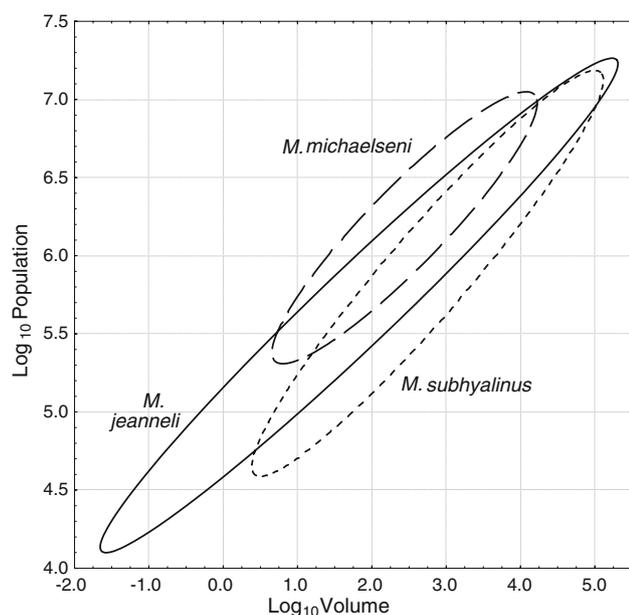
Fig. 4 Log–log relationship between the termite population and their mound volume (dm^3) computed for the three *Macrotermes* species that were sampled after fumigation, showing the 90% concentration ellipses. The ellipse for *M. jeanneli* is large because the number of mounds is small ($n = 7$)
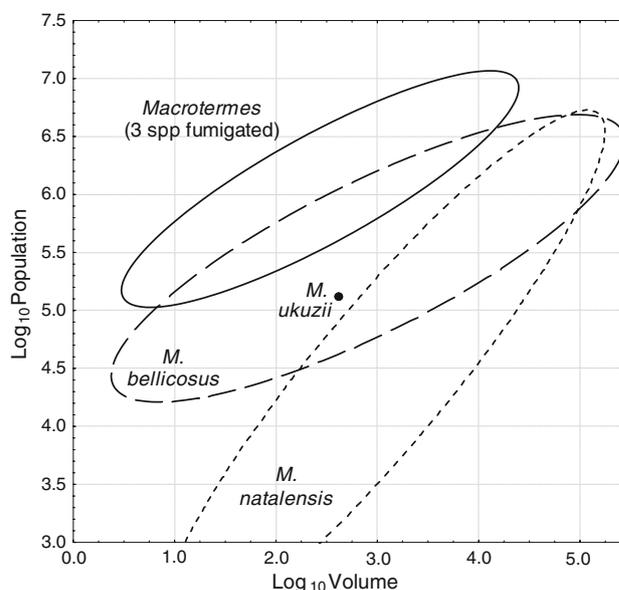
Fig. 5 Log–log relationship between the termite population and their mound volume (dm^3) computed for the *Macrotermes* species: a comparison between species that were sampled after fumigation and otherwise sampled, showing the 90% concentration ellipses. *Macrotermes ukuzii* is shown by a single point (average value)

The populations of *M. natalensis* were almost certainly underestimated for the same reasons, leading to still lower densities within their mounds (Fig. 5). On the other hand, the very low percentages of larvae (Table 2) might be an outcome of the rough sampling method using an industrial vacuum cleaner; the termites' heads were frequently found to be detached from the abdomens (Meyer et al., 2000) and many larvae may have been squashed and not retrieved in the subsequent flotation.

The architecture of the *O. obesus* mounds, externally ridged with hollow buttresses and internally hollowed in a wide central shaft (Roonwal, 1960), suggests a ventilation system, although it has not yet been described. These mounds look like the savannah nests of *M. bellicosus* (see Fig. 3 in Singh and Singh, 1981, miscaptioned as a nest of *O. redemanni*). The mounds of *O. redemanni* are more massive, but might have a ventilation system too (Mukerji and Mitra, 1949, quoted by Darlington, 1997). Therefore, it is expected to find populations of *Odontotermes* that are similar to those of *Macrotermes*. Even though Singh and Singh (1981) reported that the larva percentages showed strong seasonal fluctuations, the low percentages at the time of sampling (6 and 9% in *O. obesus* and *O. redemanni*, respectively) and the low population densities suggest that the populations were seriously underestimated (Fig. 6). Even the much higher figures provided by Gupta (1953) for *O. obesus* are still low in comparison with *Macrotermes* and seem incompatible with the legendary high fecundity of the queens of this species (Roonwal, 1960).

In conclusion, regarding the subfamily Macrotermitinae, only the *Macrotermes* mounds that were sampled after fumigation provide trustworthy population assessments (Figs. 4, 5, 6). The regressions have gentle slopes ($0.33 \leq b < 0.67$) pointing to a trade-off between a surface and a linear regulation and even to a linear regulation for *M. jeanneli*. Another conclusion is that a high coefficient of determination is not a reliable criterion for the quality of the population assessment; it only shows that there are no striking outliers amongst the data.
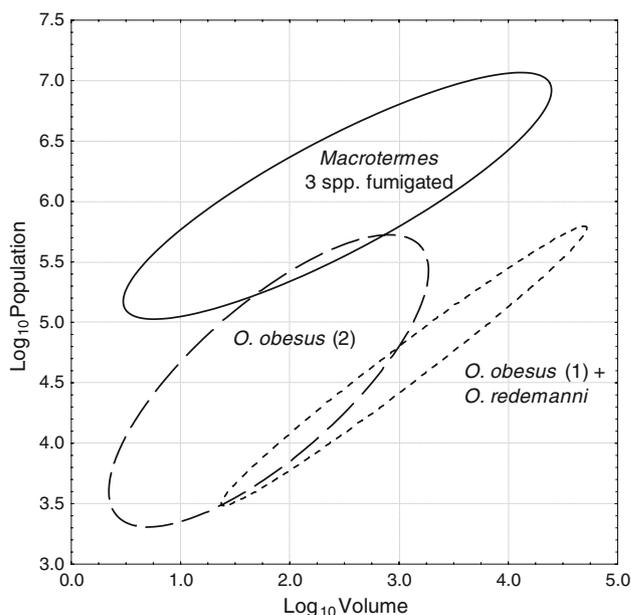
Fig. 6 Log–log relationship between the termite population and their mound volume (dm^3) computed for five Macrotermitinae species: a comparison between species that were sampled after fumigation and the *Odontotermes*, otherwise sampled, showing the 90% concentration ellipses for (a) the three *Macrotermes* species that were sampled after fumigation, (b) *O. obesus* (from Gupta, 1953) and (c) *O. obesus* + *O. redemanni* (from Singh and Singh, 1981)

All species

If we do not consider 2 out of the 3 Apicotermitinae (because of their paradoxical negative regression) and the Macrotermitinae mounds that were not fumigated prior to sampling, the remaining 18 mound-building species provide a global and significant relation (Table 3, Fig. 7).

This regression is a complex result of various parameters: gas exchanges (depending on mound architecture and wall porosity) and termite size. It provides a useful tool for estimating roughly the termite populations of epigeal mounds independently of the species.

Table 3 Relations between termite numbers and mound volumes: log–log linear regressions and determination coefficients for pooled species

Species	n	Regression[a]	r^2	
Selected 18 species (10 genera) (see text)	330	Log N = 3.90 + 0.70 log V	0.72	Fig. 7
Mounds with soil walls and large individuals (FM > 4 mg) (*Cubitermes* + *Thoracotermes* + *Trinervitermes* + *Constrictotermes*)	195	Log N = 3.76 + 0.57 log V	0.82	Fig. 8
Mounds with soil walls and small individuals (FM < 2 mg) + carton mounds (*Dicuspiditermes* + *Homallotermes* + *Anoplotermes* + *Nasutitermes*)	56	Log N = 4.44 + 0.67 log V	0.80	Fig. 8
Large Macrotermitinae mounds (*Macrotermes* sampled after fumigation)	55	Log N = 4.96 + 0.45 log V	0.73	Fig. 8

[a] Logarithm base 10, N = number of individuals, V = epigeal volume in dm^3
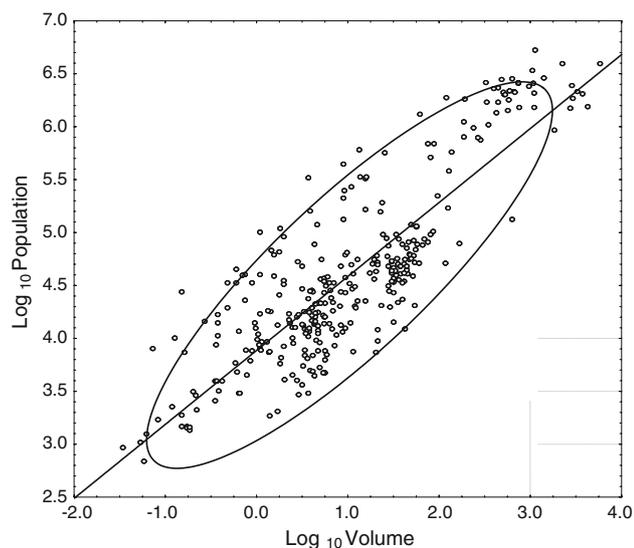
Fig. 7 Log–log regression between the termite population and their mound volume (dm^3) computed for 18 species (10 genera). In the case of the Macrotermitinae, only three species sampled after fumigation are used; in the case of Apicotermitinae only one species (*A. banksi*) is included. The regression equation is shown in Table 3
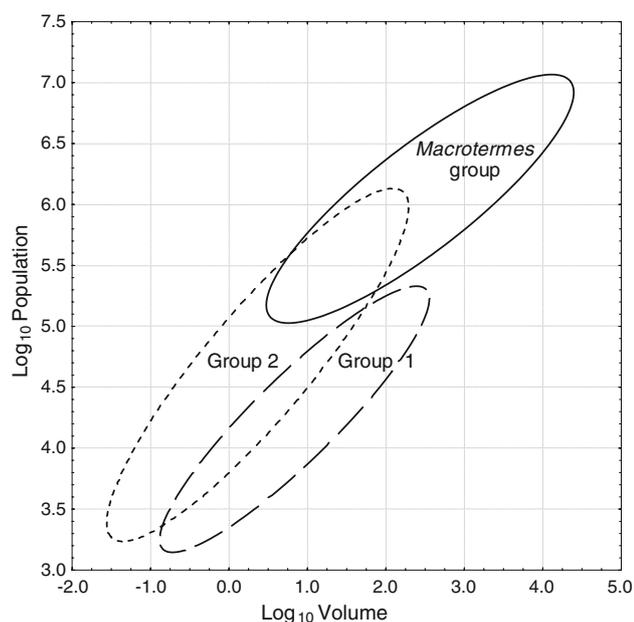
Fig. 8 Log–log regression between the termite population and their mound volume (dm^3) computed for three groups, showing the 90% concentration ellipses for (a) mounds with soil walls and rather large individuals, (b) for either mounds with soil walls and rather small individuals or for carton mounds and (c) for large Macrotermitinae mounds. The regression equations are shown in Table 3

However, a more accurate assessment will be reached if a more appropriate model is applied (Table 3, Fig. 8).

The elevation of the regression provides a good indication of the size of the society when it starts to build an epigeal mound. The elevation is between three and four

(populations between 1,000 and 10,000 individuals) in most species building small soil mounds (most Termitinae, *Trinervitermes*) and between four and five (populations between 10,000 and 100,000 individuals) either in small species building small soil mounds (*Dicuspiditermes*, *Anoplotermes*), in species building carton nests (*Nasutitermes*, *Homallotermes*) or in species building large soil mounds (*Macrotermes*).

It should be remembered that the use of these regressions on the one hand may result in population overestimations, because the nests that were suspected of housing senescent societies were regularly discarded from our analyses and it is not always easy to recognize them in the field (Martius and Ribeiro, 1996). On the other hand, there is always an unknown fraction of the population away from their nests at the time of sampling, which is thus not taken into account in the regressions.

Conclusions

The results of this meta-analysis generally support the following hypothesis: amongst the various functions of the epigeal termite mounds (see Noirot and Darlington, 2000), their size is regulated by the necessity of respiratory gas exchanges and by the limiting factor of these exchanges. Such exchanges can be achieved in three different ways:

1. The *volume-regulated mounds* grow mainly by getting taller; their surface/volume ratio and the density of termites per volume unit both stay constant. The inner architecture is compartmentalized and the limiting parameter is molecular diffusion through the outside wall (*Noditermes*).
2. In the *surface-regulated mounds*, the density of termites per volume unit decreases as the nest gets larger. The inner architecture is either compartmentalized or labyrinthine with large passages; the limiting parameter is molecular diffusion through the outside wall (most Termitinae, *Nasutitermes*).
3. In the *line surface-regulated nests* the inner architecture allows gas convection; gas exchanges can be limited either by gas convection or by gas diffusion. Therefore, the mound size regulation is a trade-off between a surface and a line regulation (*Trinervitermes*, *Macrotermes*).

More information is required to support these conclusions and to understand the functioning of the termite mounds. More accurate samplings are required, especially for large mounds, and to achieve this it is recommended to kill the termites in their mound prior to sampling.

Several ratios (Table 2) can be used to assess the sampling quality:

4. The percentage of larvae, in most cases, should not be lower than 35%. Lower percentages can indeed be observed in senescent colonies (Lepage and Darlington, 2000) or in species with long-living workers as in *Trinervitermes geminatus* (Josens, 1982; Ohiagu, 1979) or during seasonal fluctuations.

5. The population density (i.e. the number of individuals per cm^3) varies in inverse proportion to the volume of the nest and depends also, of course, on the size of the individuals. In most cases, it should not be lower than 0.5 individuals/cm^3. Lower densities can be observed in senescent colonies and possibly during seasonal fluctuations.

6. The ratio of sterile individuals to queen fresh mass: only a little information is available on this criterion; the available data range between 45 and 400 sterile individuals/mg FM queen (Table 2).

7. In the case of the Macrotermitinae, the ratio of sterile individuals to fungus comb dry mass: here also little reliable information is available; the available data range between 70 and 350 sterile individuals/g DM fungus comb. This criterion is also subject to seasonal fluctuations (Lepage and Darlington, 2000).

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