

The Role of Termites in the Decomposition of Wood and Leaf Litter in the Southern Guinea Savanna of Nigeria

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Summary. This is part of a study on the litter dynamics of Southern Guinea savanna, with special reference to the role of termites (Isoptera) as decomposers of wood and leaves.

The biomass of accumulated wood litter on the 6 ha study area varied from 2.299 to 3.488 t ha⁻¹, with a mean of 2.821 t ha⁻¹. Leaf litter biomass varied from 0.290 to 1.643 t ha⁻¹, with a mean of 0.903 t ha⁻¹. The measured decomposition constant for wood of 51% a⁻¹ agreed well with a calculated value of 49% a⁻¹. Leaf decomposition was calculated as 264% a⁻¹. Termites removed an estimated 835.5 kg ha⁻¹a⁻¹ of wood litter (60% of annual wood-fall), and 68.4 kg ha⁻¹a⁻¹ of leaf litter (3% of annual leaf-fall), i.e. 24% of total annual litter production. Conversely, the annual bush-fire removed 1.173 t ha⁻¹a⁻¹ (49%) of annual leaf-fall but only 3 kg ha⁻¹a⁻¹ (0.2%) of annual wood-fall, i.e. 31% of total annual litter production. Baiting studies showed that the fungus-growing Macrotermitinae took 95% of the litter removed by termites (23% of annual litter production).

The ability of the Macrotermitinae to utilise fresh litter is a diagnostic feature of decomposition processes in Southern Guinea and other savanna ecosystems. Their fungus combs produce a processed diet which allows the Macrotermitinae to feed in a seasonally arid environment where the curtailment of free fungal and microbial activity inhibits feeding by other decomposer invertebrates.

Introduction

The accumulation and decomposition of wood and leaf litter in cool temperate latitudes have been extensively studied and reviewed (Dickinson and Pugh 1974). Burges (1967) has described the general pathways for decomposition of plant litter, which may be summarised and simplified as follows. After development of phylloplane microflora, the litter is colonised by saprophytic micro-organisms whose degradation of plant structural polysaccharides is an essential prelude to feeding by soil invertebrates. Once well-rotted, the litter is comminuted and ingested by the soil invertebrates. Finally, litter fragments and invertebrate faeces are incorporated into the soil, where further microbial action results in the formation of humus.

As Wood (1976) has pointed out, the ability of many termites to feed on fresh litter opens up a completely new pathway in tropical decomposition processes. In savanna regions, where fresh litter-feeding termites are dominant, considerable quantities

of plant material may be consumed before being attacked by saprophytic micro-organisms. There are examples of important fresh litter-feeders in most subfamilies, including the lower termites (e.g. *Hodotermes*), but the main groups involved are the higher termite subfamilies Nasutitermitinae and Macrotermitinae. There are grass-feeding nasute genera in South America (*Syntermes*), the Old World (*Trinervitermes*) and Australia (*Tumulitermes*), all of which are believed to have symbiotic, cellulolytic bacteria in their guts. The main fresh wood-feeders in Australia are also nasutes (e.g. *Nasutitermes*) but in the Old World the Macrotermitinae, that culture fungi on faecal residues within their nests, usually dominate this niche. Population studies in West African Sahel and derived savannas have suggested that the Macrotermitinae are important decomposers of litter in these ecosystems (Lepage 1974; Josens 1972, 1977; Lamotte 1975).

The Southern Guinea savanna vegetation zone was chosen for a major project on the role of termites in agricultural and natural ecosystems, organised jointly by the Centre for Overseas Pest Research (Overseas Development Administration, London) and the Institute for Agricultural Research (Ahmadu Bello University, Zaria, Nigeria). Ohiagu and Wood (1979) and Ohiagu (1979a, b) have described the production and decomposition of grasses in the savanna, and assessed the importance of grass-feeding termites. Studies on the soil populations have shown that the Macrotermitinae are dominant in terms of numbers (Wood and Sands 1978; Table 9.6) and may build up to pest proportions under certain agricultural regimes (Wood et al. 1977). This paper is part of a quantitative study on the role of the Macrotermitinae in decomposition processes in the natural savanna; publications other concentrate on the energetics and populations of *Macrotermes bellicosus* (Smeathman), whose towering nests are a prominent feature of the landscape (Collins 1977a, b, 1979a, 1981a, b).

Experimental Plots

The study site was near Ahmadu Bello University's Agricultural Research Station at Mokwa (9°18' N, 5°04' E) in Niger State, Nigeria. In this region the mean annual rainfall of 1,175 mm peaks during September, in the April to October rainy season. The Harmattan, a dust-laden north-easterly wind, blows from December to February during the dry season, when there is almost no rain. Mean monthly minimum temperatures range from 12–25° C, while maxima range from 30–39° C, with the hottest period during March. The topography is gently undulating and the soils are deep, undifferentiated red Ferrisols with a sandy surface and clay content gradually increasing with depth

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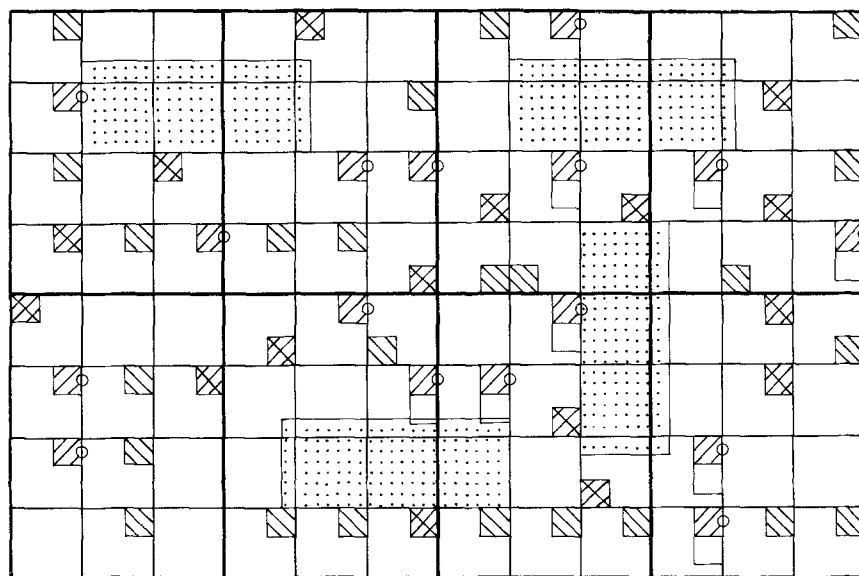


Fig. 1. The layout of the study area

to a B horizon of sandy clay or clay at 30–64 cm (Dangappe Series), or 64–150 cm (Kulfo Series) (Valette 1973).

The savanna vegetation is open-canopy deciduous woodland reaching 15 m and dominated by Caesalpiniaceae legumes such as *Burkea africana* Hook., *Azelia africana* Sm. and *Detarium microcarpum* Guill. & Per. There is a dense field layer of grasses up to 2 m, most of which is burnt off in the January bush-fires. The annual leaf- and wood-fall have been described in an earlier publication (Collins 1977b). Leaf-fall was $2.387 \text{ t ha}^{-1} \text{ a}^{-1}$ ($47,055 \times 10^3 \text{ kJ ha}^{-1} \text{ a}^{-1}$) with a peak from November to February and a maximum after the January fires. Annual wood-fall was $1.391 \text{ t ha}^{-1} \text{ a}^{-1}$ ($31,812 \times 10^3 \text{ kJ ha}^{-1} \text{ a}^{-1}$) and was less seasonal, but with two peaks, from January–March after the fires and May–July during the rains.

The 6 ha study area was in primary woodland on a well-drained site with a slight north-westerly slope, between the villages of Ndayako and Zugurma on the Mokwa to New Bussa road (see Ohiagu and Wood 1979, Fig. 1). The entire study area was divided into eight blocks of twelve $25 \times 25 \text{ m}$ sub-plots and sub-divided in a stratified random way into $10 \times 10 \text{ m}$ quadrats for the estimation of litter production, accumulation and decomposition, as required (Fig. 1). Plots for baiting (see below) were put in positions that avoided interference with other quadrats while still giving a good coverage of the study area.

Methods

Litter Accumulation

The biomass of accumulated wood litter was estimated five times between March 1975 and March 1976. On the first occasion all woody litter and standing dead wood on the eight $10 \times 10 \text{ m}$ tree survey quadrats (Fig. 1) was weighed and sub-sampled for dry weight. On subsequent sampling occasions totals of wood litter on the ground plus standing dead wood of diameter $< 5 \text{ cm}$ at breast height (d.b.h.) were weighed on 24 $10 \times 10 \text{ m}$ quadrats selected in a stratified random manner from the eight blocks of the study area. Collections were made on 30.7.75, 30.12.75

(pre-fire), 12.1.76 (post-fire) and 3.3.76. All samples were replaced after weighing and samples for dry weight estimation were taken from outside the quadrats. In the collection of 3.3.76, the relative proportions of 'twigs' of diameter $< 2 \text{ cm}$ and 'logs' $> 2 \text{ cm}$ diameter were estimated.

Standing dead items of d.b.h. $> 5 \text{ cm}$ were very scattered and after the first sampling occasion they were estimated only once, in March 1976, but over the whole study area. The biomass is taken to be relatively stable throughout the year and this single estimate is used as an annual mean. The height and d.b.h. of each item were recorded and the volume calculated from the equation:

$$Vp = \frac{\pi \cdot r^2 \cdot h}{2}$$

where Vp = volume of wood, r = radius of tree at breast height and h = tree height (Newbould 1967). To convert volume into biomass the mean density of eight common species of wood was calculated by weighing and measuring the water displacement of dry samples.

The biomass of leaf litter was estimated six times during the year. On the first occasion (25.3.75) the standing crop on seven of the eight tree survey quadrats was measured by raking the entire quadrat, weighing the leaves and sub-sampling for dry weight estimation. On subsequent sampling occasions three 0.5 m^2 wire quadrats were thrown at random on each of the 24 standing crop quadrats, the leaves within were collected, dried for 48 h at 100° C and weighed. Samples were taken before and after the annual fire and, as with the wood litter, any weight differences were attributed to the fire.

Litter Decomposition

Sixteen stratified random $10 \times 10 \text{ m}$ quadrats were cleared of woody litter and on 7.1.75 10 kg of paint-marked air-dry logs (mainly 4–10 cm diameter and 30–40 cm long) were scattered over each quadrat. In addition, 5 kg of air-dry twigs ($< 2 \text{ cm}$ diameter) were placed under two 1 m^2 pieces of chicken wire

pegged to the ground. The total of 15 kg per 100 m² quadrat was similar to the natural biomass of fallen litter and was therefore not unduly attractive to termites or other decomposers. The wood samples had been collected indiscriminately from living trees outside the study area, air-dried for two weeks and sub-sampled for dry weight estimation. These wood samples were re-weighed every six weeks for one year, during which time samples for dry weight estimation were taken from surrounding areas. All samples were removed before the 1976 bush-fire.

In addition, three sets of log and twig samples were set aside for decomposition measurements with the exclusion of termites. Litter bags and insecticides were considered but the method chosen was to tie the samples in bundles and suspend them off the ground. As with any exclusion method, this one had its weaknesses. Drier surroundings may have slowed decomposition and invertebrates other than termites would also have been excluded. However, termites are widely believed to be the most important decomposers in tropical soils (Lamotte 1975; Nye 1961; Hopkins 1966; Collins 1977a), and at least some other decomposers could reach the suspended samples. By the end of the year the attacks of wood-boring beetles (Scolytidae and Bostrychoidea) were much in evidence.

Observations during 1974 suggested that leaf litter was not attacked by termites to the same extent as wood but that some species, notably *Macrotermes bellicosus*, did take some during the rainy season, when leaf litter accumulation was high and wood litter low. Accordingly, three 160 g air-dry samples (148 g d.w.) were placed in each of the 16 decomposition quadrats under three 1 m² pieces of chicken wire pegged to the ground. Samples were examined (but not weighed) weekly from June to October 1975 and the amount removed by termites was calculated from the difference between attacked and unattacked samples in the final weighings. Termite activity was always accompanied by very obvious mud galleries.

Baiting

The proportion of litter removal attributable to the various species of termites present was examined by attracting them to softwood baits cut from planks of cottonwood (*Ceiba pentandra* (Linn.) Gaertn.) and arranged in a 4 m grid on four 32 × 80 m plots (Fig. 1). A total of 160 pre-weighed baits per plot, each measuring ca. 15 × 2.5 × 2.5 cm and weighing 30–50 g dry weight, were put in place in January 1975 and at the beginning of every second month thereafter for one year. In the early morning of every second day after bait placement, they were examined for termite attack by quickly turning them over and replacing them. The identity of termites present was recorded and after 28 days (14 checks), the baits were removed, brushed, dried and re-weighed. Removal of wood by organisms other than termites was assessed on eight unattacked control baits per plot. By collating records of termite attack and individual bait weight loss, it was possible to calculate the total wood loss attributable to each species. In the case of baits attacked by more than one species, it was assumed that each removed a proportion equal to that taken overall from baits attacked by only one species. These proportions were applied to the data from the wood decomposition studies to obtain values for removal of natural wood by each type of termite.

Various assumptions are implicit in these methods. For example, it is assumed that all termite species found the cottonwood as palatable as natural wood litter. To assess whether the use of softwood conferred a disproportionate advantage on one or

other of the major species, four inter-rows of hardwood baits were put on each of two plots in May 1975 and checked in the usual way. Checking the baits undoubtedly disturbed the termites to some extent (which is why this method was not applied to the natural timbers used in the decomposition studies) and it is also assumed that all species were disturbed equally. The extent of disturbance was measured by placing four inter-rows of softwood baits on each of two plots in July 1975 and leaving them unchecked until the final collection. The weight of cottonwood baits on the plots averaged 23.1 kg ha⁻¹, which is less than 1% of the standing crop of dead wood and is therefore believed to have had no effect on the distribution of the termite populations.

Results

Litter Accumulation

Data for the standing crop of accumulated wood and leaf litter are given in Table 1. The biomass of standing dead wood (1.090 t ha⁻¹) was estimated from a total volume of 10.077 m³ on the 6 ha study area, and a mean wood density (eight species) of 0.649 ± 0.101 g cc⁻¹ (Collins 1977a). The total biomass of dead wood varied from 2.299 to 3.488 t ha⁻¹, with a calculated mean (allowing for the irregular sampling periods) of 2.821 t ha⁻¹. The biomass of leaf litter was more variable, ranging from 0.290 to 1.643 t ha⁻¹, with a calculated mean of 0.903 t ha⁻¹. Losses of wood litter to the fire were very low; only 3 kg ha⁻¹ were burnt, representing 0.2% of the annual wood-fall. Losses of standing dead items were not estimated and are also assumed to be low. Conversely, 49.1% of the annual leaf-fall was lost to the fire, the biomass dropping from 1.463 to 0.290 t ha⁻¹. An additional study by the author and T.G. Wood showed that the same fire removed 1 t ha⁻¹ of grass and grass litter, representing 81.4% of the standing crop of 1.23 t ha⁻¹ present before the fire and 36.6% of the annual grass production of 2.731 t ha⁻¹ (Ohiagu and Wood 1979).

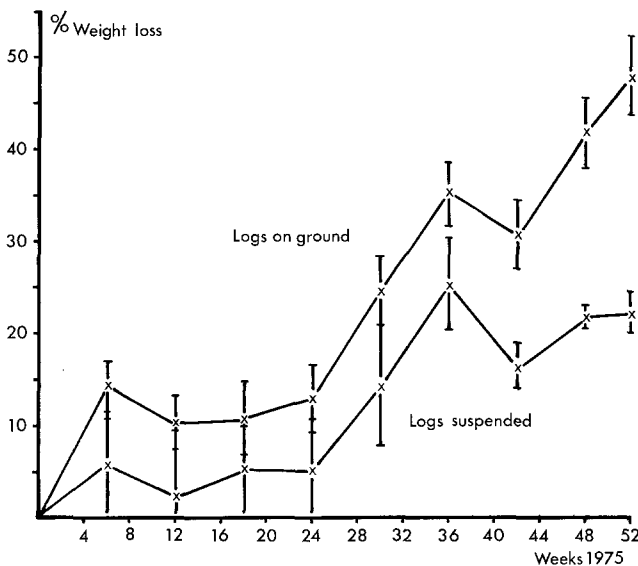
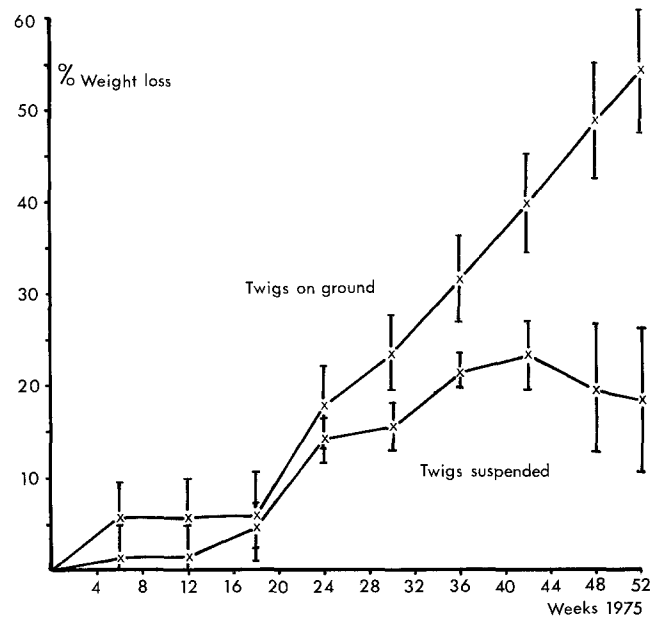
Litter Decomposition

Results for the decomposition of log and twig samples are given in Figs. 2 and 3. Termite mud which accumulated in the samples was removed prior to the last weighing but constituted an error in intermediate data. More substantial errors resulted from dry weight estimations and, as can be seen in Figs. 2 and 3, there were some inconsistent fluctuations in the weight loss. However, only the original and final weights were used in the calculations and these were reliable since the samples themselves were sub-sampled for dry weight. The rate of disappearance of wood increased quickly after week 18 and although this was undoubtedly partly due to the onset of the rainy season, the use of fresh timber cut from trees may have slowed the initial phase. The samples were dried for two weeks prior to impalement but they were still fresher than natural litter, which may be subjected to lengthy attack of various kinds prior to falling. For example, the attacks of wood-boring beetles noted on the suspended samples may normally occur before the timber falls. Hence, the losses to termites may be under-estimated, although this may be offset by the exclusion of decomposers other than termites from the suspended samples.

The decomposition constants are given in Table 2 and the percentage weight loss attributable to termites is calculated by subtraction of weight loss of suspended samples from weight loss of samples on the ground. The mean decomposition constant

Table 1. Calculations of the annual mean standing crops of accumulated wood and leaf litter

Date	Wood					
	25.3.75	30.7.75	30.12.75	12.1.76	3.3.76	
Standing crop excluding standing dead items with d.b.h. > 5.0 cm, kg ha ⁻¹	—	2,398 ± 1,029	1,409 ± 687	1,406 ± 678	1,267 ± 622	
Standing crop of standing dead items with d.b.h. > 5.0 cm, kg ha ⁻¹	—	1,090 ± 306 (measured once only, March 1976)				
Total standing crop of woody litter, kg ha ⁻¹ (L(w))	2,299 ± 1,333	3,488 ± 1,335	2,499 ± 993	2,496 ± 984	2,357 ± 928	
No. days at this level (T)	74.5	140	80.5	32	39	
Annual mean	from: $\Sigma(L(w) \cdot T) / \Sigma T = 2.821 \text{ t ha}^{-1} \text{ d.w.}$					
Date	Leaves					
	25.3.75	12.8.75	23.10.75	30.12.75	12.1.76	3.3.76
Standing crop of leaf litter kg ha ⁻¹ (L(l))	1,643 ± 412	618 ± 92	474 ± 73	1,463 ± 173	290 ± 118	846 ± 103
No. days at this level (T)	81	106	70	40.5	32	36.5
Annual mean	from: $\Sigma(L(l) \cdot T) / \Sigma T = 0.903 \text{ t ha}^{-1} \text{ d.w.}$					

**Fig. 2.** The progressive weight loss from logs (> 2 cm diameter) lying on the ground or suspended in the air, ± 95% c.l.**Fig. 3.** The progressive weight loss from twigs (< 2 cm diameter) lying on the ground or suspended in the air, ± 95% c.l.

is corrected for the proportional annual fall of log and twig litter:

$$\text{Mean } k = \left(k(\text{logs}) \cdot \frac{A(\text{logs})}{A(\text{total})} \right) + \left(k(\text{twigs}) \cdot \frac{A(\text{twigs})}{A(\text{total})} \right)$$

where k = decomposition constant expressed as % weight loss per year, A = annual litter production (from Collins 1977b; Table 4). This is equal to:

$$\left(47.86 \cdot \frac{681.825}{1,390.756} \right) + \left(53.98 \cdot \frac{708.931}{1,390.756} \right), \text{ i.e. } 50.98\% \text{ a}^{-1}.$$

Heavy attack of the log and twig samples is demonstrated by records of species found feeding in the 16 decomposition quadrats at each check, given in Table 3.

The annual disappearance of wood litter attributable to termites can be calculated as:

$$\left(A(\text{logs}) \cdot \frac{k(\text{termites on logs})}{k(\text{total logs})} \right) + \left(A(\text{twigs}) \cdot \frac{k(\text{termites on twigs})}{k(\text{total twigs})} \right)$$

equal to:

$$\left(681.825 \cdot \frac{25.66}{47.86} \right) + \left(708.931 \cdot \frac{35.78}{53.98} \right)$$

i.e.: 365.558 kg ha⁻¹a⁻¹ of logs and 469.906 kg ha⁻¹a⁻¹ of twigs, or a total of 835.464 kg ha⁻¹a⁻¹. With a mean energetic equivalent of wood of 22.87 kJ g⁻¹ (Collins 1977b; Table 6), this is equivalent to 19,107 × 10³ kJ ha⁻¹a⁻¹.

Results for the attack of leaf litter samples are given in

Table 2. Summarised decomposition data with calculations of the impact of termites. For calculation of mean k , see text

Items	Decomposition rate in years ($1/k$)	Decomposition constant (k)
Logs on ground	2.09	47.86% a ⁻¹
Logs suspended	4.50	22.20% a ⁻¹
Termites on logs	—	25.66% a ⁻¹
Twigs on ground	1.85	53.98% a ⁻¹
Twigs suspended	5.49	18.20% a ⁻¹
Termites on twigs	—	35.78% a ⁻¹
Mean (logs and twigs on ground)	1.96	50.98% a ⁻¹

Table 4. Of the 48 × 148 g (d.w.) samples put out, 13 were unattacked by termites, 22 were attacked by *Macrotermes bellicosus*, 11 were attacked by other species of termites and 2 were attacked by *M. bellicosus* and others. These latter were ignored in the self-explanatory calculation in Table 4. During the June–October study period, leaves decomposed by 66.29%, 5.9% being due to termites. To calculate the weight of leaves removed by termites

from the study area, the standing crop of leaves at the start of the experiment was estimated from a graph of standing crop data (Table 1) as 1.16 t ha⁻¹. Decomposition at 66.29% during the period gives an expected value of 0.391 t ha⁻¹ at the end, given no input. Leaf litter production from 20.6.75 to 9.10.75 was in fact 192 kg ha⁻¹ (Collins 1977b), some of which would have decomposed during that time. Therefore the measured standing crop of leaf litter of 0.474 t ha⁻¹ on 23.10.75 was roughly what would be expected. Termites took 5.90%, equivalent to 68.44 kg ha⁻¹, 5.49% (63.684 kg ha⁻¹, 1,255 × 10³ kJ ha⁻¹) was taken by *M. bellicosus* and 0.41% (4.756 kg ha⁻¹, 94 × 10³ kJ ha⁻¹) by other termites (mainly *Odontotermes* spp., to which the whole of this amount is attributed in future calculations). The energetic equivalents have been calculated from a figure for mixed leaf litter of 19.71 kJ g⁻¹ (Collins 1977b). Since there was no observable activity on leaves in the dry season, these figures are taken as annual estimates of leaf removal by termites.

The total litter taken by termites can be calculated as 835.464 kg ha⁻¹a⁻¹ of wood (60.1% of annual wood-fall) plus 68.44 kg ha⁻¹a⁻¹ of leaves (2.9% of leaf-fall), i.e. 903.904 kg ha⁻¹a⁻¹ in all (23.9% of total litter-fall), equivalent to 20,456 × 10³ kJ ha⁻¹a⁻¹ (29.9% of total litter-fall energetic equivalent).

Table 3. The species of termites recorded at checks of the log (L) and twig (T) samples

Termite	Date	No. of decomposition quadrats upon which termites were recorded on each date (maximum 16)																Total (twigs)	Total (logs)	Rank (twigs)	Rank (logs)		
		19.2.75		2.4.75		20.5.75		25.6.75		6.8.75		17.9.75		29.10.75		6.12.75						8.1.76	
		T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L					T	L
* <i>Microtermes</i> spp.	—	—	—	—	7	10	4	4	8	3	6	7	3	4	1	5	1	2	30	35	4	4	
* <i>Ancistrotermes cavithorax</i>	10	6	9	10	16	15	15	15	12	15	14	14	15	12	16	15	11	12	118	114	1	1	
* <i>Odontotermes</i> spp.	2	2	4	3	—	—	—	—	—	1	—	1	—	1	2	2	—	1	8	11	5	5	
* <i>Macrotermes bellicosus</i>	2	1	3	6	3	4	2	6	4	3	4	5	3	7	6	8	4	7	31	47	3	3	
* <i>Macrotermes subhyalinus</i>	1	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	2	3	7	7	
† <i>Microcerotermes parvulus</i>	3	7	2	8	8	9	7	4	5	3	9	5	4	3	3	13	—	4	41	56	2	2	
† <i>Amitermes evuncifer</i>	—	—	—	—	—	1	1	2	—	1	1	1	1	1	—	—	—	—	3	6	6	6	
† <i>Basidentitermes potens</i> Silv.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	0	1	9	9	
** <i>Trinervitermes</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	0	1	9	9	
** <i>Fulleritermes tenebricus</i> (Silv.)	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	0	1	9	9	

* Macrotermitinae, † Termitinae, ** Nasutitermitinae

Table 4. Summary of the leaf decomposition experiment, with calculations of the impact of termites in removing leaf litter

	Unattacked samples	Samples attacked by <i>M. bellicosus</i>	Samples attacked by other termites	Totals
Dry weight of leaves put out (g)	1,924 (13 samples)	3,256 (22 samples)	1,628 (11 samples)	6,808
Dry weight of leaves taken in after 20 weeks (g)	762	916	617	2,295
Dry weight of leaves lost (g)	1,162	2,340	1,011	4,513 (66.29%)
Dry weight of leaves lost to factors other than termites (g)	1,162 (89.38 g/sample)	1,966.36 (89.38 × 22)	983.18 (89.38 × 11)	4,111.54 (60.39%)
Dry weight of leaves taken by termites (g)	0	373.64 (5.49%)	27.82 (0.41%)	401.46 (5.90%)

Table 5. Mean consumption of baits per species per plot, with calculation of the proportion removed by each species over the year

Species of termite	Mean consumption of baits per plot $\pm 95\%$ c.i. (g.d.w.)						Annual mean consumption per plot (g)	% of annual total per species	<i>t</i> -test, <i>P</i> =
	January	March	May	July	September	November			
<i>Microtermes</i> 5 spp	1.97 ± 5.02	10.68 ± 21.95	313.68 ± 193.05	209.42 ± 109.34	257.12 ± 112.76	46.77 ± 32.29	839.64 ± 368.26	35.966	<0.1
<i>Macrotermes bellicosus</i>	75.45 ± 125.42	9.80 ± 18.15	74.50 ± 113.96	119.85 ± 77.61	48.03 ± 60.57	166.49 ± 177.08	494.12 ± 406.02	21.166	n.s.
<i>Ancistrotermes cavithorax</i>	25.88 ± 36.00	40.59 ± 35.57	177.93 ± 234.25	126.99 ± 147.44	59.43 ± 19.00	8.20 ± 0.78	439.03 ± 290.68	18.806	n.s.
<i>Odontotermes smeathmani</i> & <i>O. pauperans</i>	85.49 ± 81.03	31.22 ± 32.05	62.43 ± 127.61	15.34 ± 19.07	28.71 ± 27.36	114.96 ± 131.05	338.15 ± 353.26	14.485	<0.1
<i>Microcerotermes fuscotibialis</i>	25.51 ± 27.04	50.19 ± 44.89	9.77 ± 19.17	5.82 ± 10.73	5.87 ± 11.14	15.06 ± 17.99	112.22 ± 115.86	4.807	n.s.
<i>Macrotermes subhyalinus</i>	40.55 ± 70.17	9.93 ± 15.69	0.69 ± 2.21	17.20 ± 27.59	10.11 ± 15.26	24.19 ± 44.67	102.67 ± 146.49	4.398	n.s.
<i>Amitermes evuncifer</i>	—	—	5.65 ± 17.99	—	0.94 ± 3.00	—	6.59 ± 17.23	0.282	n.s.
<i>Trinervitermes</i> sp.	0.14 ± 0.46	—	—	0.30 ± 0.71	0.70 ± 2.22	0.98 ± 1.97	2.12 ± 2.61	0.09	n.s.
Totals	255.00 ± 148.2	152.41 ± 75.86	644.66 ± 230.04	494.92 ± 203.72	410.90 ± 93.95	376.65 ± 95.87	2334.55 ± 480.91	100.0	

Table 6. Calculation of the estimated consumption of wood and leaf litter by termites, with energetic equivalents

Species	Proportion taken (%)	Wood-litter consumption (kg ha ⁻¹ a ⁻¹ (CWsp))	Leaf-litter consumption (kg ha ⁻¹ a ⁻¹)	Total consumption (kg ha ⁻¹ a ⁻¹)	Total consumption (kJ ha ⁻¹ a ⁻¹)
<i>Microtermes</i> 5 spp.	35.966	300.483	~0	300.483	6,872 $\times 10^3$
<i>Macrotermes bellicosus</i>	21.166	176.834	63.684	240.518	5,299 $\times 10^3$
<i>Ancistrotermes cavithorax</i>	18.806	157.117	~0	157.117	3,593 $\times 10^3$
<i>Odontotermes</i> 2 spp.	14.485	121.017	4.756	125.773	2,861 $\times 10^3$
<i>Microcerotermes parvulus</i>	4.807	40.161	0	40.161	918 $\times 10^3$
<i>Macrotermes subhyalinus</i>	4.398	36.744	~0	36.744	840 $\times 10^3$
<i>Amitermes evuncifer</i>	0.282	2.356	0	2.356	54 $\times 10^3$
<i>Trinervitermes</i> sp.	0.09	0.752	0	0.752	17 $\times 10^3$
Totals	100	835.464 (CWt)	68.440	903.904	20,456 $\times 10^3$

^a Energetic equivalents (used throughout this paper), wood: 22.87 kJ g⁻¹, leaves: 19.71 kJ g⁻¹ (Collins 1977b)

Baiting

The complete data from the baiting plots are given in Collins (1977a) and are summarised in Table 5. The 95% confidence limits for the mean consumption per species are wide, mainly because of the limited number of plots. However, an analysis of variance of the total consumption per species per plot gave an insignificant variance ratio between plots (0.39 *a* 3 and 31 d.f.), indicating their homogeneity, while the variance ratio between species (11.74 *a* 7 and 21 d.f.) was highly significant ($p < 0.001$). A *t*-test analysis of consumption per species gave

no significance values of less than $P = 0.1$ (Table 5), but three sets of species feeding levels were indicated. *Microtermes* spp. consumed the largest proportion (35.79%) while *Macrotermes bellicosus*, *Ancistrotermes cavithorax* and the two *Odontotermes* spp. (*O. smeathmani* (Fuller) and *O. pauperans* (Silvestri)) also took large amounts (21.17%, 18.81% and 14.49% respectively). At a lower level, *Microcerotermes parvulus* (Sjöstedt) and *Macrotermes subhyalinus* (Rambur) took 4.81% and 4.40% respectively, while *Amitermes evuncifer* Silvestri and *Trinervitermes* sp. took less than 1%. In Table 6, the proportions taken from baits by each species are used to calculate amounts of wood litter

Table 7. Records of termites found on baits attacked by one or several species during May 1975

Baiting results: May 1975	No. baits attacked by one species	Rank	No. baits attacked by > 1 species	Rank
<i>Microtermes</i> spp.	126	1	228	1
<i>Ancistrotermes cavithorax</i>	82	2	213	2
<i>Odontotermes</i> spp.	32	3	67	3
<i>Macrotermes bellicosus</i>	19	4	65	4
<i>Macrotermes subhyalinus</i>	1	6.5	9	6
<i>Microcerotermes parvulus</i>	8	5	23	5
<i>Amitermes evuncifer</i>	1	6.5	0	7.5
<i>Trinervitermes</i> sp.	0	8	0	7.5

Spearman correlation coefficient: 0.98, $p = < 0.01$

Table 8. Consumption of hardwood and softwood baits on two plots during May 1975. There were twice as many softwood as hardwood baits

Species	Consumption of hardwood (g)	Rank	Consumption of softwood (g)	Rank
<i>Microtermes</i> spp.	203.7	2	436.2	2
<i>Ancistrotermes cavithorax</i>	212.3	1	482.4	1
<i>Odontotermes</i> 2 spp.	67.2	3	214.1	3
<i>Macrotermes bellicosus</i>	61.7	4	145.7	4
<i>Macrotermes subhyalinus</i>	0	6	2.8	6
<i>Microcerotermes parvulus</i>	19.5	5	24.7	5

consumed, using the expression:

$$CW_{\text{sp}} = CW_{\text{t}} \cdot \frac{\overline{CB}_{\text{sp}}}{\overline{CB}_{\text{t}}}$$

where CW_{sp} = annual wood litter consumption per species, CW_{t} is the total wood litter consumption by all species (835.464 kg $\text{ha}^{-1}\text{a}^{-1}$, see above), $\overline{CB}_{\text{sp}}$ = total mean consumption of baits per species and \overline{CB}_{t} = mean total consumption per plot (equal to 2334.54 g, Table 5).

The method assumes that species of termites foraged independently of each other and removed similar proportions of wood from baits attacked by one or several species. Table 7 is a comparison of the number of baits attacked by each species alone and in conjunction with others during one month, May 1975. A Spearman rank correlation test showed a significant correlation ($P < 0.01$) for this and all other months, suggesting that foraging behaviour is similar in both cases and consumption rates are therefore unlikely to be affected.

It is also assumed that the cottonwood was equally palatable to all the termite species and that, in being relatively fresh, the baits were representative of natural woods as used in the decomposition work. A survey of natural wood litter over eight 100 m^2 plots by the author, R.A. Johnson, C.E. Ohiagu and T.G. Wood in April 1975 revealed that less than 5% of items showed any sign of rotting. All the major species of termites on the study area normally feed on fresh litter. *Amitermes evuncifer* may prefer rotten wood but was a rare species.

Use of one bait size assumed no partiality for food of any particular dimensions by various termite species. Size and presentation of baits have been found to be important in timber testing experiments (Usher and Ocloo 1974) and T.G. Wood (pers. comm.) has recently demonstrated size selection at Mokwa. In

view of these new data, the particular bait size used may have under-estimated *Microtermes* and possibly *Ancistrotermes* consumption since these genera tend to attack smaller items. Although Table 3 shows a 100% rank correlation of attacks on logs and twigs, even the twigs may have been too large to detect selective attack.

Data from the consumption of hardwood and softwood baits put down in May 1975 are given in Table 8, which is a combination of results from two plots. On each plot there were twice as many softwood as hardwood baits so the consumption figures for softwood are higher. However, ranking shows a 100% correlation and no suggestion of preferences by any species for either hardwood or softwood.

The assumption that bait checking did not disproportionately disturb the termite species feeding on them could not be verified in the field. On collection, the four unchecked rows of baits placed during July 1975 were 29.6% lighter than checked baits in one plot, and 22.1% lighter in the other. Clearly, checking did slow down the disappearance of the baits, but the assumption that all termites were equally affected stands untested.

Discussion

Calculated and Experimental Decomposition Rates

Nye's (1961) equation relating litter standing crops (L) and litter production (A) can be used to calculate the decomposition constant (k):

$$A \cdot dT = kL \cdot dT.$$

The annual leaf-fall of 2.387 $\text{t ha}^{-1}\text{a}^{-1}$ and mean standing crop of leaf litter of 0.903 $\text{t ha}^{-1}\text{a}^{-1}$ give a calculated mean decomposition constant of 264.3% a^{-1} . This is comparable with other data from West Africa quoted by John (1973) and adapted for Table 9. Since the decomposition studies on leaves were not continued throughout the year, the calculated decomposition constant cannot be checked.

The decomposition constant for wood litter may be calculated from the ratio of annual wood-fall of 1.391 $\text{t ha}^{-1}\text{a}^{-1}$ to the mean standing crop of wood of 2.821 t ha^{-1} , as 49.31% a^{-1} . John (1973) recorded calculated decomposition rates of a similar order of magnitude from Kade, Ghana, where twigs decomposed at 83.3% a^{-1} , small wood at 76.9% a^{-1} and medium-sized wood at 10.9% a^{-1} . Hopkins (1966) recorded 50–100% a^{-1} for small blocks of obeche (*Triplochiton scleroxylon* K. Schum.) in savanna and forests in Southern Nigeria, but this species decomposes rapidly and may not be representative of a range of woods.

The measured mean decomposition constant of 50.98% a^{-1} compares very favourably with the calculated constant of 49.3% a^{-1} , but some anomalies in the data must also be noted. The total standing crop of dead wood on 3.3.76 (2.357 t ha^{-1}) was 12.28% twigs. Extrapolating this figure to the mean annual standing crop (2.821 t ha^{-1}) gives an estimate of 0.346 t ha^{-1} of twigs and 2.475 t ha^{-1} of logs and standing dead wood. The annual wood litter production (1.391 $\text{t ha}^{-1}\text{a}^{-1}$) consisted of 0.709 $\text{t ha}^{-1}\text{a}^{-1}$ of twigs and 0.682 $\text{t ha}^{-1}\text{a}^{-1}$ of logs (Collins 1977b). The decomposition constants for twigs and logs may thus be calculated as 204.9% a^{-1} and 27.6% a^{-1} respectively, which are in very poor agreement with the measured constants of 53.98% a^{-1} and 47.86% a^{-1} (Table 2). The reason for these discrepancies is uncertain but further estimates of the proportions of various litter sizes and more detailed decomposition studies to include standing dead wood would seem to be needed.

Table 9. A comparison of leaf decomposition data from various West African localities

Locality	Leaf decomposition constant, k (% a ⁻¹)	Leaf decomposition rate, $1/k$ (Years for decay)	Source
Kade, Ghana	250	0.4	John 1973
Ibadan, Nigeria	250	0.4	Madge 1965
Olokomeji, Nigeria	500	0.2	Hopkins 1966
Omo, Nigeria	250	0.4	Hopkins 1966
Banco, Ivory Coast	333–250	0.3–0.4	Bernhard 1970
Yapo, Ivory Coast	333	0.3	Bernhard 1970
Mokwa, Nigeria	264	0.379	Present study

Usher (1975) recorded a weight loss from wood blocks protected from soil arthropods of 12.68% in 16 weeks. Extrapolation of the data suggests a possible loss of 20.3% a⁻¹, which is very similar to the results for suspended wood samples at Mokwa of 18.2% a⁻¹ and 22.2% a⁻¹ (Table 2).

Olson (1963) examined total litter production and accumulation from data in the literature and found a general inverse correlation. Since the decomposition constant (k) is the ratio of litter production: accumulation it follows that k increases with litter production and therefore, in West Africa south of the Sahara, with proximity to the equator (Collins 1977b). In tropical forests, Olson calculated k -values ranging from 100 to 400% a⁻¹, while in temperate latitudes they ranged from 1.56 to 25% a⁻¹. He calculated values in terms of total carbon but values using energetic equivalents would not be expected to differ greatly. In these terms, the overall k -value for the present study, 95.8% a⁻¹, agrees well with Olson's data, being higher than temperate and lower than rain forest values.

Seasonality of Litter Accumulation

Seasonal variation in wood litter accumulation was considerable, with a maximum in July/August (Table 1). According to the data, litter fall of at least 1.2 t ha⁻¹ would be required to make up the disparity between April and August values, even if decomposition was zero. Actual litter production during that period was about 0.8 t ha⁻¹ (Collins 1977b). Confidence limits were wide as result of localised wood-falls and the change in methodology between the first and second estimates of wood accumulation may have aggravated the discrepancy.

Leaf litter accumulation was also seasonally variable, with a major peak in March (dry season) and a smaller one in December before the fires. Madge (1965) recorded a single peak from November through to April in Ibadan, Nigeria, and this would have been the case in Mokwa but for the fires in January. The rise from a minimum in January 1976 to a peak such as that in March 1975 implies a leaf-fall of at least 1.35 t ha⁻¹. Actual leaf-fall from January to March 1976 was similar, at about 1.2 t ha⁻¹ (Collins, 1977b). Differences between leaf litter accumulation in the early months of 1975 and 1976 (Table 1) may have been due to variation in the effectiveness of the annual fire.

Seasonality of Termite Activity

The bait consumption figures in Table 5 reflect seasonal foraging patterns on this type of food, but it should be borne in mind

that substrates other than wood litter are widely used, and often preferred. Three indistinct foraging patterns are indicated in the species of Macrotermitinae. *Microtermes* and *Ancistrotermes* have strong peaks in the wet season, *Odontotermes* and *Macrotermes subhyalinus* have less distinct peaks in the dry season, and *Macrotermes bellicosus* is more constant all year round. These patterns are the result of several parameters, of which feeding preferences and nest structure appear to be particularly important.

Both *Microtermes* and *Ancistrotermes* have small individuals, possibly more susceptible to dehydration than the other genera. The nests are polycalic systems of small, diffuse (*Microtermes*) or clustered (*Ancistrotermes*, Josens 1977) subterranean fungus combs, which are used as a dry season food source (Wood and Johnson 1978) but provide little microclimatic amelioration other than that of the soil alone. *Ancistrotermes*, unlike *Microtermes*, may take some tree bark during the dry season, feeding under soil sheeting built over tree trunks and lower boughs. The extent of feeding at these sites was not estimated, but the amount of surface bark removed appeared small compared to consumption of woody litter.

Odontotermes smeathmani and *O. pauperans* also construct subterranean combs, but they are generally aggregated and larger (up to 30 cm diameter). Both species will feed on tree bark in the dry season and *O. pauperans* in particular feeds extensively on grass litter at that time. *Macrotermes subhyalinus* is similarly more active in the dry season, feeding largely on the abundant grass litter, but taking woody litter as well. This species builds a complex epigeal or hypogean nest with a single agglomeration of fungus combs.

Macrotermes bellicosus builds the largest and most complex nest in the savanna ecosystem. The single mass of combs is up to 3 m across, supported on a clay pillar and plate in a habitacle beneath a hollow mound up to 6 m high (Collins 1979a). The mound resists the extremes of the external climate and the metabolism of the combs helps to maintain the nest microclimate at optimal levels (Collins, in prep.). Foraging by this species was at a more steady level, but still low in the driest period, during March. There were suggestions from nest studies that the combs were depleted at that time. *M. bellicosus* took some tree bark during the dry season, but the amount was believed to be small. In further studies on populations and consumption rates of *M. bellicosus* it was calculated that the annual removal of litter by the species was 239 kg ha⁻¹a⁻¹ (Collins 1981 b). This is in very close agreement with the estimate of 240.5 kg ha⁻¹a⁻¹ found by the independent baiting studies described here.

Hence, there are indications that, amongst the Macrotermitinae, the wood-feeders with simple nests (*Microtermes*, *Ancistrotermes*) are more active in the rainy season, while *M. bellicosus*, with a more substantial nest, is able to feed all year round. The grass/wood-feeders (*Odontotermes*, *M. subhyalinus*) are mainly active in the dry season when grass litter is abundant. Their nests are more protective than the simple structures of *Microtermes* and *Ancistrotermes* but less advanced than that of *M. bellicosus*.

Termites other than Macrotermitinae were of minor importance as consumers of fallen wood and leaf litter on the soil surface. *Microcerotermes parvulus* builds a carton nest near or inside woody roots and, although very numerous (1,148 m⁻²; Wood and Sands 1978), the species usually feeds inside roots and stems and was not adequately sampled by the methods used. *Amitermes evuncifer* also feeds mainly on rotten roots but, unlike *Microcerotermes*, was rare in the study area. *Trinervi-*

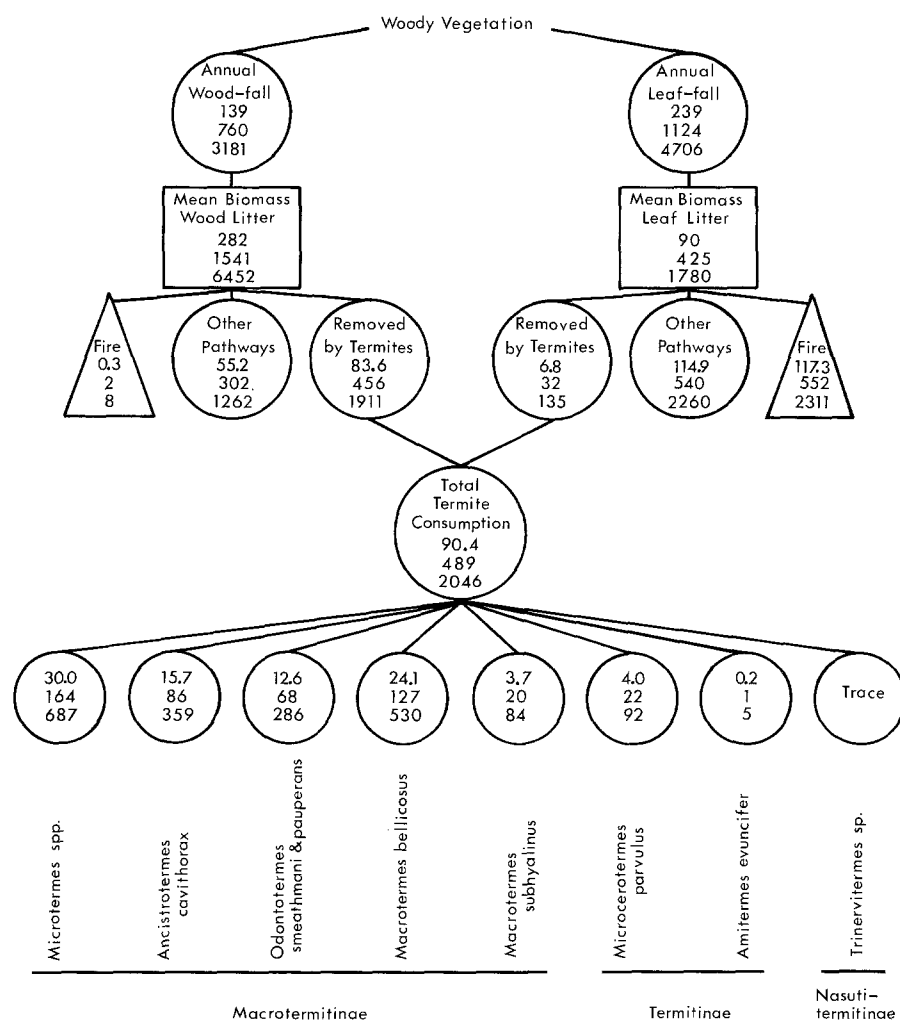


Fig. 4. Flow diagram summarising litter production and decomposition in Southern Guinea savanna. Standing crop values are in boxes, flux values in circles and losses to fire in cones. In each compartment the upper figure is the biomass ($\text{g m}^{-2}(\text{d.w.})$), the centre figure is the calorific equivalent (kcal m^{-2}) and the lower figure is the joule equivalent (kJ m^{-2})

termes feeds almost entirely on grass and its occurrence on the baits was unusual.

Termites and Decomposition Processes in Southern Guinea Savanna

The data on litter production and decomposition are summarised in terms of both biomass and energetic equivalents in Fig. 4. Almost 24% of the total annual litter production was consumed by termites and a further 31% was destroyed by the annual fire. These two factors were complementary in that termites took 60% of wood-fall and only 3% of leaf-fall, while the fire destroyed 49% of leaf-fall and only 0.2% of wood-fall.

The Macrotermitinae quite clearly dominated the other sub-families of termites by taking 22.8% (0.861 t ha^{-1}) of the annual litter production. In Table 10 the data are compared with other ecosystems where the fungus-growers are prevalent. With the inclusion of Ohiagu's (1979a, b) data on grass consumption, termites as a whole took 34.9% of all litter production, very similar to the 28% taken by termites in derived savanna in the Ivory Coast (Josens 1972). The data from rain forest at Pasoh are for leaves only, of which the fungus-growing *Macrotermes carbonarius* (Hagen) was a dominant consumer. Pasoh, being unusually dry, may not be typical of Old World equatorial

forest and much lower populations of Macrotermitinae have been found in wetter forests in Sarawak (Collins 1979b, 1980a, b).

Since litter decomposition and rotting are inhibited by lack of water (van der Drift 1963), an ability to take fresh litter is of greater advantage in drier climates. Wood and Sands (1978) have demonstrated the increasing proportion of energy consumption taken by Macrotermitinae at higher latitudes in West Africa. The Macrotermitinae may also survive well where the microclimate has been artificially changed by land management practices. Collins (1980b) has noted that the Macrotermitinae survive in soils subjected to desiccation after clearance of dipterocarp forest in Sarawak and Wood et al. (1977) have found that they may become pests in land cleared for agriculture in Nigeria.

Studies on leaf litter have shown that decomposition may also be inhibited by low content of bases (Broadfoot and Pierre 1939), or nitrogen (Williams and Gray 1974), and by high content of polyphenols (Janzen 1975). In all these respects woody litter is of poor quality, but the Macrotermitinae are independent of the restrictions of food quality on feeding and assimilation. *Termitomyces*, the symbiotic basidiomycete fungus maintained on faecal fungus combs within the nests of Macrotermitinae, is a white-rot genus, capable of digesting polyphenols (R.J. Thomas, pers. comm.). In addition, the fungus combs may moderate the microclimate of the nest and moisture content of the food

Table 10. Records of consumption by termites (mainly Macrotermitinae) in some tropical ecosystems. (Revised from Wood and Sands 1978)

	Annual litter production (g m ⁻² a ⁻¹)	Annual consumption by termites (g m ⁻² a ⁻¹)	% of litter consumed by termites	Authorities
Sahel savanna Senegal				Lepage 1974
Total	160	12.5	7.8	Bille 1973 a, b
S. Guinea savanna Nigeria				
Wood	139	83.5	60.1	Collins 1977b
Leaves	239	6.8	2.9	Present study
Grass	162	98.0	60.5	Ohiagu and Wood 1979
Total	540	188.3	34.9	Ohiagu 1979b
Derived savanna Ivory Coast				
Total	480	135	28.1	Josens 1972
Rain forest Malaysia				
Leaves	630	{ 202 (Plot 1)	{ 32.0	Matsumoto 1976
Other	430	{ 149 (Plot 2)	{ 23.5	Matsumoto and Abe 1979
Total	1,060	—	—	Ogawa 1974

stores (if present) through production of metabolic heat and water (Collins 1979a, in prep.; Luscher 1951). Studies on the combs of *Macrotermes bellicosus* and *M. carbonarius* (Collins 1977a; Matsumoto 1976) have shown that the fresh faeces, with a high C:N ratio and polyphenol content, are gradually reduced by the fungus to a substrate of low C:N ratio which can be utilised as a food source by the termites. *Termitomyces* achieves this by metabolising the polysaccharides while immobilising nutrients such as nitrogen in the fungal conidiophores and mycelium. Similar processes have been described in the rotting of free woody litter (Hungate 1940; Swift 1977).

In effect therefore, the maintenance of a symbiotic fungus in their nests provides the Macrotermitinae with an external digestive system which decomposes their faeces to produce a high quality, easily assimilated diet. They are thus able to maintain high populations in the seasonally arid savannas (Wood and Sands 1978), where the curtailment of free fungal and microbial activity restricts the feeding of other decomposer invertebrates. A large proportion of the food collected by the termites is metabolised by the *Termitomyces* and the weight-specific consumption of the Macrotermitinae is necessarily higher than that of other subfamilies (Wood 1978). As a result of their high populations and consumption rates, the Macrotermitinae play a major role in the decomposition of litter in the savannas of West Africa.

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References

Bernhard F (1970) Étude de la litière et de sa contribution au cycle des éléments minéraux en forêt ombrophile de Côte d'Ivoire. *Oecol Plant* 5:247–266
 Bille JC (1973a) Graines et diaspores des plantes herbacées du Sahel. Production et dynamique. ORSTOM-Sahel. Rapport du Centre du Dakar, p 45

Bille JC (1973b) L'écosystème sahélien de Fété-Olé. Essai de bilan au niveau de la production primaire nette annuelle. ORSTOM-Sahel, Rapport du Centre de Dakar, p 66
 Broadfoot WM, Pierre WH (1939) Forest soil studies: 1) Relation of rate of decomposition of tree leaves to their acid-base balance and other chemical properties. *Soil Sci* 48:329–348
 Burges A (1967) The decomposition of organic matter in the soil. In: Burges A, Raw F (eds) *Soil biology*. Academic Press, New York and London, pp 479–492
 Collins NM (1977a) The population ecology and energetics of *Macrotermes bellicosus* (Smeathman) Isoptera. Ph. D. thesis, London
 Collins NM (1977b) Vegetation and litter production in Southern Guinea savanna, Nigeria. *Oecologia (Berl)* 28:163–175
 Collins NM (1979a) The nests of *Macrotermes bellicosus* (Smeathman) from Mokwa, Nigeria. *Insectes Soc* 26:240–246
 Collins NM (1979b) A comparison of the soil macrofauna of three lowland forest types in Sarawak. *Sarawak Mus J* 27:267–282
 Collins NM (1980a) The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. *Oecologia (Berl)* 44:263–275
 Collins NM (1980b) The effect of logging on termite (Isoptera) diversity and decomposition processes in lowland dipterocarp forests. In: Furtado JI (ed) *Tropical ecology and development*. International Society of Tropical Ecology, Kuala Lumpur, pp 113–121
 Collins NM (1981a) Populations, age structure and survivorship of *Macrotermes bellicosus* (Isoptera:Macrotermitinae). *J Anim Ecol* 50:293–311
 Collins NM (1981b) Consumption of wood by artificially isolated colonies of the fungus-growing termite *Macrotermes bellicosus*. *Entomologia exp appl* 29:313–320
 Dickinson CH, Pugh GJF (1974) *Biology of plant litter decomposition*. 2 vols. Academic Press, London and New York
 Drift J van der (1963) The disappearance of litter in mull and mor in connection with the weather conditions and the activity of the macrofauna. In: Doekson J, Drift J van der (eds) *Soil organisms*. North-Holland, Amsterdam, pp 125–133
 Hopkins B (1966) Vegetation of the Olokemeji Forest Reserve. IV. The litter and soil with special reference to their seasonal changes. *J Ecol* 54:687–703
 Hungate RE (1940) Nitrogen content of sound and decayed coniferous woods and its relation to loss in weight during decay. *Bot Gaz* 102:389–392
 Janzen DH (1975) *Ecology of plants in the tropics*. Arnold, London
 John DM (1973) Accumulation and decay of litter and net production of forest in tropical W. Africa. *Oikos* 24:430–435
 Josens G (1972) Études biologique et écologique des termites (Isoptera)

- de la savanne de Lamto-Pakobo (Côte d'Ivoire). These et Sciences, Bruxelles
- Josens G (1977) Recherches sur la structure et le fonctionnement des nids hypogés de quatre espèces de Macrotermitinae (Termitidae) communes dans les savanes de Lamto (Côte d'Ivoire). Mem Acad r Belg Cl Sci 8° Sér II, T XLII: 5
- Lamotte M (1975) The structure and function of a tropical savannah ecosystem. In: Golley FB, Medina E (eds) Tropical ecological systems. Ecological studies 11. Springer-Verlag, Berlin, pp 179–222
- Lepage M (1974) Les termites d'une savane sahélienne (Ferlo-Septentrional, Sénégal): peuplement, populations, consommation, rôle dans l'écosystème. D. Sc. Thesis, Dijon
- Lüscher M (1951) Significance of fungus gardens in termite nests. Nature 167:34
- Madge DS (1965) Leaf-fall and litter disappearance in a tropical forest. Pedobiologia 5:273–278
- Matsumoto T (1976) The role of termites in an equatorial rain forest ecosystem of West Malaysia. Oecologia (Berl) 22:153–178
- Matsumoto T, Abe T (1979) The role of termites in an equatorial rain forest ecosystem of West Malaysia. II. Leaf litter consumption on the forest floor. Oecologia (Berl) 38:261–274
- Newbould PJ (1967) Methods for estimating the primary production of forests. IBP Handbook No. 2. Blackwell, Oxford
- Nye PH (1961) Organic matter and nutrient cycles under moist tropical forest. Pl Soil 13:333–346
- Ogawa H (1974) Litter production and carbon cycling in Pasoh Forest. Malaysian IBP Synthesis Meeting, Kuala Lumpur
- Ohiagu CE (1979a) Nest and soil populations of *Trinervitermes* spp, with particular reference to *T. geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in Southern Guinea savanna, Mokwa, Nigeria. Oecologia (Berl) 40:167–178
- Ohiagu CE (1979b) A quantitative study of seasonal foraging by the grass harvesting termite, *Trinervitermes geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in Southern Guinea savanna, Mokwa, Nigeria. Oecologia (Berl) 40:179–188
- Ohiagu CE, Wood TG (1979) Grass production and decomposition in Southern Guinea savanna, Nigeria. Oecologia (Berl) 40:155–165
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331
- Swift MJ (1977) The roles of fungi and animals in the immobilisation and release of nutrient elements from decomposing branch-wood. In: Soil organisms as components of ecosystems. Ecol Bull (Stockholm) 25:180–192
- Usher MB (1975) Studies on a wood-feeding termite community in Ghana, W. Africa. Biotropica 7:217–233
- Usher MB, Ocloo JK (1974) An investigation of stake size and shape in graveyard field tests for termite resistance. J Inst Wood Sci 9:32–36
- Valette J (1973) The reconnaissance soil survey of the Mokwa-Kontagora-Kainji area, North-Western and Kwara States, Nigeria. Soil Survey Bull (Samaru) 44:1–109
- Williams ST, Gray TRG (1974) Decomposition of litter on the soil surface. In: Dickinson CH, Pugh GJF (eds) Biology of plant litter decomposition, vol II. Academic Press, London and New York, pp 611–632
- Wood TG (1976) The role of termites (Isoptera) in decomposition processes. In: JM Anderson, A Macfadyen (eds), The role of terrestrial and aquatic organisms in decomposition processes. Blackwell, Oxford, pp 145–168
- Wood TG (1978) Food and feeding habits of termites. In: Brian MV (ed) Production ecology of ants and termites. University Press, Cambridge, pp 55–80
- Wood TG, Johnson RA (1978) Abundance and vertical distribution in soil of *Microtermes* (Isoptera: Termitidae) in savanna woodland and agricultural ecosystems at Mokwa, Nigeria. Memorabilia Zool 29:203–213
- Wood TG, Johnson RA, Ohiagu CE (1977) Populations of termites (Isoptera) in natural and agricultural ecosystems in Southern Guinea savanna near Mokwa, Nigeria. Geo Eco Trop 1:139–148
- Wood TG, Sands WA (1978) The role of termites in ecosystems. In: MV Brian (ed) Production ecology of ants and termites. University Press, Cambridge, pp 245–292

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