# THE POPULATION ECOLOGY AND ENERGETICS
# OF *MACROTERMES BELLICOSUS*
# (SMEATHMAN) (ISOPTERA)

by

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A thesis submitted for the degree of Doctor
of Philosophy of the University of London and
for the Diploma of Imperial College.

JUNE 1977

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## ABSTRACT

This thesis is an enquiry into the ecology of a litter-feeding termite, Macrotermes bellicosus, which builds large mounds in the savanna zones of tropical Africa. The study was carried out in Southern Guinea savanna at Mokwa, Nigeria ($9^{\circ}18'$N, $5^{\circ}04'$E). In the preliminary section the climatic, edaphic and vegetational features of the area are described.

The second section is concerned with plant litter dynamics; estimates of litter production, accumulation and decomposition are given. Termites removed 60.1% of wood-fall and 2.9% of leaf-fall while fire destroyed 0.9% and 49.1% respectively. Of the 25.9% of total litter production removed by termites, 95.2% was taken by the Macrotermitinae, a group in which the faeces (fungus combs) are degraded by a symbiotic basidiomycete fungus, Termitomyces sp., prior to reingestion. The ability of the Macrotermitinae to feed on fresh litter is considered to be an important element in the high turnover rate of litter and distinguishes decomposition processes in savanna from the essentially fungal and microbial based patterns found in equatorial and temperate regions.

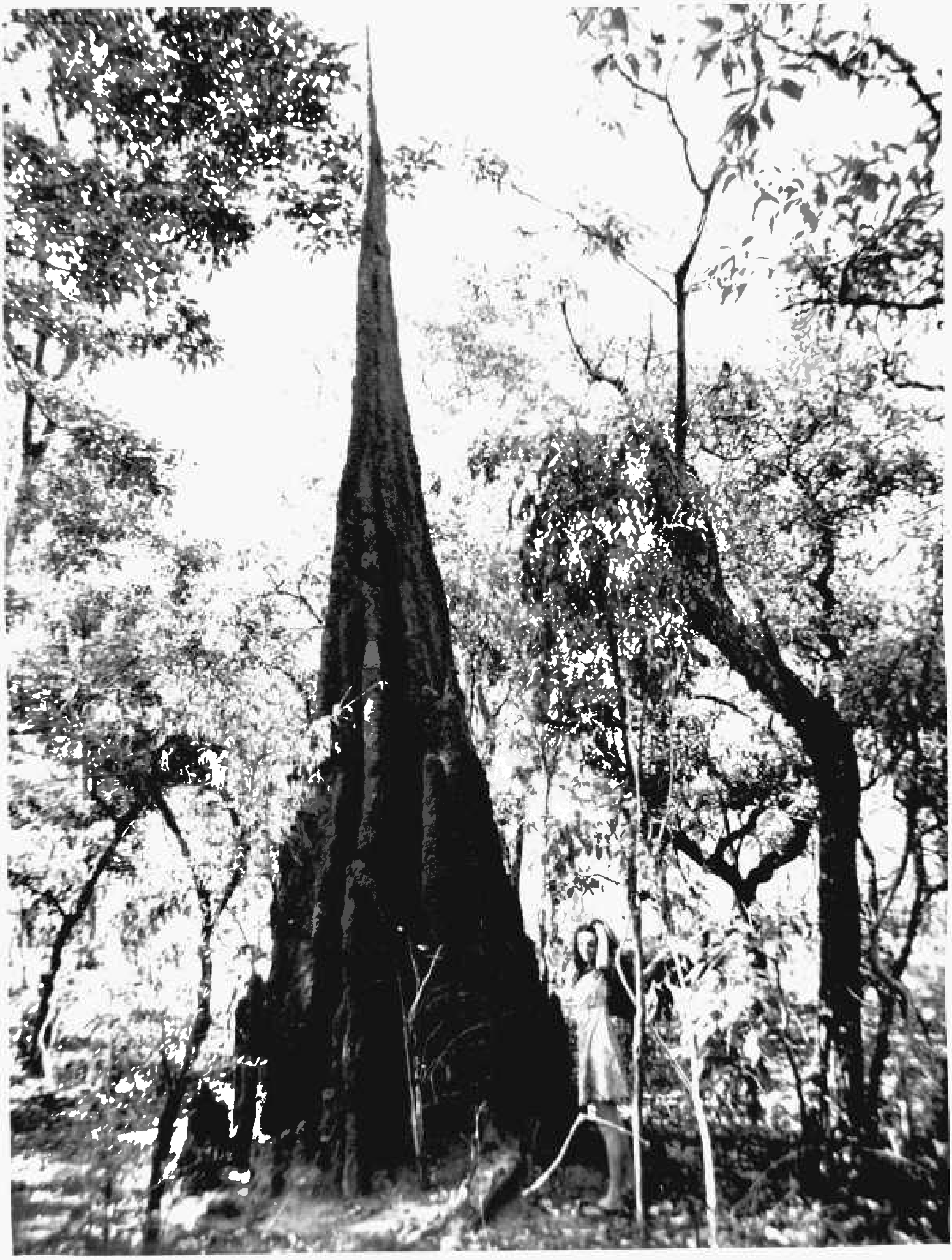
The third section is concerned with the energetics of Macrotermes bellicosus. A new type of nest is described and colony populations and densities discussed. Data on colony growth, caste composition, biomass and survivorship are given. Field consumption measurements were checked using isolated colonies and faeces production was calculated from fungus comb biomass and turnover rate. Respiration rates were measured using Gilson respirometers and extrapolated to the field population. Production was calculated from alate production, larval populations and larval turnover rate.

It is concluded that the fungal symbiont Termitomyces sp. concentrates nutrients in the combs by respiration of organic carbon. The heat evolved is used in maintaining an optimal homoeostatic microclimate by the construction of a highly complex nest. The high quality diet permits a high termite production to biomass ratio, which renders the termite-fungus symbiosis an important link in the nutrient flux from plant litter to the consumer food chain.

Note: A brief review of the quantitative data may be found in the summary.

# FRONTISPIECE

The above-ground portion of a nest of *Macrotermes bellicosus*, (Macrotermitinae : Isoptera). This exceptionally tall example was over 7 m high. The mound is hollow and constructed in such a way that it helps to maintain an optimal microclimate within the main nursery, which is below ground level. The size and complexity of these nests is largely the result of co-adaptation between the termites and their fungal nest symbiont, *Termitomyces* sp.



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# GENERAL INTRODUCTION

The hemimetabolous insect order Isoptera, commonly known as the termites, comprises approximately 1900 living and fossil species, most of them found within the tropics. In accordance with the works of Krishna (1969) and Sands (1972b), the order can be divided into the following families and sub-families:

1) MASTOTERMITIDAE
2) KALOTERMITIDAE
3) HODOTERMITIDAE
    - Termopsinae
    - Stolotermitinae
    - Porotermitinae
    - Cretatermitinae (fossil)
    - Hodotermitinae
4) RHINOTERMITIDAE
    - Psammotermitinae
    - Heterotermitinae
    - Stylotermitinae
    - Coptotermitinae
    - Termitogetoninae
    - Rhinotermitinae
5) SERRITERMITIDAE
6) TERMITIDAE
    - Apicotermitinae
    - Termitinae
    - Macrotermitinae
    - Nasutitermitinae

Termites are polymorphic social insects which live in highly integrated colonies in nests of their own making. They are most closely related to the cockroaches (Blattaria : Dictyoptera), but have no known subsocial groups. They all feed on plant material, either living, dead or in the process of decay. The majority are detritivores or humivores. The lower termites (all families except Termitidae) exhibit stomodeal and proctodeal inter-caste feeding and possess symbiotic gut protozoans upon which they depend for digestion of cellulose. The higher termites (Termitidae) comprise the largest family and have no gut protozoa of any importance but are constantly associated with large numbers of gut bacteria, believed to be symbiotic. This group exhibits only stomodeal inter-caste feeding.

The sub-family Macrotermitinae (with which this work is mainly concerned), is comprised of twelve genera, of which ten occur in the Ethiopian region and five in the Oriental region. They are not found in the Americas or Australasia. The genera are characterised by their comparatively primitive gut anatomy, the fact that faeces are not used in the fabric of their nests and by their symbiotic relationship with Basidiomycete fungi of the genus Termitomyces (except Sphaerotermes). The fungi grow on faecal structures (fungus combs) which are re-eaten by the termites following a period of fungal degradation.

For further information on the taxonomy and biology of the Isoptera the texts of Harris (1961), Krishna and Weesner (1969, 1970) and Lee and Wood (1971), should be consulted.

The work described here was part of an integrated ecological study of termites in agricultural and natural ecosystems, organised jointly by the Centre for Overseas Pest Research, (Ministry of Overseas Development), London, and the Institute for Agricultural Research, Amadu Bello University, Zaria, Nigeria. It was based at the Agricultural Research Station, Mokwa, Nigeria, in the Southern Guinea Savanna climatic and vegetation zone of West Africa.

In the savannas of West Africa in particular, the Macrotermitinae are notorious for causing damage in buildings, crops and reafforestation programmes. In addition to studies of population changes in cropping systems, it was considered necessary to study the ecological impact of the Macrotermitinae in natural woodland and to examine the populations and energetics of one species in particular, Macrotermes bellicosus. This species builds large mounds in the belt of savanna from West to East Africa and is an important component not only of the landscape, but also of the ecosystem.

This thesis is divided into four sections. The first section is largely introductory and includes accounts of soils, climate, vegetation and termite species in the area. The second section examines the litter dynamics in natural woodland, with particular reference to the role of the Macrotermitinae. In the third section the populations and energetics of Macrotermes bellicosus are studied in detail, while in the final section the data are synthesised and discussed.

There have been no previous studies of litter dynamics in Southern Guinea Savanna and no previous complete studies of the energetics of a termite species. It is hoped that this work not only provides some insight into the function and importance of the fungus-termite symbiosis found in the Macrotermitinae, but also offers some idea of the importance of this group in decomposition processes in Southern Guinea Savanna.

# SECTION ONE

## CLIMATIC, EDAPHIC AND VEGETATIONAL FEATURES, WITH AN INVENTORY OF TERMITE SPECIES AND A DESCRIPTION OF THE STUDY AREA

## SECTION 1.1

## CLIMATE

Mokwa Agricultural Research Station is situated in Niger State, Nigeria, at longitude $5^{o}04'$E, latitude $9^{o}18'$N. It lies within the Southern Guinea savanna climatic and vegetational zone (Fig. 1.1.1). Mean annual rainfall is 1175 mm and is distinctly seasonal. The warm wet season runs from April - October with two rainfall peaks, one from May - July and one in September (Table 1.1.1). Valette (1973) however, suggests that on average one year in three has a single peak of rainfall. During the dry season there is normally no rain at all and a dry dust-laden north-easterly wind,the Harmattan, blows from December to February.

Mean monthly temperatures range from $12^{o}$-$40^{o}$C with a maximum during March, in the dry season (Table 1.1.1).

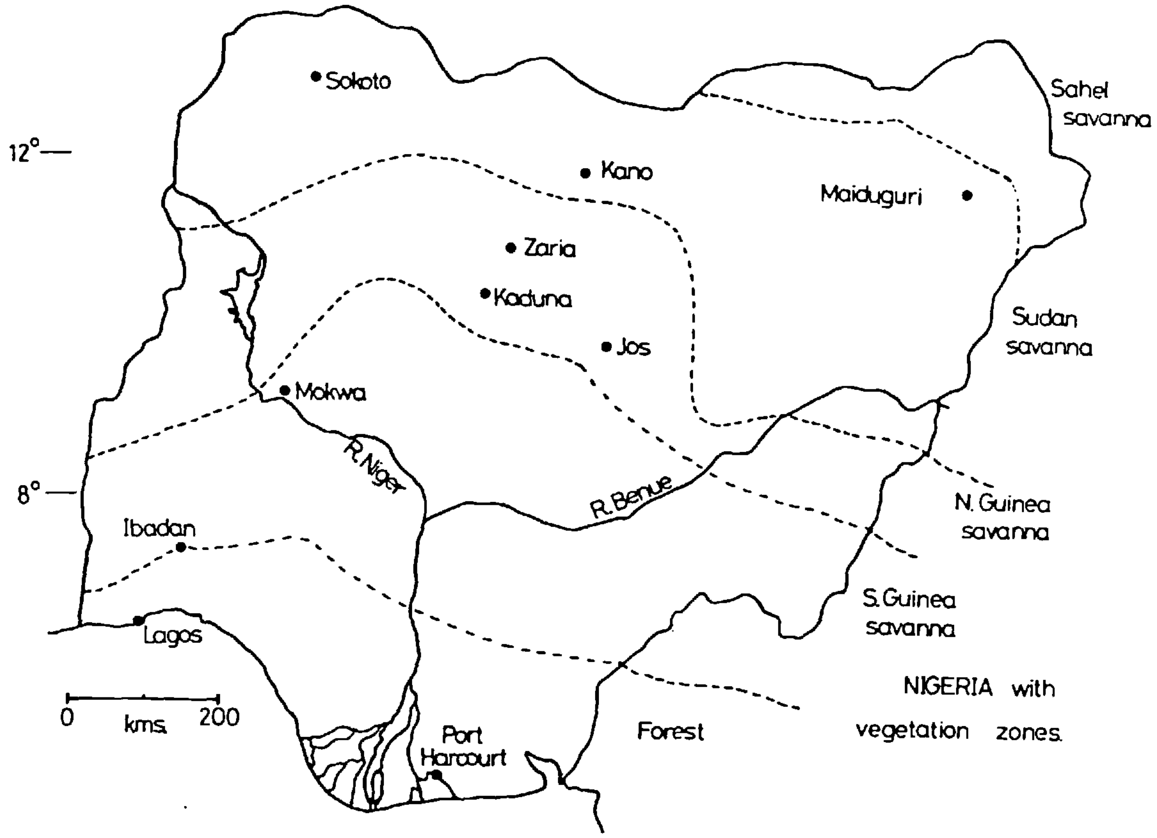


FIGURE 1.1.1 Nigeria with vegetation zones, (after Keay 1959).

## TABLE 1.1.1 CLIMATIC MEASUREMENTS 1974/1975

| | | JAN | FEB | MAR | APR | MAY | JUN | JUL | AUG | SEP | OCT | NOV | DEC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RAINFALL mm | 1974 | 0.3 | 0 | 7.4 | 41.4 | 167.6 | 119.4 | 206.8 | 183.9 | 332.0 | 56.6 | 0 | 0 |
| | 1975 | 0 | 0 | 26.9 | 68.8 | 160.3 | 169.9 | 174.2 | 131.8 | 258.3 | 55.9 | 0 | 0 |
| MEAN MAXIMUM TEMPERATURE °C | 1974 | 32.96 | 37.04 | 39.05 | 37.17 | 33.41 | 31.91 | 30.11 | 29.89 | 30.48 | 31.72 | 33.63 | 33.23 |
| | 1975 | 33.76 | 36.97 | 37.71 | 36.82 | 33.04 | 31.52 | 29.73 | 29.19 | 29.85 | 32.19 | 34.18 | 34.61 |
| MEAN MAXIMUM TEMPERATURE °C | 1974 | 15.63 | 19.64 | 23.48 | 24.41 | 23.40 | 22.15 | 21.90 | 21.83 | 25.54 | 21.47 | 16.94 | 13.24 |
| | 1975 | 12.91 | 19.13 | 23.33 | 24.44 | 22.96 | 22.32 | 21.74 | 21.17 | 21.33 | 16.99 | 18.09 | 12.33 |

TOTAL:
111.54 cm

TOTAL:
104.61 cm

Courtesy of Mm. Bagudu Agaie, Meteorological Observer,
A.R.S. Mokwa.

## SECTION 1.2

## SOILS

### GENERAL DESCRIPTION (after Valette 1973)

The Mokwa-Zugurma region is gently undulating with broad interfluves (6-10 km or more). The soils are of the Kulfo association which are developed on the parent rock of coarse, sometimes conglomeratic, deeply-weathered Nupe sandstone. Most of the soils are deep undifferentiated red Ferrisols with a moderately low cation exchange capacity and low base saturation with a sandy surface layer (Table 1.2.1) with low water retention capacity (Tables 1.2.2, 1.2.3). Clay content gradually increases with depth to form a B horizon of sandy clay to clay within 30-64 cm (Dangappe Series), 64-150 cm (Kulfo Series) or of sandy clay loam within 91 cm (Takumah Series). The study area was on a mosaic of Dangappe and Kulfo Series which differ only in the depth of the B horizon and are generally found on upper slopes.

### ANALYSIS OF PROFILES, SOIL MOISTURE AND SOIL TEMPERATURES

Chemical and particle size analyses of soils from the study area are given in Table 1.2.1. The particle size analysis bears out Valette's (1973) description of high sand content with clay increasing with depth. The organic carbon content of the soil is very low.

Soil moisture was measured during every second month of 1975 at depths of 5 and 50 cm. Ten 5 cm auger samples were taken at each depth at random from each of the four baiting areas, (Section 1.4), stored in small weighed sealed aluminium containers and weighed before and after drying at 70-80$^{o}$C for 48 hours. Soil moisture did not exceed 12% even at the height of the rainy season, emphasising the low water-retention capacity of the soil, (Tables 1.2.2, 1.2.3).

Soil temperatures for 1974-5 are recorded in Table 1.2.4 (courtesy Mm. Bagudu Agaie, Met. Observer, Mokwa). At a depth of 30 cm the range was 25-34°C while at 120 cm it was 27-34°C. The readings are monthly means of observations taken daily at 09.00 hours local time.

TABLE 1.2.1 CHEMICAL AND PARTICLE SIZE ANALYSIS OF SOILS FROM PRIMARY WOODLAND AT MOKWA. (T.G. Wood. pers.comm)

| | PARTICLE SIZE (%) | | | % | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| DEPTH cm | SAND | SILT | CLAY | ORGANIC C | N | K | Ca | Mg | C.E.C. Me/100g |
| 0-5 | 72 | 15 | 13 | 0.90 | 0.131 | 0.14 | 2.0 | 0.71 | 3.09 |
| 5-25 | 72 | 13 | 15 | 0.50 | 0.065 | 0.09 | 1.1 | 0.56 | 2.00 |
| 25-50 | 65 | 9 | 26 | 0.50 | 0.075 | 0.09 | 0.9 | 0.69 | 2.45 |
| 50-75 | 47 | 10 | 43 | 0.48 | 0.088 | 0.11 | 1.0 | 0.49 | 2.68 |
| 75-100 | 39 | 10 | 51 | 0.35 | 0.075 | 0.27 | 1.1 | 0.59 | 2.97 |

TABLE 1.2.2 % SOIL MOISTURE AT 5 cm DEPTH

| MEASURED DURING LAST WEEK OF: | FEB 1975 | APR | JUN | AUG | OCT | DEC |
|---|---|---|---|---|---|---|
| MEAN OF 10 SAMPLES, AREA :1 | 0.613 | 10.050 | 11.717 | 9.595 | 4.156 | 1.995 |
| ± 95% CONF. LIMITS | 0.168 | 1.499 | 0.911 | 1.115 | 0.762 | 0.458 |
| :2 | 0.817 | 12.504 | 12.320 | 12.000 | 5.969 | 2.415 |
|  | 0.186 | 1.602 | 1.292 | 1.701 | 1.131 | 1.080 |
| :3 | 1.109 | 9.573 | 10.218 | 9.708 | 3.986 | 1.337 |
|  | 0.281 | 1.273 | 1.494 | 1.947 | 0.923 | 0.422 |
| :4 | 1.067 | 7.374 | 11.013 | 11.031 | 3.396 | 1.393 |
|  | 0.383 | 0.911 | 1.558 | 1.310 | 0.614 | 0.327 |
| OVERALL MEAN | 0.902 | 9.875 | 11.317 | 10.584 | 4.377 | 1.785 |
| ± 95% CONF. LIMITS | 0.128 | 0.801 | 0.628 | 0.707 | 0.474 | 0.303 |

TABLE 1.2.3 % SOIL MOISTURE AT 50 cm DEPTH

| MEASURED DURING LAST WEEK OF: | FEB 1975 | APR | JUN | AUG | OCT | DEC |
|---|---|---|---|---|---|---|
| MEAN OF 10 SAMPLES, AREA :1 | 4.356 | 5.820 | 7.742 | 9.807 | 7.940 | 5.075 |
| ± 95% CONF. LIMITS | 0.582 | 1.341 | 1.595 | 0.407 | 0.778 | 0.699 |
| :2 | 5.159 | 6.497 | 9.788 | 10.998 | 9.043 | 5.566 |
|  | 1.068 | 1.404 | 1.896 | 1.116 | 1.291 | 1.444 |
| :3 | 5.572 | 8.503 | 9.829 | 10.342 | 8.904 | 4.884 |
|  | 0.889 | 2.590 | 1.758 | 0.402 | 1.663 | 0.622 |
| :4 | 5.869 | 7.237 | 10.268 | 11.085 | 9.279 | 6.653 |
|  | 1.081 | 1.411 | 2.188 | 1.355 | 1.274 | 1.748 |
| OVERALL MEAN | 5.239 | 7.014 | 9.407 | 10.558 | 8.791 | 5.545 |
| ± 95% CONF. LIMITS | 0.425 | 0.799 | 0.838 | 0.417 | 0.560 | 0.554 |

TABLE 1.2.4 SOIL TEMPERATURES AT 30 cm AND 120 cm DEPTH

| | MEAN SOIL TEMPERATURE AT 30 cm DEPTH | | MEAN SOIL TEMPERATURE AT 120 cm DEPTH | |
|---|---|---|---|---|
| | 1974 | 1975 | 1974 | 1975 |
| JAN | 26.62 | 25.86 | 28.16 | 27.95 |
| FEB | 26.96 | 29.98 | 28.93 | 29.27 |
| MAR | 33.61 | 32.14 | 31.79 | 31.42 |
| APR | 33.72 | 33.64 | 33.3 | 33.19 |
| MAY | 30.63 | 30.95 | 31.11 | 32.32 |
| JUN | 30.01 | 29.74 | 31.39 | 30.84 |
| JUL | 28.32 | 28.51 | 29.96 | 29.84 |
| AUG | 28.31 | 27.73 | 29.46 | 28.94 |
| SEP | 27.75 | 26.14 | 28.99 | 28.37 |
| OCT | 28.24 | 28.36 | 28.27 | 28.83 |
| NOV | 27.72 | 27.94 | 29.21 | 28.94 |
| DEC | 26.21 | 27.34 | 28.44 | 28.94 |

## SECTION 1.3

## VEGETATION

Mokwa lies within the Southern Guinea savanna vegetation zone of West Africa, the characteristic vegetation being fairly open deciduous woodland reaching 15 m height with a dense field layer of grasses up to 2 m. The annual fires, normally started in January by local people, quickly remove grasses and leaf litter and kill leaves on trees. Some of the common tree species appear to have fire-resistant qualities such as thickened bark (e.g. *Butyrospermum paradoxum*) or deciduous bark (e.g. *Detarium microcarpum*).

Table 1.3.1 shows the results of a survey of the trees in 8 10 x 10 m quadrats in the study area. The survey was only intended to give indicationsof the more common trees. There were 1425 ± 402 (95% limits) trees $ha^{-1}$. Three Caesalpiniaceous legumes, *Burkea africana*, *Afzelia africana* and *Detarium microcarpum* made up nearly 53% of the trees examined. All 16 species were fairly common in the study area, as was *Entada africana* (Mimosaceae) which was not represented in the survey quadrats.

A comprehensive survey of tree heights, crown widths and other vegetational features was beyond the scope of the study but an idealised profile diagram (Figure 1.3.1) shows approximate vertical distribution and crown shape.

*Daniellia oliveri* and *Afzelia africana* reached the greatest heights (up to 15 m) with *Burkea africana* and *Butyrospermum paradoxum* dominating the intermediate levels around 10 m. *Uapaca togoensis*, although well represented on the study area, was not consistently common elsewhere. At the 5 m level *Detarium microcarpum* was common with *Parinari polyandra*, *Entada africana* also numerous. Below 2 m *Grewia mollis* and *Annona senegalensis* occurred frequently.

No quantitative studies were made on the field layer but a list of common grass species is given here:

(C.E. Ohiagu, pers. comm.)

| | | |
|---|---|---|
| 1) | *Andropogon gayanus*. | Kunth. |
| 2) | *Hyparrhenia dissoluta*. | (Hochst.) Chiov. |
| 3) | *Microchloa indica*. | (Linn.) Beav. |
| 4) | *Imperata cylindrica*. | Linn. |
| 5) | *Pennisetum pedicellatum*. | Trin. |
| 6) | *Cymbopogon giganteus*. | (Hochst.) Chiov. |
| 7) | *Ctenium newtonii*. | Hack. |
| 8) | *Eragrostis tremula*. | Hochst ex Steud. |
| 9) | *Cynodon dactylon*. | Linn. Pers. |
| 10) | *Chloris gayana*. | Kunth. |
| 11) | *Digitaria diagonalis*. | (Nees.) Stapf. |
| 12) | *Bracharia brizantha*. | (Hochst ex A. Rich.) Stapf. |
| 13) | *Cyperus* sp. | |

Species 1), 2) and 8) were very common, *Andropogon gayanus* reaching 2-3 m height.

TABLE 1.3.1 The trees found on 8 100 m$^2$ plots on the study area. Species and authorities after Hopkins and Stanfield (1966) and Keay et al. (1960 and 1964).

| Species | CODE FIG. 1.3.1 | NUMBER OF TREES IN EACH PLOT | | | | | | | | TOTALS |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| *Burkea africana* Hook.<br>(Caesalpiniaceae) | Bu. | 6 | 6 | 6 | 5 | 3 | 2 | 3 | 2 | 33 |
| *Afzelia africana* Sm.<br>(Caesalpiniaceae) | Af. | 3 | 2 | 3 | 5 | | | 2 | | 15 |
| *Detarium microcarpum* Guill. & Per.<br>(Caesalpiniaceae) | De. | | 1 | | | 6 | 2 | 1 | 2 | 12 |
| *Parinari polyandra* Benth.<br>(Rosaceae) | Pa. | | | | 6 | 1 | 2 | 2 | | 11 |
| *Uapaca togoensis* Pax.<br>(Euphorbiaceae) | Ua. | 1 | 1 | 3 | | 3 | | | | 8 |
| *Grewia mollis* Juss.<br>(Tiliaceae) | Gr. | | 2 | | | 1 | 4 | | | 7 |
| *Daniellia oliveri* (Rolfe) Hutch. & Dalz.<br>(Caesalpiniaceae) | Da. | | | | 1 | 2 | 1 | 1 | | 5 |
| *Hymenocardia acida* Tul.<br>(Euphorbiaceae) | Hy. | | | | | 1 | 2 | 2 | | 5 |
| *Annona senegalensis* Pers.<br>(Annonaceae) | An. | | | | | 1 | 1 | 1 | 2 | 5 |
| *Butyrospermum paradoxum* (Gaertn.f.) Hepper (Sapotaceae) | But. | | | | | | 1 | 1 | 1 | 3 |
| *Lannea kerstingii* Engl. & K. Krause.<br>(Annacardiaceae) | La. | | 1 | | 2 | | | | | 3 |
| *Combretum sp.* Loefl.<br>(Combretaceae) | Co. | | | | 3 | | | | | 3 |
| *Terminalia avicennioides* Guill. & Perr.<br>(Combretaceae) | Te. | 1 | | | | | | | | 1 |
| *Antidesma venosum* Tul.<br>(Euphorbiaceae) | Ant. | | | | | 1 | | | | 1 |
| *Monotes kerstingii* Gilg.<br>(Dipterocarpaceae) | Mo. | | | 1 | | | | | | 1 |
| *Securidaca longepedunculata* Fres.<br>(Polygalaceae) | Se. | | | | | 1 | | | | 1 |
| *Entada africana* Guill & Perr.<br>(Mimosaceae) | En. | | | | | | | | | 0 |

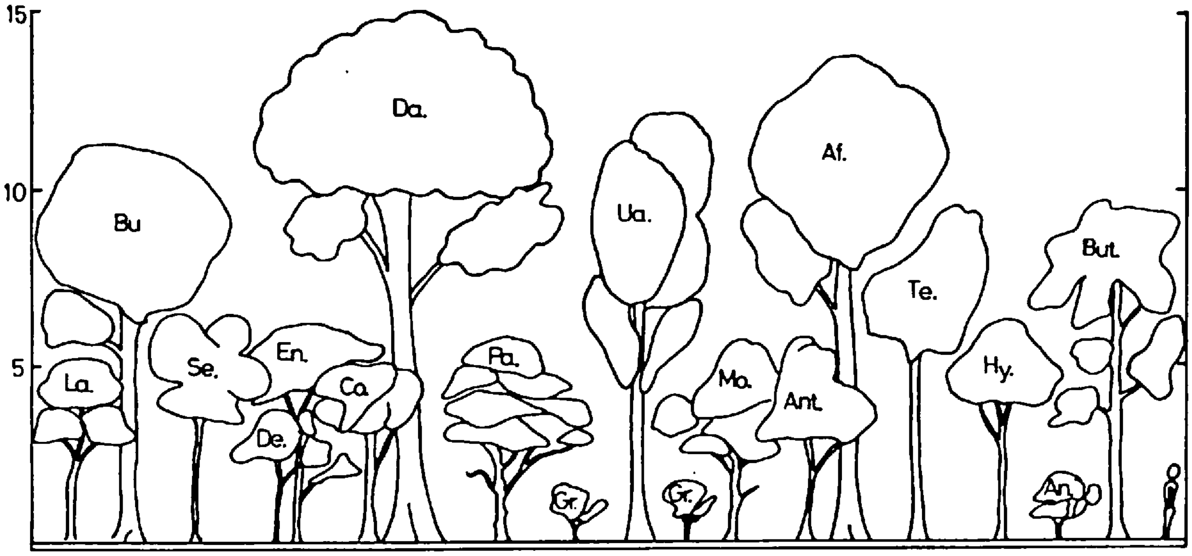


FIGURE 1.3.1 Idealised profile diagram of the heights and shapes of common trees on the study area in Southern Guinea savanna. For key to names see Table 1.3.1. Height is given in metres.

## SECTION 1.4

## LAYOUT OF THE STUDY AREA

The study area was 15 km NW of Mokwa on the Mokwa-Zugurma-New Bussa road. It lay at an altitude of 200 m on a well-drained gentle slope with a NW aspect. The area was fairly homogeneous and accessible, lying between the approximate boundaries of cultivation of Ndayako and Zugurma (Figure 1.4.1). It was reputed to have been undisturbed by farmers for at least 100 years and showed minimal signs of biotic disturbance other than the annual burning.

The study area itself (Figure 1.4.2) was 6 ha of woodland (300 x 200 m) lying roughly east-west and set back from the road. A number of quadrats designed and situated for the quantification of various features were marked inside the area:-

1) Map quadrats. The entire area was divided into 96 (12 x 8), 25 x 25 m quadrats marked with corner posts and used for enumeration, measurement and mapping of occupied and abandoned _Macrotermes bellicosus_ mounds, (Section 3.2). These quadrats were also used for estimating biomass of standing dead trees (Section 2.2).

2) Litter fall quadrats. Sixteen 10 x 10 m quadrats were used for collecting weekly samples of woody plant litter, (Section 2.1). They were positioned in the NE corners of map quadrats selected randomly in a stratified manner, with two in each of blocks 1-8 (Figure 1.4.2). One 0.25 $m^2$ leaf trap was positioned on the boundary of each quadrat.

3) Decomposition quadrats. In each of blocks 1-8, two 10 x 10 m

quadrats were used to measure decomposition of wood and leaves (Section 2.3). They were not put in the same map quadrats as litter fall quadrats, nor were they put in adjacent corners.

4) Standing crop quadrats. Similarly, 24 quadrats for measuring standing crop of wood and leaf litter were selected, three in each of blocks 1-8. Map quadrats already containing other quadrats were avoided.

5) Baiting and soil coring areas. (Section 1.2 and 2.4). Four areas 80 x 32 m were marked in a 4 m grid using aluminium foil flags on wire pegs. They were put in positions that avoided interference with other quadrats and still gave a good coverage of the study area. They were used to assess the role of each wood-feeding species of termite in wood decomposition and also for taking cores for soil moisture content.

6) Tree survey quadrats (Section 1.3). Eight 10 x 10 m quadrats were used to assess the number and species of common trees present in the study area.

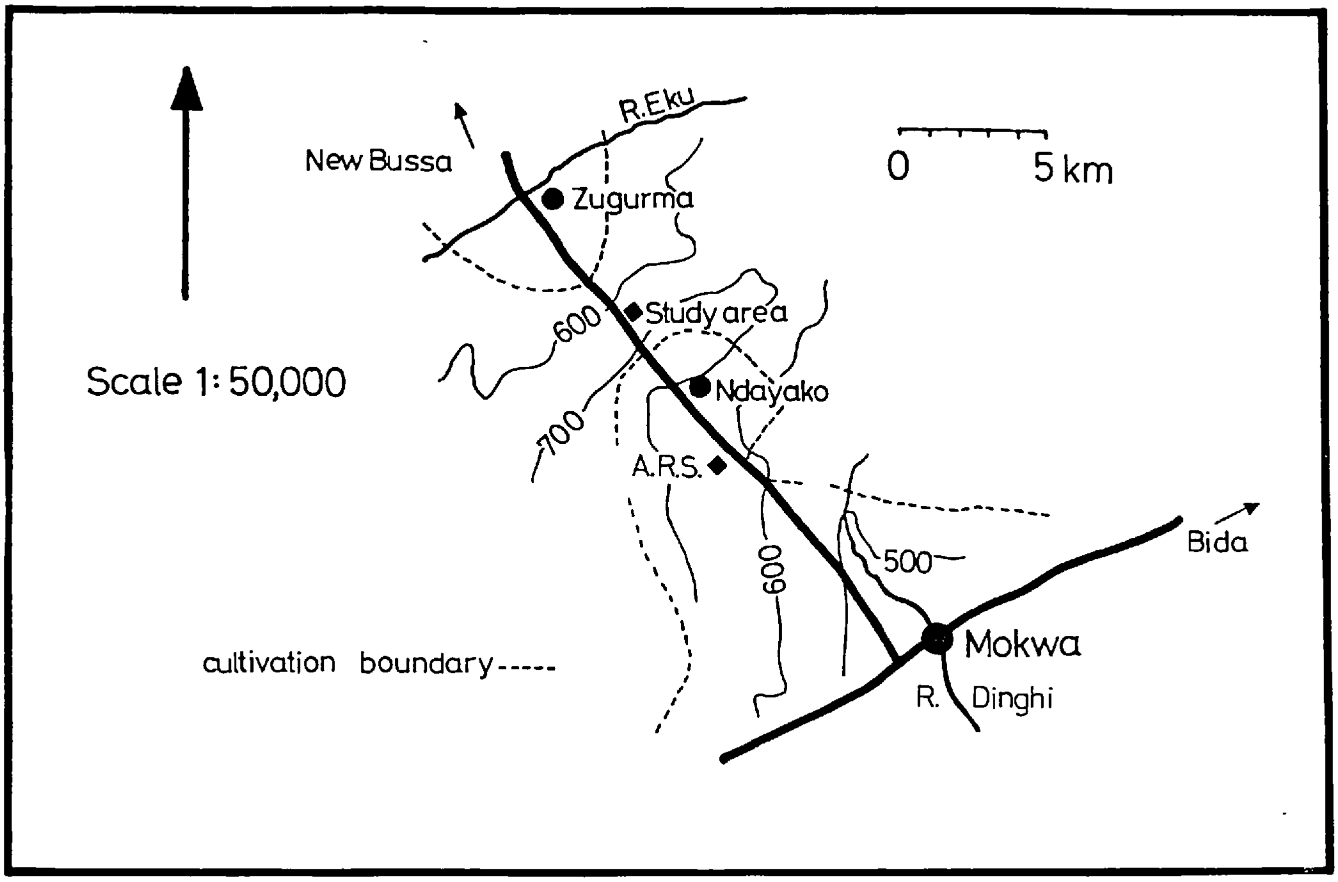


FIGURE 1.4.1 Map showing the position of the study area in relation to Mokwa, Ndayako, Zugurma and the Agricultural Research Station (A.R.S.).

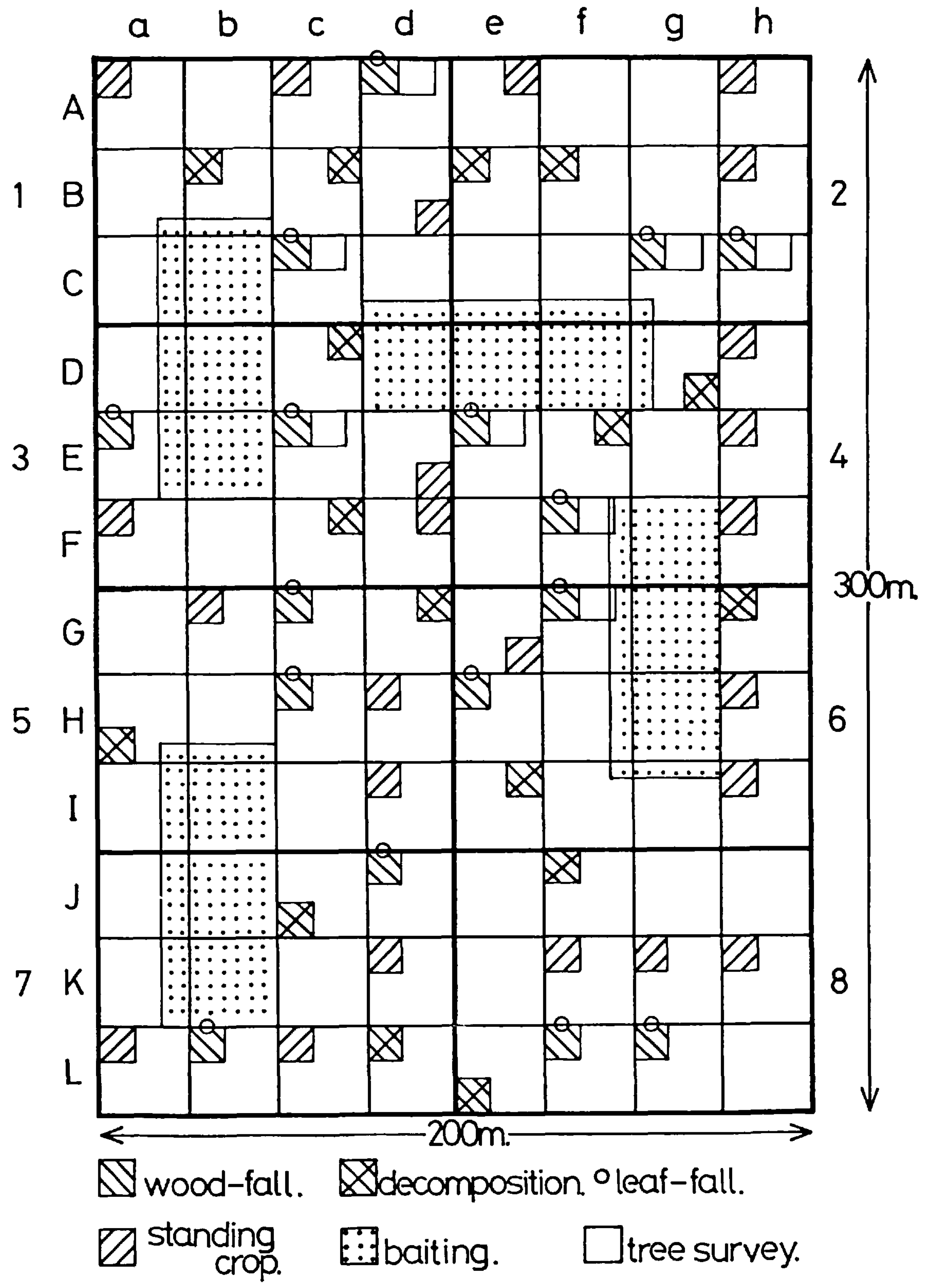


FIGURE 1.4.2 The layout of the study area.

# SECTION 1.5

# SPECIES OF TERMITES AND THEIR HABITS

## 1.5.1 SPECIES FOUND IN THE STUDY AREA

ORDER : ISOPTERA

FAMILY : RHINOTERMITIDAE Light.

SUB-FAMILY : COPTOTERMITINAE Holmgren.

*Coptotermes* Wasmann 1896.

*Coptotermes* sp.

FAMILY : TERMITIDAE Westwood.

SUB-FAMILY : TERMITINAE Sjöstedt.

*Amitermes* Silvestri 1901.

*Amitermes evuncifer* Silvestri 1912.

*Amitermes stephensoni* Harris 1957.

*Microcerotermes* Silvestri 1901.

*Microcerotermes* sp.

*Basidentitermes* Holmgren 1912.

*Basidentitermes* sp.

*Promirotermes* Silvestri 1914.

*Promirotermes* sp.

*Cubitermes* Wasmann 1906.

*Cubitermes* sp.

*Noditermes* Sjöstedt 1924.

*Noditermes* sp.

*Pericapritermes* Silvestri 1914.

*Pericapritermes* sp.

SUB-FAMILY : APICOTERMITINAE Grassé and Noirot.

*Adaiphrotermes* Sands 1972.

- *Adaiphrotermes* sp.
- *Anenteotermes* Sands 1972.
  - *Anenteotermes* sp.
- *Astalotermes* Sands 1972.
  - *Astalotermes* sp.

SUB-FAMILY : MACROTERMITINAE.

- *Microtermes* Wasmann 1902.
  - *Microtermes usambaricus* Sjöstedt 1926.
  - *Microtermes* 4 spp.
- *Ancistrotermes* Silvestri 1912.
  - *Ancistrotermes cavithorax* Sjöstedt 1899.
- *Odontotermes* Holmgren 1912.
  - *Odontotermes smeathmani* Fuller 1924.
  - *Odontotermes pauperans* Silvestri 1912.
- *Allodontermes* Silvestri 1912.
  - *Allodontermes* sp.
- *Macrotermes* Holmgren 1910.
  - *Macrotermes bellicosus* Smeathman 1781.
  - *Macrotermes subhyalinus* Rambur 1842.

SUB-FAMILY : NASUTITERMITINAE

- *Trinervitermes* Holmgren 1912.
  - *Trinervitermes geminatus* Wasmann 1897.
  - *Trinervitermes occidentalis* Sjöstedt 1904.
  - *Trinervitermes oeconomus* Träghardh 1904.
  - *Trinervitermes togoensis* Sjöstedt 1899.
  - *Trinervitermes trinervius* Rambur 1842.
- *Fulleritermes* Coaton 1962.
  - *Fulleritermes* sp.
- *Eutermellus* Silvestri 1912.
  - *Eutermellus* sp.

Total 30 species of 19 genera.

### 1.5.2 SUMMARY OF THE HABITS OF EACH SPECIES

RHINOTERMITIDAE : COPTOTERMITINAE

*Coptotermes* sp. Forages and nests in standing dead trees, sometimes extending into living tissues. Distribution is influenced by behaviour of alates which, after release in the dry season, fly until a vertical object is encountered. The female then "calls", a tandem forms and the pair moves up the substrate in search of a nesting place. The nest is fairly diffuse and contains lamellae of faecal carton.

TERMITIDAE : TERMITINAE

*Amitermes evuncifer*, *A. stephensoni*, *A. evuncifer*, the more common species, usually feeds on rotten wood. The nest is normally hypogeal, but may be partially or totally epigeal, and is made of mud with a dark faecal lining to the galleries.

*Microcerotermes fuscotibialis*. A wood litter feeder, sometimes found in standing dead items and often feeding on dead roots near the carton nest, which is frequently under the base of a tree.

*Basidentitermes* sp. A rarely encountered subterranean soil feeder, occasionally found under wet rotten logs.

*Promirotermes* sp. A very rare subterranean soil feeder.

*Cubitermes* sp., *Noditermes* sp., *Pericapritermes* sp. *Cubitermes* is quite common, *Noditermes* and *Pericapritermes* quite rare; all are soil feeders. *Cubitermes* and *Pericapritermes* were found in the soil or nesting in old *Trinervitermes* mounds. *Noditermes* was found nesting in the wall of an abandoned nest of *Macrotermes bellicosus* (C. Longhurst pers. comm.).

TERMITIDAE : APICOTERMITINAE

*Adaiphrotermes* sp. *Anenteotermes* sp. *Astalotermes* sp. Soil feeding soldierless species with simple hypogeal nests of soil and excrement. Foragers are encountered to a depth of over 2 m (T. G. Wood pers. comm.), but are rarely found near the surface. *Anenteotermes* is primarily a sub-soil feeder while *Adaiphrotermes* consumes organic rich top soil.

TERMITIDAE : MACROTERMITINAE

*Microtermes usambaricus*, *Microtermes* spp. The genus *Microtermes* is taxonomically confused but there appears to be a complex of 5 species at Mokwa (R.A. Johnson pers. comm.). The commonest genus in the savanna areas, *Microtermes* is primarily a wood feeder but is occasionally found in leaf litter. The nest consists of scattered subterranean cavities each containing a fungus comb and found to, and probably below 1.5 m, (R.A. Johnson pers. comm.). Fungus combs are also common in abandoned mounds of *Macrotermes bellicosus* and in the walls of the subterranean habitacles of living colonies.

*Ancistrotermes cavithorax*. A very common species feeding on wood litter, standing dead items and the outer bark of living trees. Foraging is under covered galleries of sub-soil. The nest is hypogeal, again consisting of a complex of fungus comb cavities at various levels in the soil.

*Odontotermes smeathmani* and *O. pauperans*. Essentially wood litter feeders but take leaves early in the rainy season. *O. pauperans* also feeds extensively on bark and grass litter. The nest is a mass of fungus combs up to 30 cm across, usually hypogeal but also in the walls of abandoned *Macrotermes bellicosus* mounds.

*Allodontermes* sp. A rare litter feeder with hypogeal nest of scattered fungus comb cavities.

*Macrotermes bellicosus*. A very common species, occurring in the savanna zones in a belt right across Africa (Ruelle 1970). The nest structure is variable, but in the Mokwa region mounds may reach 6 m high and are a prominent feature of the landscape. The mass of fungus combs is maintained in a spherical habitacle beneath the mound, (see Section 3.1 for details). The species is a wood litter feeder, also taking bark in the dry season and some leaf litter early in the rainy season. Foraging occurs under sheet-like earth coverings, mainly of brown topsoil.

Macrotermes subhyalinus. Another very common species found in the savannas of West, Central and East Africa, sometimes in forest and also in South West Africa, (Ruelle 1970). This is the largest species found in the area; it feeds on wood, leaf and grass litter under earth (mainly sub-soil) galleries. The nest is a closely associated system of cavities containing fungus combs and may be hypogeal or partially epigeal. At low elevations (e.g. around the houses and buildings of the Agric. Res. Stat. Mokwa) the nest always has irregularly domed epigeal portions, up to 1.5 m high and 2 m across. In the study area they were always hypogeal, being discernible only by a slightly domed and often bare area of hard red sub-soil on the ground surface. Alates fly throughout the rainy season, unlike M. bellicosus which flies only late April-early May, and piles of discarded wings can be found at the base of trees and fence posts. Nests are often located at the base of trees.

TERMITIDAE : NASUTITERMITINAE

Trinervitermes spp. This genus comprises the "snouted harvester termites" whose nests are a dominant feature of African savanna regions. They are essentially grass feeders, foraging in the open, cutting down grass fragments and storing them in the nest. Sands (1965a) studied 5 species in 3 areas near Zaria, N. Nigeria and found some distinct differences in nesting habits. T. geminatus (as T. ebenerianus) nests were frequent in open unshaded sites. Mounds were domed and brittle with faecal-lined galleries and often a number of satellite storage mounds around the reproductive centre. *T. oeconomus* does not store food but builds similar mounds in shady areas. At Mokwa, *T. occidentalis* built no nest of its own but usually occupied abandoned *T. geminatus* nests (C.E. Ohiagu pers. comm.). *T. togoensis* may store grass but is also restricted to abandoned nests of other species. *T. trinervius* tends to build on raised sites such as natural hummocks and old *Macrotermes* mounds. Some *Trinervitermes* spp. occasionally take wood litter.

*Fulleritermes* sp. Another nasute species which occurs frequently in woodland but disappears under clearing and cultivation (Wood 1975). The carton nest is found inside large logs but the carton-covered foraging galleries may extend up trees and into adjacent wood-litter.

*Eutermellus* sp. A rare soil-feeding nasute species with a hypogeal nest.

### 1.5.3 DISCUSSION

#### Latitude, Species Diversity and Feeding Trends.

Species lists, *per se*, are often of little interest except to the specialist and collector. However, there have been several collections made from different latitudes in W. Africa and some basic underlying principles are suggested from comparison.

Table 1.5.1 describes the number of termite species and their feeding habits from five W. African localities. Termites are almost entirely tropical or sub-tropical in distribution and the collections illustrate the general principle that the diversity of species tends to increase with proximity to the equator (e.g. Krebs 1972). The number of species is small in comparison with, e.g. Fischer's (1960) record of 222 species of ants from Brazil, and reflects the fact that termites are not a particularly diverse group of insects with about 1900 described species (Krishna 1969). This may be correlated with a lack of diversity in feeding habits. Their ecological importance is the result of their abundance and nest-building behaviour which exercise a heavy impact on tropical ecosystems.

Wood and Sands (in press) note that in the drier northerly latitudes a high proportion of species feed on fresh plant material while in the lower latitudes there are more humivores.

TABLE 1.5.1 NUMBER OF SPECIES OF TERMITES AND THEIR FEEDING HABITS IN DIFFERENT ECOSYSTEMS IN WEST AFRICA

| | Latitude | Total number of Species | Living wood and Fresh woody Litter | Grass and Herbaceous Litter | Decomposing Wood | Soil |
|---|---|---|---|---|---|---|
| Sahel savanna Senegal (1) | 16° 30'N | 19 | 11 | 8 | 0 | 3 |
| Northern Guinea Savanna Nigeria (2) | 11°N | 19 | 9 | 11 | 1 | 5 |
| Southern Guinea Savanna Nigeria (3) | 9°N | 31 | 15 | 10 | 2 | 9 |
| "Derived" savanna Ivory Coast (4) | 6°N | 36 | 18 | 11 | 3 | 13 |
| Rain-forest Cameroon (5) | 3° 36'N | 43 | 8 | 2 | 4 | 31 |

1) Lepage (1974) Total area 100 ha.

2) Sands (1965a,b) Area 1, 4 ha.

3) Wood, Johnson and Ohiagu (in press), present work. Includes primary and secondary woodland at Mokwa (7 ha).

4) Josens (1972a) Including sparsely wooded and densely wooded savanna but not including other vegetation types in the area.

5) Collins (submitted) Primary rain forest in the Cameroons, (1·5 ha).

(After Wood and Sands, in press).

# SECTION TWO

## LITTER DYNAMICS AND THE ROLE OF TERMITES IN LITTER DECOMPOSITION

In Section 1, I have briefly described the climatic, edaphic, topographic and vegetational features of Mokwa and included a species list for the study area.

There have been no previous studies on the litter dynamics of Southern Guinea savanna. In order to assess the quantitative significance of the energy flow through the population of *Macrotermes bellicosus*, it was necessary to examine the production, accumulation and decomposition of litter on the study area. *Macrotermes bellicosus* is only one of several litter-feeding species found at Mokwa and the latter part of this section describes studies designed to quantitatively separate the role of each of these species in litter removal.

# SECTION 2.1

## ANNUAL WOOD AND LEAF FALL

In this section I will describe the annual wood and leaf fall at Mokwa, the seasonality of the fall and the relationship between my results and other similar studies in West Africa.

### 2.1.1 METHODS

In some previous studies in the tropics, (e.g. Cornforth 1970, Madge 1965), fallen litter was collected in trays supported off the ground. Although such trays help to slow down decomposition between collections, they do not sample larger litter very well. For this reason 10 x 10 m quadrats marked on the ground were used for woody items.

Woody litter-fall was collected from two such quadrats positioned at random in each of the eight study area blocks (Fig.1.4.2). They were cleared of all woody litter one week before the first collection on 23 May 1974. Wood-litter of all sizes (including woody seed-pods of e.g. *Afzelia africana* Sm.) was removed at weekly intervals until 22 May 1975. It was oven-dried at 100°C for 48 hours except for very large items which were weighed wet and sub-sampled for conversion to dry weight. Weekly collections were divided into four size categories:

1) Diameter $< 0.5$ cm.
2) Diameter 0.5 - 1.0 cm.
3) Diameter 1.0 - 2.0 cm.
4) Diameter $> 2.0$ cm.

Since litter from the ground could be attacked by termites between the weekly collections, an approximation of the magnitude of this source of error was calculated by weighing separately all the items showing this attack in the last 11 weekly samples.

Leaf litter was collected in a circular, cellular-cotton, bag leaf trap of diameter 56.4 cm, depth 60 cm and catchment area 0.25m$^2$ placed on the boundary of each of the 16 litter-fall quadrats. The design was based on Newbould (1967 Fig. 3a). Leaves were collected at fortnightly intervals from 3 October 1974 to 2 October 1975, dried at 100°C for 48 hours and weighed. Two leaf-nets were absent for some of the sampling time, Ff was stolen but is included in standard error and mean calculations since it was only absent for a short period at a time of little leaf-fall. Jd was accidentally burnt and absent for several weeks. No attempt was made to categorise wood and leaves into species groups and flowers were included in leaf-fall.

Calorific values and ash content for wood from eight common species of trees were measured by taking drillings through logs (to include all parts of the log), grinding in a Glen Creston ball-mill and burning samples in a Gallenkamp ballistic bomb calorimeter. Calorific values for leaves were determined similarly using a sample of leaf litter collected during February 1976.

## 2.1.2 RESULTS

### 2.1.2.1 Wood Fall.

The regular, comparatively steady, fall of small woody items could be measured with some statistical confidence and seasonal variations noted (Table 2.1.1 (summary), Appendix 2 (in full)). Occasional larger falls of entire trees or large boughs were considered separately (Table 2.1.2) since they were not frequent enough for statistical analysis and would tend to obscure the underlying seasonal nature of the fall of smaller items. The two groups were designated as minor and major falls with the arbitrary distinction that any fall on one quadrat of over 5 kg in one week was a major fall. The final results were: total wood litter fall 1.391 t $ha^{-1}$ $a^{-1}$, of which 933.5 kg $ha^{-1}$ $a^{-1}$ were from minor wood falls and 457.5 kg $ha^{-1}$ $a^{-1}$ from major wood falls. The large proportion constituted by the major falls throws some doubt upon the accuracy of the total figure but parallel measurements of wood litter standing crop (Section 2.2) and mean decomposition rate (Section 2.3) gave results of 2.821 t $ha^{-1}$ and 50.98% $a^{-1}$ respectively, giving a calculated wood litter fall for steady state woodland of 1.438 t $ha^{-1}$ $a^{-1}$. This figure is in close agreement with the measured one.

The size-classes of wood fall are summarised in Table 2.1.3 and given in full in Appendix 2. Approximately half of the annual wood fall consisted of items of diameter $>$ 2.0 cm (size 4). Parallel decomposition rate measurements (Section 2.4) revealed that such items decompose more slowly per unit weight than small items ($<$ 2.0 cm diameter) and the proportion of fall of large and small items was accounted for in the annual decomposition rate quoted above.

Malaisse et al. (1975) working in miombo woodland near Lubumbashi, Zaire (11°41'S), provide the only comparable data. This vegetation type is similar to Northern Guinea savanna (Keay 1959). They reported wood fall $<$ 2.0 cm diameter as 0.87 t $ha^{-1}$ $a^{-1}$ but for larger items (not including trunks) 4.4 t $ha^{-1}$ $a^{-1}$ - a very high figure. Fanshawe (1971) regards miombo woodland as a recent vegetation type resulting from the destruction of dry evergreen forest and maintained as a pyroclimax by annual fires. Malaisse et al. (1973) note that it may or may not be in equilibrium. The ratio of leaf-fall to total litter-fall of 0.355 is certainly low in comparison with data from West African sites, (see Section 2.1.3.2 for further values), and suggests an abnormally high production of woody litter.

The levels of termite attack in the last 11 weekly samples are recorded in Table 2.1.4. Only 9.02% of the total weight of wood collected showed any sign of termite attack and since damage was invariably slight, errors from this source are ignored.

The calorific values and ash content for eight species of wood are given in Table 2.1.5. Five samples were taken for each species and the mean of all species calculated as 5.4634 ± 0.1399 kcal $g^{-1}$ (95% c. limits). John (1973) obtained a lower figure of 4.830 kcal $g^{-1}$ for twigs from Kade, Ghana, in semi-deciduous forest. The annual woody litter production is equivalent to 7,598,256 kcal $ha^{-1}$ $a^{-1}$.

### 2.1.2.2 Leaf Fall

Results from the 16 leaf traps are recorded in Table 2.1.1 (summary), Figure 2.1.1, and Appendix 2 (in full). Total annual leaf fall is estimated at 2.387 t $ha^{-1}$ $a^{-1}$. This is the only figure available from S.Guinea savanna but Malaisse et al. (1975) report a similar figure of 2.9 t $ha^{-1}$ $a^{-1}$ from miombo woodland in Zaire. Figure 2.1.2 shows that leaf-fall is highly seasonal with a dry-season peak from November to February. The bush-fires in January cause a temporary and rapid increase of up to 222 kg $ha^{-1}$ $wk^{-1}$ by killing, but not burning, leaves on the trees. Leaf nets were removed prior to burning and replaced immediately afterwards.

Decomposition losses from leaf traps between collections have been calculated by Kirita and Hozumi (1969). My own figures suggest that such losses are negligible at Mokwa. An equation derived by Nye (1961),

$$A \times dT = kL \times dT$$

where A = annual litter fall, L = standing crop of litter and k = decomposition constant, when applied to my data for standing crop of leaf litter, (0.903 t $ha^{-1}$ $a^{-1}$, Section 2.2.), indicates a maximum decomposition of 10.14% during a 2-week period. Assuming constant continuous leaf-fall into the nets (between collections), this is reduced to a rate of 5.4% 2 $wk^{-1}$. Wood (1974) found a positive linear correlation between decomposition, due to micro-organisms and leaching, and the annual rainfall:

$$Wm = 57.54 + 0.114\ R$$

where Wm = decomposition rate, equivalent to 1/k above, R = rainfall. His calculations were based on decomposition of alfalfa leaves in the Americas reported by Jenny et al. (1949). Applied to the Mokwa data (R = 1175 mm), the maximum decomposition is 2.71% 2 $wk^{-1}$. Errors between 2.71% and 5.4% are small enough to be ignored.

Calorific values and ash content for leaves were 4.7077 kcal $g^{-1}$ ± .2320 (95% c. limits) with 5.7% ash (Table 2.1.5). John (1973) reported comparable results of 4.856 ± 0.136 kcal $g^{-1}$ for leaf litter from semi-deciduous forest at Kade, Ghana. The total annual leaf fall is equivalent to $\underline{11{,}238{,}932\ \text{kcal ha}^{-1}\ \text{a}^{-1}}$.

TABLE 2.1.1

| QUADRAT & NET NUMBER | TOTAL ANNUAL WOOD-FALL g $100m^{-2}$ QUADRAT | TOTAL ANNUAL LEAF-FALL g $0.25m^{-2}$ net |
|---|---|---|
| Ad | 8512 | 111.571 |
| Cc | 5849 | 45.350 |
| Cg | 5430 | 38.395 |
| Ch | 7651 | 33.764 |
| Ea | 4997 | 13.482 |
| Ec | 14294 | 30.859 |
| Ee | 7526 | 80.154 |
| Ff | 8673 | 40.602 |
| Gc | 9136 | 57.622 |
| Gf | 10823 | 70.368 |
| Hc | 9297 | 81.221 |
| He | 14711 | 60.418 |
| Jd | 13561 | (9.559) |
| Lb | 10124 | 44.388 |
| Lf | 4975 | 64.575 |
| Lg | 13790 | 125.755 |
| MEAN<br>95% CONF. | 9334.31<br>±1775.10 | 59.902<br>±15.407 |

| WEEK NUMBERS AND DATES | WOOD-FALL kg $ha^{-1}$ ±95% conf.lts. | % OF TOTAL 4 $wk^{-1}$ | LEAF-FALL kg $ha^{-1}$ ±95% conf.lts. | % OF TOTAL 4 $wk^{-1}$ |
|---|---|---|---|---|
| 1-4<br>23.5-19.6.74 | 105.269<br>±40.370 | 11.28 | (1975) 40.118<br>±17.925 | 1.68 |
| 5-8<br>20.6-17.7 | 119.368<br>±52.301 | 12.79 | 32.383<br>±17.185 | 1.36 |
| 9-12<br>18.7-14.8 | 69.070<br>±41.451 | 7.40 | 55.868<br>±38.344 | 2.34 |
| 13-16<br>15.8-11.9 | 60.912<br>±23.347 | 6.53 | 39.988<br>±36.373 | 1.63 |
| 17-20<br>12.9-9.10 | 69.082<br>±23.103 | 7.40 | 63.724<br>±21.567 | 2.67 |
| 21-24<br>10.10-6.11 | 45.962<br>± 9.627 | 4.92 | (1974) 153.274<br>±56.235 | 6.42 |
| 25-28<br>7.11-4.12 | 32.157<br>± 6.512 | 3.45 | 312.263<br>±142.681 | 13.08 |
| 29-32<br>5.12-1.1.75 | 31.595<br>± 9.582 | 3.38 | 381.293<br>±67.254 | 15.97 |
| 33-36<br>2.1-29.1 | 70.957<br>±20.359 | 7.60 | 682.072<br>±392.642 | 28.57 |
| 37-40<br>30.1-26.2 | 83.613<br>±12.361 | 8.96 | 373.678<br>±181.706 | 15.65 |
| 41-44<br>27.2-26.3 | 67.400<br>±10.753 | 7.22 | 133.240<br>±45.425 | 5.58 |
| 45-48<br>27.3-23.4 | 61.194<br>±11.560 | 6.56 | 82.008<br>±43.112 | 3.44 |
| 49-52<br>24.4-22.5 | 116.857<br>±88.630 | 12.52 | 38.443<br>±28.332 | 1.61 |
| TOTALS | 933.431<br>kg $ha^{-1}$ $a^{-1}$ | 100 | 2387.351<br>kg $ha^{-1}$ $a^{-1}$ | 100 |

Summary of the minor wood-fall and leaf-fall data. Collections have been grouped into 4-week blocks.

| QUADRAT NUMBER | WEEK NUMBER | WOOD-FALL g | ANNUAL WOOD-FALL kg ha$^{-1}$ |
|---|---|---|---|
| Jd | 29 | 13431 | |
| Jd | 48 | 54543 | |
| He | 48 | 5198 | |
| TOTALS | | 73172 | 457.325 |

TABLE 2.1.2 Data from all major wood falls during the year.

| SIZE-CLASS | | TOTAL ANNUAL FALL, g 1600m$^{-2}$ | TOTAL FALL kg ha$^{-1}$ a $^{-1}$ | % OF TOTAL IN EACH CLASS |
|---|---|---|---|---|
| MINOR WOOD-FALL | 1 | 59629 | 372.681 | 26.797 |
| | 2 | 26405 | 165.031 | 11.866 |
| | 3 | 27395 | 171.219 | 12.311 |
| | 4 | 35920 | 224.500 | 49.026 |
| MAJOR WOOD-FALL (4) | | 73172 | 457.325 | |
| | | 222521 | 1390.756 | 100.00 |

TABLE 2.1.3 The size distribution of all wood litter fall during the year.

| WEEK NUMBER | TOTAL WOOD-FALL g | WEIGHT OF WOOD SHOWING SIGNS OF TERMITE ATTACK g | % OF TOTAL |
|---|---|---|---|
| 42 | 2168 | 0 | 0 |
| 43 | 3807 | 486 | 12.77 |
| 44 | 2088 | 84 | 4.02 |
| 45 | 2275 | 154 | 6.77 |
| 46 | 1905 | 92 | 4.83 |
| 47 | 2758 | 693 | 25.13 |
| 48 | 2853 | 578 | 20.26 |
| 49 | 4807 | 127 | 2.64 |
| 50 | 6900 | 387 | 5.61 |
| 51 | 1434 | 134 | 9.34 |
| 52 | 5556 | 562 | 10.12 |
|  | 36551 | 3297 | 9.02% |

TABLE 2.1.4 The weight of items showing signs of termite attack in the final 11 weekly wood litter collections.

TABLE 2.1.5

| ITEM | MEAN CALORIFIC VALUE (K cal $g^{-1}$) | 95% CONFIDENCE LIMITS | MEAN % ASH |
|---|---|---|---|
| *Afzelia africana* | 5.2925 | ± 0.1237 | 3.018 |
| *Daniellia oliveri* | 5.3349 | ± 0.1971 | 1.565 |
| *Butyrospermum paradoxum* | 5.4725 | ± 0.0759 | 1.730 |
| *Burkea africana* | 5.8019 | ± 0.1351 | < 0.5 |
| *Entada africana* | 5.4851 | ± 0.1636 | 0.725 |
| *Detarium microcarpum* | 5.5225 | ± 0.1403 | < 0.5 |
| *Parinari polyandra* | 5.2912 | ± 0.0983 | < 0.5 |
| *Uapaca togoensis* | 5.5069 | ± 0.0984 | 1.3124 |
| Mean all trees | 5.4634 | ± 0.1399 | |
| Leaves | 4.7077 | ± 0.2320 | 5.702 |

Calorific values of various woods and leaves from Southern Guinea savanna, Mokwa.

## 2.1.3 DISCUSSION

### 2.1.3.1 Seasonal Variation in Litter Fall

The pattern of leaf fall in the tropics varies greatly with latitude. In the rain forest of Colombia (Jenny et al. 1949) and Malaya (Mitchell in Bray and Gorham 1964) litter fall was shown to be continuous throughout the year with a tendency to be slightly higher in the first six months. In drier conditions near the savanna edge Madge (1965) in Ibadan, Nigeria (7.5$^{o}$N), John (1973) in Kade, Ghana (6$^{o}$N) and Bernhard (1970) at Banco, Ivory Coast (5.5$^{o}$N) all recorded high seasonal variation with a peak at January - March. These figures from Mokwa (9$^{o}$N) are the first recorded for W.African savanna. Leaf fall was markedly seasonal, being high from October to April with a peak in January, (Fig. 2.1.1.)

Clearly, in the more northerly tropical latitudes the climate is more seasonal, evergreen forests are replaced by deciduous woodland and the leaf fall becomes increasingly seasonal.

Wood fall is less seasonal. John (1973) recorded no significant differences between monthly falls in Kade, Ghana. At Mokwa, however, minor wood fall has a small peak in February after the fires and a more obvious peak in May - July which may be due to heavy rain storms bringing down dead timber (Fig. 2.1.1.).

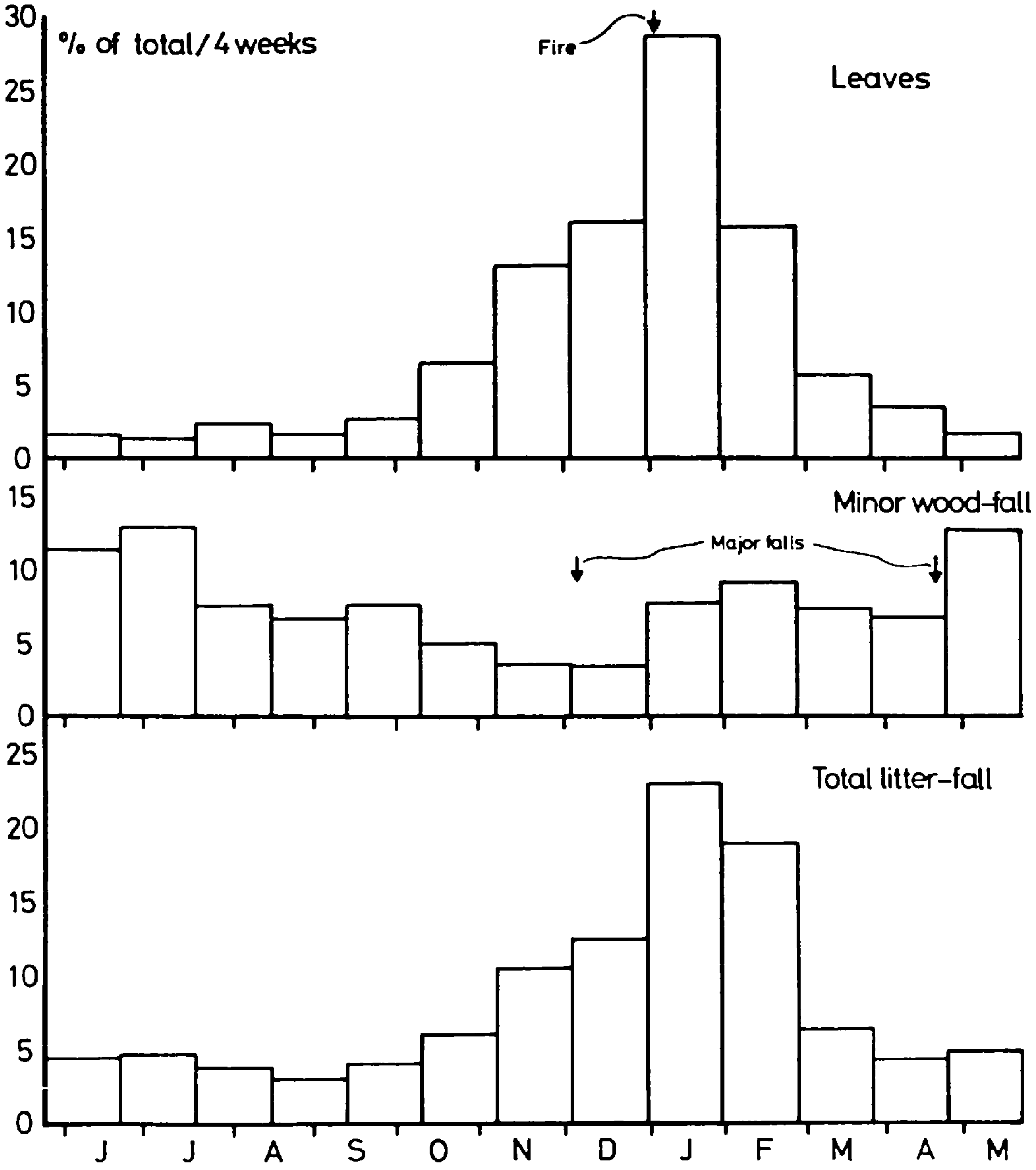


FIGURE 2.1.1 The seasonal distribution of leaf fall, minor wood fall and total litter fall, shown in four-week blocks. Note that wood and leaf fall were not measured entirely contemporaneously.

### 2.1.3.2 Litter Production and Latitude

An inverse relationship between latitude and litter production in the forests of the world was noted by Bray and Gorham (1964). The maximum level of about 15 t $ha^{-1}$ $a^{-1}$ at the equator declined to less than 1 t $ha^{-1}$ $a^{-1}$ at 65°N in the Arctic. There was a shortage of data between 6° and 30° of latitude and the work of the last 15 years in West Africa now permits a more detailed review of this zone.

Latitudes 6 - 30°N in West Africa extend from rain forest to the Sahara Desert and Table 2.1.6 summarises information on litter production for the region. Hopkins' (1966) figures for leaf fall have been extrapolated to total litter fall using a mean ratio of leaf fall to total litter fall of 0.683, derived from my own study (0.632), Madge (1965, 0.666), Nye (1961, 0.666) and John (1973, 0.767). This extrapolation is not justified for the leaf fall figures of Brynaert et al. (in Bray and Gorham 1964) since there is no comparable published information from equatorial rain forests.

A linear regression of annual litter production against latitude ($p < 0.001$) is combined with part of Bray and Gorham's (1964) Fig. 1 in Figure 2.1.2. A better fit to the data is a linear regression of log total litter fall against latitude:

$$y = 1.225 - 0.055x, \quad r = 0.9098, \quad p < 0.001$$

In general the figures for leaf fall, although fewer, are in agreement with the relationship.

It is clear from Figure 2.1.2 that Bray and Gorham's generalisation, while broadly correct, does not hold in the restricted zone of rapid climatic change north of the equator in West Africa. Here, litter production declines rapidly from about 15 t $ha^{-1}$ $a^{-1}$ to 1-2 t $ha^{-1}$ $a^{-1}$ at the edge of the Sahara Desert. Since deserts tend to occur on all major land masses at similar latitudes, the same probably occurs elsewhere. North of the desert the production will increase again, (dashed line Fig. 2.1.2 - no supporting data), and then decline as temperature becomes prohibitive with higher latitude, in accordance with Bray and Gorham's (*loc. cit.*) hypothesis.

TABLE 2.1.6 Litter production in various W. African localities.

| LOCATION | LATITUDE NORTH | RAINFALL mm | VEGETATION | LITTER-FALL $t\ ha^{-1}\ yr^{-1}$ |  |  |  | LOG TOTAL | AUTHORITY |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | LEAVES | GRASS | OTHER | TOTAL |  |  |
| Zaire, Yangambi | 1° | 1700 | Mixed rain-forest |  |  |  | 12.3 | 1.0899 | Bartholomew et al.(1953) |
| " " | 1° | 1700 | Young secondary forest |  |  |  | 14.9 | 1.1732 | Laudelout and Meyer(1954) |
| " " | 1° | 1700 | <u>Macrolobium</u> forest |  |  |  | 15.3 | 1.1847 | " |
| " " | 1° | 1700 | Mixed forest |  |  |  | 12.4 | 1.0934 | " |
| " " | 1° | 1700 | <u>Brachystegia</u> forest |  |  |  | 12.3 | 1.0899 | " |
| Zaire, Ituri | 2° |  | <u>Eucalyptus saligna</u> | 8.3 |  |  |  |  | Brynaert et al. in Bray & Gorham (1964) |
| " " | 2° |  | <u>Cupressus lusitanica</u> | 2.9 |  |  |  |  | " |
| " " | 2° |  | Mixed forest | 8.5 |  |  |  |  | " |
| Ivory Coast, Banco | 5.5° | 2100 | Moist evergreen forest | 8.12 |  | 2.72 | 10.84 | 1.0349 | Bernhard (1970) |
| " ", Yapo | 5.8° | 1800 | Moist evergreen forest | 6.69 |  | 2.64 | 9.33 | 0.9700 | " |
| Ghana, Kade | 6° | 1630 | Moist semi-deciduous | 7.02 |  | 3.52 | 10.54 | 1.0228 | Nye (1961) |
| " " | 6° | 1630 | Moist semi-deciduous | 7.41 |  | 2.25 | 9.66 | 0.9850 | John (1973) |
| Ivory Coast, Lamto | 6° | 1297 | "Derived" savanna |  |  |  | 4.80 | 0.6812 | Josens (1972) |
| Nigeria, Omo | 7° | 2072 | Moist evergreen | 7.17 |  | 3.33 (2) | 10.50 (2) | 1.0212 | Hopkins (1966) |
| " , Olokomeji | 7.5° | 1232 | Dry semi-deciduous | 4.67 |  | 2.18 (2) | 6.85 (2) | 0.8357 | " |
| " , Ibadan | 7.5° | 1200 | Mixed dry lowland forest | 3.73 |  | 1.87 | 5.60 | 0.7482 | Madge (1965) |
| " , Mokwa | 9° | 1175 | Southern Guinea savanna | 2.39 (3) | 1.55 | 1.39 | 5.33 | 0.7267 | Present work |
| Senegal, Fétè-Olé | 16.5° | 435 (1) | Sahel savanna |  | 1.50 | 0.10 | 1.60 | 0.2041 | Bille (1973a & b) in Lepage (1974) |

Key: 1) Mean of Podar and Linguere, not drought years, (Lepage 1974). 2) Calculated data. 3) T.G. Wood and C.E. Ohiagu, unpubl. data.

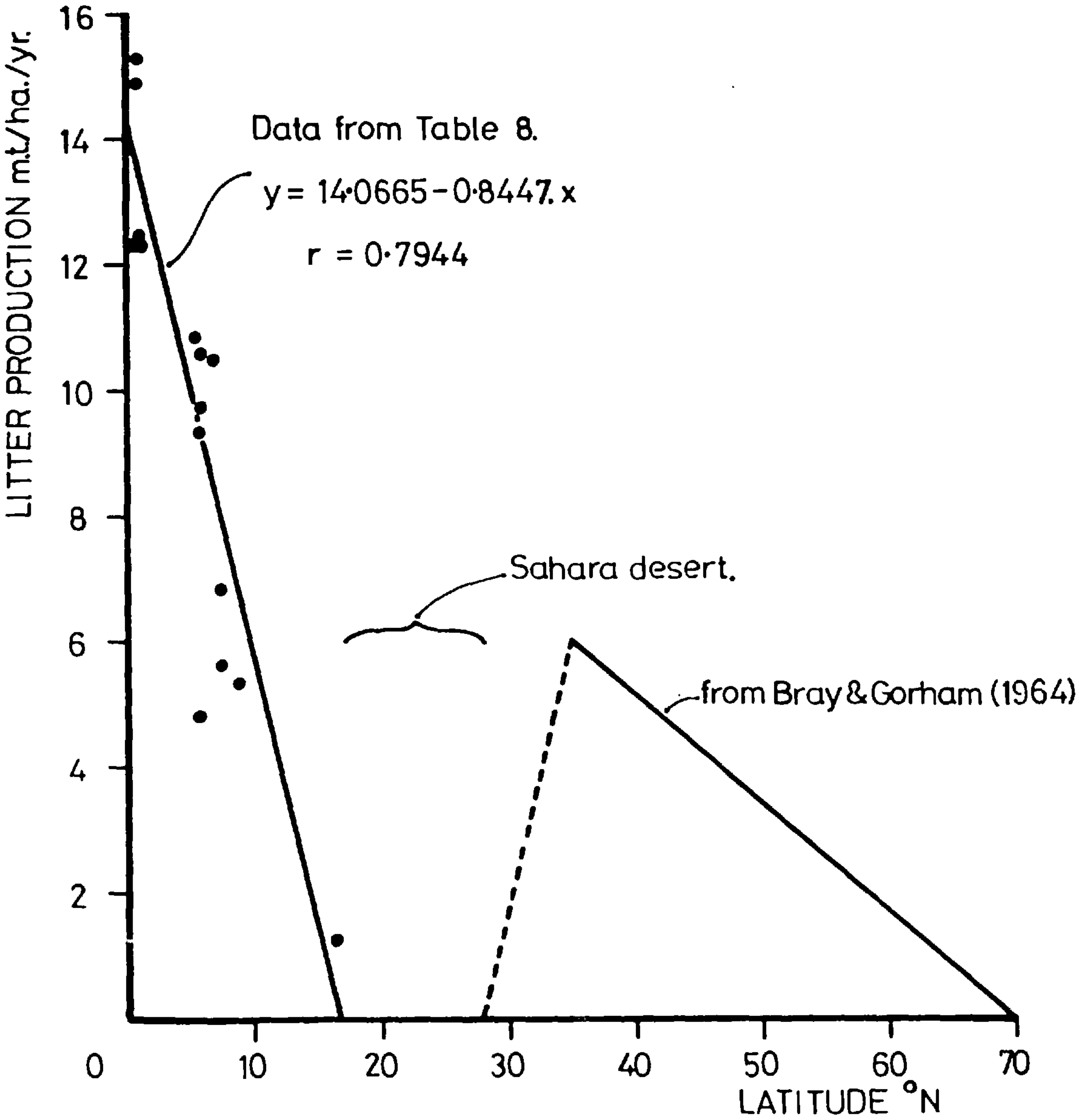


FIGURE 2.1.2 Annual production of total litter in relation to latitude using data from Table 2.1.6 and Bray and Gorham (1964).

### 2.1.3.3 Litter Production and Environmental Factors

Bray and Gorham's (1964) assumption that temperature is the controlling factor at all latitudes is clearly not valid in West Africa. From 6 - 30$^{o}$N, the litter production falls rapidly while the mean temperature is rising. Rainfall, however, declines very rapidly with latitude. Madge (1965) found little correlation between litter production and rainfall but addition of more recent data (Table 2.1.6) suggests a very strong positive correlation illustrated in Figure 2.1.3. ($p < 0.001$), suggesting that rainfall is a powerful factor in limiting litter production in these latitudes.

Whittaker (1970 Fig. 4.1) found a similar correlation between net annual primary production and rainfall and noted that the production supported by a given rainfall may be affected by the seasonal distribution of the precipitation. The data from Yangambi in Zaire (Fig. 2.1.3) show a departure from the linear correlation in higher latitudes. Litter production is very high but the annual rainfall is only 1700 mm. An examination of rainfall patterns has shown that all sites in Table 2.1.6 except Yangambi have two or more months with little or no rainfall, the length of the dry season increasing with latitude. At Yangambi the rainfall is more evenly distributed, the lowest in any month being 53 mm (courtesy Met. Office, Bracknell). This can be compared to Kade, Ghana with 1630 mm of rain but with two months with less than 20 mm.

Hence, although annual rainfall is an important factor in litter production, there is a suggestion, in keeping with Whittaker's contention, that the annual distribution of the rain may also be a limiting factor outside the equatorial rain forests. Data from an area of very high rainfall and low seasonality such as the Cameroon rain forest would be most valuable since in this region the absolute maximum litter production in West Africa might be expected.

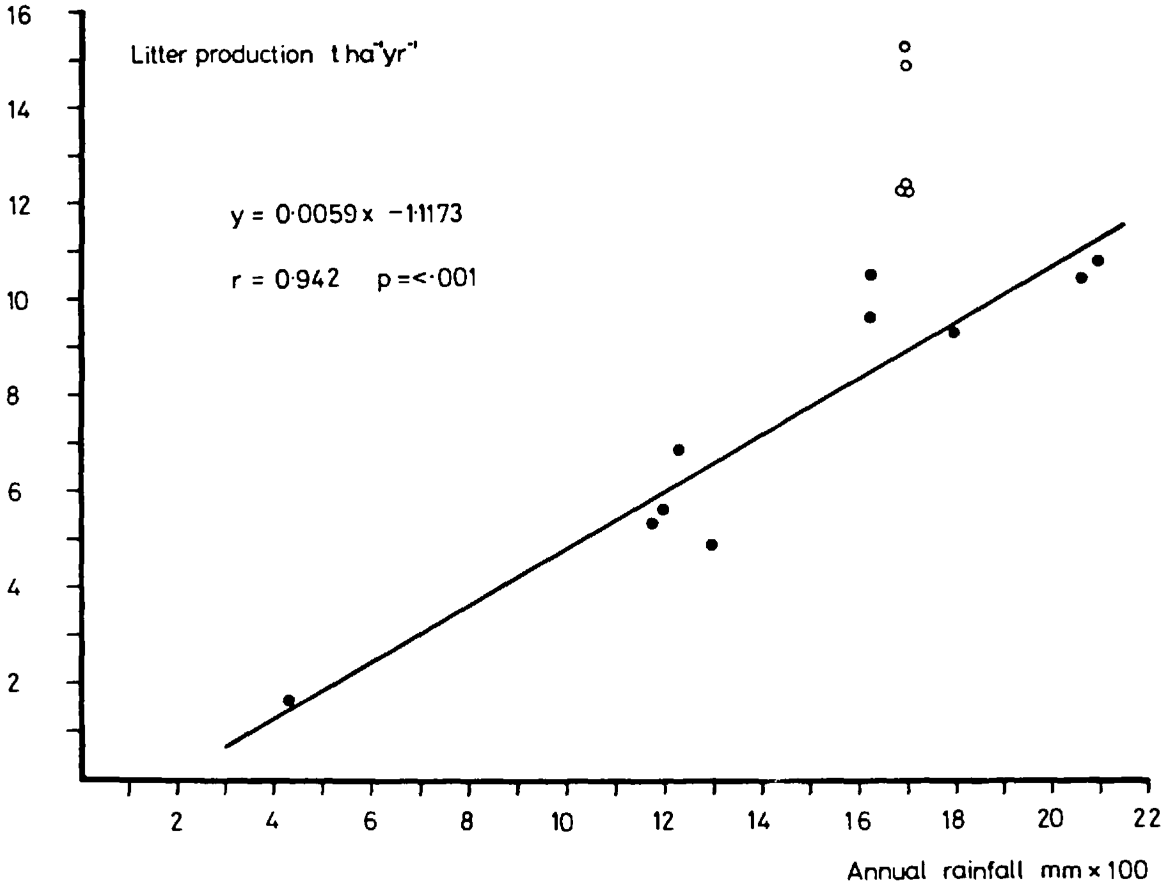


FIGURE 2.1.3 The relationship between rainfall and litter production in West Africa. Open circles (Yangambi data) have been excluded from the correlation (see text).

# SECTION 2.2

## THE STANDING CROPS OF WOOD AND LEAF LITTER

### 2.2.1 METHODS

The standing crops of wood and leaf litter were measured between March 1975 and March 1976. The main purpose was to provide a check on annual wood and leaf fall and decomposition rates using Nye's (1961) equation:

$$A \times dT = kL \times dT$$

where A = annual litter fall, L = standing crop, k = the decomposition constant. A for wood and leaves has been discussed in Section 2.1 and k for wood is given in Section 2.3.

Samples were taken on 30.12.1975 and 12.1.1976 to assess the significance of fire in removal of litter. The study area was burnt on 9 and 10 of January and the differences between the standing crops are taken as losses caused by fire.

#### 2.2.1.1 Wood Litter

The programme for dead wood was in two sections:

a) Totals of wood litter on the ground plus standing dead items of diameters < 5 cm at breast height (d.b.h.) were estimated four times in 10 x 10 m quadrats selected by stratified random means. On each occasion 24 such samples, i.e. three from blocks 1-8 of the study area, were examined, (Figure 1.4.2). Quadrats were positioned in any of the four corners of the map square selected. Collections were made on 30.7.1975, 30.12.1975 (pre-fire), 12.1.1976 (post-fire) and 3.3.1976. Wood collections were weighed on a Salter 10 kg top-loading spring balance in the field and then replaced over the quadrat. Samples for dry weight estimation were taken from outside the quadrats. The fifth estimate of the standing crop was from the eight tree survey quadrats on 25.3.1975. This included <u>all</u> standing dead items.

In the collection of 3.3.1976 the relative proportions of sticks of diameter $< 2.0$ cm and logs $> 2.0$ cm were estimated.

b) Standing dead items of d.b.h. $> 5.0$ cm were too scattered to be reliably estimated on the 24 quadrats. Thus, a survey of all such items was done on the whole study area (6 ha) in March 1976. The biomass is assumed to be relatively stable through the year and the single estimate is used as an annual mean. Height and d.b.h. of each item were recorded and volume calculated from the equation:

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

where Vp = volume of wood, r = radius of tree at breast height, h = tree height. The equation assumes that the bole of the tree approaches a paraboloid of rotations (Newbould 1967, p15) and is appropriate for most trees in S. Guinea savanna.

To convert volumes into biomass the densities of eight species of wood were measured by weighing and water displacement of dry samples; the mean of the values is used in the calculations.

### 2.2.1.2 Leaf Litter

The standing crop of leaf litter was measured five times on the 24 quadrats by throwing three 0.5 $m^2$ wire quadrats in each site (total of 72 samples), collecting the leaves within, drying for 48 hours at 100°C and weighing. In addition, the standing crop on seven of the eight tree survey quadrats was measured once on 25.3.1975 by raking the entire quadrat, weighing the leaves and sub-sampling for dry weight estimation.

## 2.2.2 RESULTS

### 2.2.2.1 Wood Litter

The standing crop results for wood litter are given in Table 2.2.1. During the year the biomass varied from 1267 to 2398 kg $ha^{-1}$ (Figure 2.2.1). The biomass of standing dead items is included in Table 2.2.1 as a total, given as a summary in Table 2.2.2 and in full in Appendix 2. The mean volume of items per map square was 104,972 cc ± 29,467 (95% limits). The mean density of eight species of dry wood (Table 2.2.3) was 0.649 g $cc^{-1}$ ± 0.101 (95% limits). The total biomass of standing dead trees of d.b.h. $>$ 5.0 cm is calculated as 6537.669 kg, this being 1090 kg $ha^{-1}$ ± 306 (95% limits). Thus the total standing crop of dead wood varied from 2.299 to 3.488 t $ha^{-1}$ (Table 2.2.1). The mean has been calculated in Table 2.2.4 as $\underline{2.821\ t\ ha^{-1}}$. The irregular sampling periods have been accounted for in calculation of the figure.

Of the samples collected on 3.3.1976, 977.5 kg $ha^{-1}$ were items $>$ 2.0 cm diameter and 289.5 kg $ha^{-1}$ $<$ 2.0 cm diameter. With the inclusion of standing dead items, 87.72% of the total weight (2357 kg $ha^{-1}$) were items of diameter $>$ 2.0 cm.

Losses of wood litter to the fire were very low. Only 3 kg were lost from the 24 quadrats, representing 12.5 kg $ha^{-1}$ or 0.9% of the annual wood fall. Losses of standing dead items were not estimated and are assumed to be very low.

TABLE 2.2.1 STANDING CROPS OF WOOD LITTER

| QUADRAT NUMBER (100 $m^2$) | S.CROP WOOD LITTER 25.3.1975 | QUADRAT NUMBER (100 $m^2$) | STANDING CROP WOOD LITTER kg | | | |
|---|---|---|---|---|---|---|
| | | | 30.7.1975 | 30.12.1975 | 12.1.1976 | 3.3.1976 |
| Ad | 10.74 | Aa | 16.38 | 7.43 | 7.82 | 6.90 |
| Cc | 7.61 | Ac | 75.02 | 34.06 | 30.26 | 33.00 |
| Cg | 55.64 | Ae | 31.53 | 14.66 | 14.46 | 16.05 |
| Ch | 10.71 | Ah | 125.33 | 84.91 | 77.58 | 78.65 |
| Gf | 54.76 | Bd | 22.16 | 13.53 | 11.84 | 10.70 |
| Ff | 17.03 | Bh | 4.17 | 2.60 | 2.45 | 3.10 |
| Ee | 18.85 | Dh | 7.63 | 16.59 | 13.83 | 13.40 |
| Ec | 28.00 | Ed | 5.00 | 2.49 | 2.23 | 2.50 |
| | | Eh | 51.07 | 27.09 | 21.38 | 19.70 |
| | | Fa | 10.62 | 3.50 | 3.27 | 3.50 |
| | | Fd | 11.28 | 7.50 | 7.47 | 7.45 |
| | | Fh | 12.1 | 4.07 | 3.53 | 2.72 |
| | | Gb | 7.40 | 4.30 | 4.49 | 5.20 |
| | | Ge | 10.51 | 4.24 | 4.09 | 5.40 |
| | | Hd | 17.25 | 9.05 | 11.32 | 11.65 |
| | | Hh | 6.63 | 2.21 | 1.50 | 1.09 |
| | | Id | 8.78 | 2.88 | 3.22 | 4.02 |
| | | Ih | 45.85 | 31.00 | 26.35 | 23.42 |
| | | Kd | 16.00 | 6.07 | 7.29 | 5.51 |
| | | Kf | 14.80 | 7.35 | 6.20 | 8.25 |
| | | Kg | 10.83 | 6.20 | 5.02 | 3.22 |
| | | Kh | 68.30 | 39.42 | 39.42 | 26.10 |
| | | La | 21.15 | 5.47 | 5.47 | 4.46 |
| | | Lc | 53.50 | 35.42 | 36.59 | 35.47 |
| Mean | 25.05 | Mean | 27.24 | 15.50 | 14.46 | 13.81 |
| ±95% limits | ±14.52 | ±95% limits | ±11.69 | ±7.56 | ±6.97 | ±6.78 |
| % Dry | As per 3/1975 | % Dry | 88.03 | 90.918 | 97.241 | 91.772 |
| Dry wt. of mean | 22.99 | Dry wt. of mean | 23.98 | 14.09 | 14.06 | 12.67 |
| kg $ha^{-1}$ dry wt | 2299 ± 1333 | kg $ha^{-1}$ dry wt | 2398±1029 | 1409±687 | 1406±678 | 1267±622 |
| | | Standing dead | 1090± 306 | 1090±306 | 1090±306 | 1090±306 |
| Total kg $ha^{-1}$ 95% limits | 2299 ±1333 | Total kg $ha^{-1}$ 95% limits | 3488 ± 1335 | 2499 ± 993 | 2496 ± 984 | 2357 ± 928 |

TABLE 2.2.2 BIOMASS OF STANDING DEAD TREES ON 96 25 x 25 m MAP SQUARES

| MAP SQUARE | STANDING DEAD TREES VOLUME | MAP SQUARE | STANDING DEAD TREES VOLUME | MAP SQUARE | STANDING DEAD TREES VOLUME |
|---|---|---|---|---|---|
| A a | 0 | F a | 0 | K a | 7540 |
| b | 101945 | b | 0 | b | 83998 |
| c | 190051 | c | 26546 | c | 77676 |
| d | 63716 | d | 9425 | d | 0 |
| e | 187553 | c | 205578 | e | 26134 |
| f | 152445 | f | 129041 | f | 484512 |
| g | 38485 | g | 0 | g | 0 |
| h | 49873 | h | 125664 | h | 0 |
| B a | 7952 | G a | 18791 | L a | 0 |
| b | 73631 | b | 517499 | b | 76341 |
| c | 46181 | c | 32142 | c | 22619 |
| d | 97487 | d | 17495 | d | 530144 |
| e | 0 | e | 736271 | e | 4811 |
| f | 11781 | f | 12723 | f | 90674 |
| g | 0 | g | 408721 | g | 80817 |
| h | 47006 | h | 356885 | h | 40212 |
| C a | 17200 | H a | 0 | | |
| b | 25447 | b | 95033 | $\bar{x}$ | 104972.21<br>± 29467.49 |
| c | 77401 | c | 0 | | |
| d | 168625 | d | 0 | | |
| e | 236878 | e | 6362 | | |
| f | 83901 | f | 253212 | | |
| g | 177618 | g | 160025 | TOTAL VOLUME | 10,077,332cc |
| h | 321228 | h | 23090 | | |
| D a | 7854 | I a | 384767 | MEAN DENSITY | 0.649 $gcc^{-1}$ |
| b | 46181 | b | 146555 | | |
| c | 90458 | c | 103436 | TOTAL BIOMASS | 6537.669 kg |
| d | 0 | d | 127549 | | |
| e | 167957 | e | 69272 | | |
| f | 9955 | f | 145299 | BIOMASS kg $ha^{-1}$ | 1089.612 |
| g | 661250 | g | 165325 | | |
| h | 11310 | h | 28373 | 95% LIMITS | ± 306 |
| E a | 12724 | J a | 0 | | |
| b | 3848 | b | 23228 | | |
| c | 5027 | c | 208444 | | |
| d | 254548 | d | 26959 | | |
| e | 20735 | e | 0 | | |
| f | 241079 | f | 0 | | |
| g | 115532 | g | 74888 | | |
| h | 79521 | h | 8875 | | |

TABLE 2.2.3 DENSITIES OF EIGHT SPECIES OF WOOD WITH MEAN VALUE

| SAMPLE SPECIES | SAMPLE DRY WEIGHT g | SAMPLE VOLUME cc | DENSITY g $cc^{-1}$ |
|---|---|---|---|
| *Daniellia oliveri* | 158 | 240 | 0.658 |
| *Afzelia africana* | 106 | 315 | 0.337 |
| *Butyrospermum paradoxum* | 83 | 112 | 0.741 |
| *Detarium microcarpum* | 96 | 141 | 0.680 |
| *Parinari polyandra* | 115 | 203 | 0.567 |
| *Entada africana* | 173 | 230 | 0.752 |
| *Burkea africana* | 141 | 176 | 0.801 |
| *Uapaca togoensis* | 117 | 178 | 0.654 |
| MEAN | | | 0.649<br>± 0.101 |

## TABLE 2.2.4 CALCULATION OF MEAN STANDING CROP OF WOOD LITTER

The mean is derived from $\frac{\Sigma\ (S.C.\ x\ T)}{366}$

| DAY | DATE | STANDING CROP, t ha$^{-1}$ (S.C.) | NUMBER DAYS AT THIS LEVEL (T) | NUMBER DAYS x STANDING (S.C. x T) |
|---|---|---|---|---|
| 1 | 15.3.75 | - | - | - |
| 11 | 25.3.75 | 2.299 | 74.5 | 171.276 |
| 138 | 30.7.75 | 3.488 | 140 | 488.320 |
| 291 | 30.12.75 | 2.499 | 80.5 | 201.170 |
| 299 | 12.1.76 | 2.496 | 32 | 79.872 |
| 355 | 3.3.76 | 2.357 | 39 | 91.923 |
| | MEAN | 2.821 | 366 | 1032.561 |

### 2.2.2.2 Leaf Litter

The standing crops of leaf litter are given in Table 2.2.5. The biomass varied greatly during the year, from 290.17 kg ha$^{-1}$ to 1643 kg ha$^{-1}$, with a calculated mean of 0.903 t ha$^{-1}$ (Table 2.2.6).

Losses of leaf litter to fire were considerable, the standing crop dropping from 1463 to 290 kg ha$^{-1}$, a loss of 1173 kg ha$^{-1}$ or 49.1% of the annual leaf fall. Practically all the leaves were burnt, only patches escaping the fire.

### 2.2.2.3 Calorific Values

Calorific values for the data recorded in this section, calculated from Table 2.1.5, are as follows:-

Mean standing crop of wood litter : 9,457,145 kcal ha$^{-1}$
Standing crop of standing dead trees : 5,955,106 kcal ha$^{-1}$
Standing crop of total dead wood : 15,412,251 kcal ha$^{-1}$
Annual losses of wood to fire : 68,293 kcal ha$^{-1}$a$^{-1}$
Mean standing crop of leaf litter : 4,248,969 kcal ha$^{-1}$
Annual losses of leaves to fire : 5,520,296 kcal ha$^{-1}$a$^{-1}$

TABLE 2.2.5 Results of leaf standing crop measurements.

| QUADRAT NO. | STANDING CROP OF LEAVES (DRY WT.) g 0.5 m$^{-2}$ 12.8.1975 | 23.10.1975 | 30.12.1975 | 12.1.1976 | 3.3.1976 |
|---|---|---|---|---|---|
| Aa | 11.1 | 12 | 60 | 16.3 | 44 |
| | 16.2 | 12 | 84 | 2.0 | 38 |
| | 22.5 | 20 | 63 | 10.3 | 42 |
| Ac | 96.5 | 17 | 74 | 13.0 | 51 |
| | 93.0 | 7 | 106 | 1.6 | 49 |
| | 73.0 | 12 | 38 | 6.6 | 57 |
| Ae | 37.0 | 14 | 130 | 3.2 | 63 |
| | 30.5 | 4 | 64 | 8.3 | 43 |
| | 56.9 | 40 | 52 | 6.6 | 82 |
| Ah | 20.4 | 38 | 59 | 4.3 | 79 |
| | 24.5 | 22 | 74 | 1.4 | 25 |
| | 67.8 | 14 | 70 | 4.7 | 55 |
| Bd | 6.2 | 19 | 38 | 1.9 | 12 |
| | 17.8 | 14 | 40 | 2.7 | 4 |
| | 7.4 | 57 | 17 | 0.3 | 25 |
| Bh | 25.7 | 57 | 140 | 17.4 | 34 |
| | 23.9 | 14 | 28 | 4.1 | 39 |
| | 21.6 | 26 | 29 | 71.0 | 39 |
| Dh | 32.0 | 13 | 15 | 1.8 | 22 |
| | 18.7 | 7 | 29 | 0.4 | 13 |
| | 57.4 | 8 | 27 | 4.3 | 29 |
| Ed | 24.7 | 18 | 59 | 3.4 | 15 |
| | 15.6 | 24 | 60 | 33.4 | 13 |
| | 20.6 | 30 | 38 | 18.4 | 26 |
| Eh | 22.5 | 9 | 42 | 0.8 | 53 |
| | 23.5 | 33 | 101 | 1.2 | 29 |
| | 24.2 | 12 | 32 | 1.2 | 41 |
| Fa | 55.4 | 29 | 63 | 9,5 | 51 |
| | 52.9 | 40 | 89 | 28.7 | 56 |
| | 49.5 | 26 | 63 | 7.9 | 87 |
| Fd | 14.2 | 26 | 50 | 18.9 | 18 |
| | 23.3 | 55 | 60 | 13.2 | 50 |
| | 28.1 | 32 | 80 | 16.8 | 55 |
| Fh | 39.9 | 10 | 31 | 11.7 | 48 |
| | 27.3 | 15 | 39 | 4.6 | 46 |
| | 11.7 | 11 | 64 | 3.6 | 61 |
| Gb | 26.7 | 18 | 83 | 3.4 | 61 |
| | 26.9 | 20 | 36 | 15.0 | 47 |
| | 13.0 | 33 | 58 | 18.1 | 76 |
| Ge | 54.7 | 28 | 134 | 10.5 | 72 |
| | 64.1 | 21 | 162 | 12.8 | 109 |
| | 56.2 | 19 | 140 | 7.4 | 110 |
| Hd | 36.0 | 10 | 120 | 4.4 | 50 |
| | 61.9 | 11 | 110 | 3.7 | 62 |
| | 13.9 | 6 | 67 | 3.5 | 33 |
| Hh | 6.0 | 23 | 50 | 6.1 | 41 |
| | 3.5 | 15 | 36 | 11.9 | 7 |
| | 17.3 | 24 | 31 | 17.7 | 27 |
| Id | 23.0 | 27 | 67 | 2.2 | 81 |
| | 14.9 | 26 | 38 | 4.4 | 16 |
| | 23.3 | 14 | 125 | 2.0 | 43 |
| Ih | 10.3 | 10 | 37 | 9.6 | 14 |
| | 16.2 | 55 | 50 | 8.6 | 30 |
| | 24.8 | 33 | 131 | 9.1 | 13 |
| Kd | 46.0 | 41 | 92 | 3.4 | 55 |
| | 43.8 | 16 | 38 | 15.1 | 22 |
| | 52.5 | 29 | 24 | 7.7 | 14 |
| Kf | 27.5 | 10 | 92 | 1.8 | 57 |
| | 40.8 | 87 | 137 | 22.8 | 18 |
| | 19.0 | 14 | 115 | 2.7 | 37 |
| Kg | 9.3 | 8 | 68 | 3.9 | 59 |
| | 21.5 | 29 | 50 | 68.0 | 34 |
| | 11.0 | 17 | 64 | 27.3 | 24 |
| Kh | 57.1 | 66 | 145 | 116 | 54 |
| | 21.6 | 35 | 94 | 105 | 36 |
| | 20.1 | 24 | 121 | 141 | 28 |
| La | 42.0 | 57 | 77 | 4.0 | 35 |
| | 38.5 | 9 | 93 | 6.9 | 30 |
| | 25.8 | 17 | 98 | 4.4 | 44 |
| Lc | 26.5 | 14 | 119 | 6.3 | 26 |
| | 16.8 | 27 | 110 | 9.6 | 50 |
| | 18.9 | 15 | 146 | 12.8 | 36 |
| Mean | 30.90 | 23.68 | 73.14 | 14.51 | 42.29 |
| 95% C limits | ± 4.59 | ± 3.67 | ± 8.67 | ± 5.92 | ± 5.15 |
| kg ha$^{-1}$ Dry wt | 618.03 | 473.61 | 1462.78 | 290.17 | 845.83 |
| 95% C limits | ±91.80 | ±73.40 | ±173.40 | ±118.40 | ±103.00 |

MARCH 1975 RESULTS

| Quadrat No. | Ad | Cc | Cg | Ch | Cf | Ff | Ee | Mean | 95% limits | kg ha$^{-1}$ | 95% limits |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dry wt. Leaves kg 100m$^{-2}$ | 24.048 | 11.016 | 14.018 | 21.036 | 21.071 | 9.891 | 13.878 | 16.43 | ±4.12 | 1643 | ±412 |

TABLE 2.2.6 CALCULATION OF MEAN STANDING CROP OF LEAF LITTER

The mean is derived from $\frac{\sum(S.C. \times T)}{366}$

| DAY | DATE | STANDING CROP, t ha$^{-1}$ (S.C.) | NUMBER DAYS AT THIS LEVEL (T) | NUMBER DAYS X STANDING CROP (S.C. x T) |
|---|---|---|---|---|
| 1 | 15.3.75 | - | - | - |
| 11 | 25.3.75 | 1.643 | 81 | 133.083 |
| 151 | 12.8.75 | 0.618 | 106 | 65.508 |
| 223 | 23.10.75 | 0.474 | 70 | 33.180 |
| 291 | 30.12.75 | 1.463 | 40.5 | 59.252 |
| 304 | 12.1.76 | 0.290 | 32 | 9.280 |
| 355 | 3.3.76 | 0.846 | 36.5 | 30.033 |
|  | MEAN | 0.903 | 366 | 330.336 |

## 2.2.3 DISCUSSION

### 2.2.3.1 Seasonal Variation in Standing Crops

Seasonal variation of wood litter standing crop is considerable with a maximum in July/August at the end of the major peak of minor wood litter fall in the rainy season (Figure 2.2.1). Litter fall of at least 1.2 t $ha^{-1}$ would be needed between April and August if decomposition was zero. During these months in 1974 and 1975 litter fall was about 0.8 t $ha^{-1}$ (Section 2.1). Confidence limits in this type of work are high and the reason for the discrepancy is difficult to assess. A single major fall on one standing crop quadrat would be sufficient to cause a sharp rise in measurement of the standing crops.

Leaf litter standing crop also varies seasonally (Figure 2.2.1) with a major peak in March during the dry season and a smaller peak in December before the litter is burnt. 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 $ha^{-1}$. From January to March 1975 leaf fall was approximately 1.2 t $ha^{-1}$ (Section 2.1), a quantity in close agreement with the expected value. Also, Figure 2.2.1 indicates that leaf litter accumulation was lower in the early months of 1976 than of 1975. The reason for this may lie in variability of leaf litter removal by the fires.

There are few comparable data from W. Africa. Often the standing crop is measured only once a year (e.g. Greenland and Kowal 1960). John (1973) made several collections but records only the mean. Madge (1965), however, records a distinct peak in leaf litter accumulation in November-April in Ibadan, Nigeria. This would also occur in Mokwa in the absence of annual fires.

### 2.2.3.2 Standing Crop, Litter Fall and Calculated Decomposition Rates

Nye's (1961) equation relating these variables has been given in

Section 2.2.1. The annual leaf fall of 2.387 t $ha^{-1}a^{-1}$ and mean standing crop of leaf litter of 0.903 t $ha^{-1}$ give a calculated mean decomposition constant of 264.3% $a^{-1}$. This compares well with other data from W. Africa quoted by John (1973) and reproduced here (Table 2.2.7).

12.83% of the standing crop collected on 3.3.1976 was of diameter < 2.0 cm. Applying this to the mean standing crop gives 346 kg $ha^{-1}$ of twigs (< 2.0 cm) and 2,475 kg $ha^{-1}$ of logs (> 2.0 cm). Total wood fall of twigs (Section 2.1) was 709 kg $ha^{-1}$ $a^{-1}$ and of logs 682 kg $ha^{-1}$ $a^{-1}$. Calculated decomposition rates are thus 0.488 years for twigs and 3.629 years for logs, the mean for all wood being 2.028 years (k = 49.31% $a^{-1}$). This mean is considered to be a reliable estimate whereas the division into twigs and logs is less so since the ratio of standing crop twigs : logs was assessed only once, in March 1976, when wood litter was at a low level.

The only other calculated estimates of decomposition rates of wood are those of John (1973) from Kade, Ghana. He recorded 1.2 years for twigs, 1.3 years for small wood and 9.2 years for medium wood. Assuming twig fall of 50%, small and medium wood fall 25% each, the mean decomposition constant is 3.23 years.

Hopkins (1966) recorded 1-2 years for small blocks of "obeche" (Triplochiton scleroxylon) in his savanna and forest sites in Southern Nigeria. Since obeche is very rapidly attacked by termites any estimate based on it would be lower than a true mean for all woods.

### 2.2.3.3 Effects of Annual Bush Fires on the Termite Community

Trapnell et al. (1976) examined the soils on old burnt and unburnt plots in Zambian deciduous woodland. They found that the soil mineral content was increased under the fire regime but the organic matter and nitrogen content remained unchanged. They showed that this was due to large populations of litter feeding termites on the unburnt plots which disposed of litter accumulation and kept soil organic matter at a low level. This suggests that the fire had a strong impact on the availability of food to termites.

As given above, the annual fire destroyed 49.4% of the annual leaf fall and 0.9% of annual wood fall. An additional study by myself and Dr. T.G. Wood showed that fire removed 1 t ha$^{-1}$ of grass and grass litter from the study area, representing 81.4% of the standing crop of grass and grass litter of 1.23 t ha$^{-1}$ present before the fire.

Hence, species feeding on leaves and grass might be expected to be the most seriously affected by the fires. The species in these categories are Trinervitermes spp, Macrotermes subhyalinus and Odontotermes spp. I have no direct experimental evidence to show whether or not populations of these species were suppressed as a result of the fires.

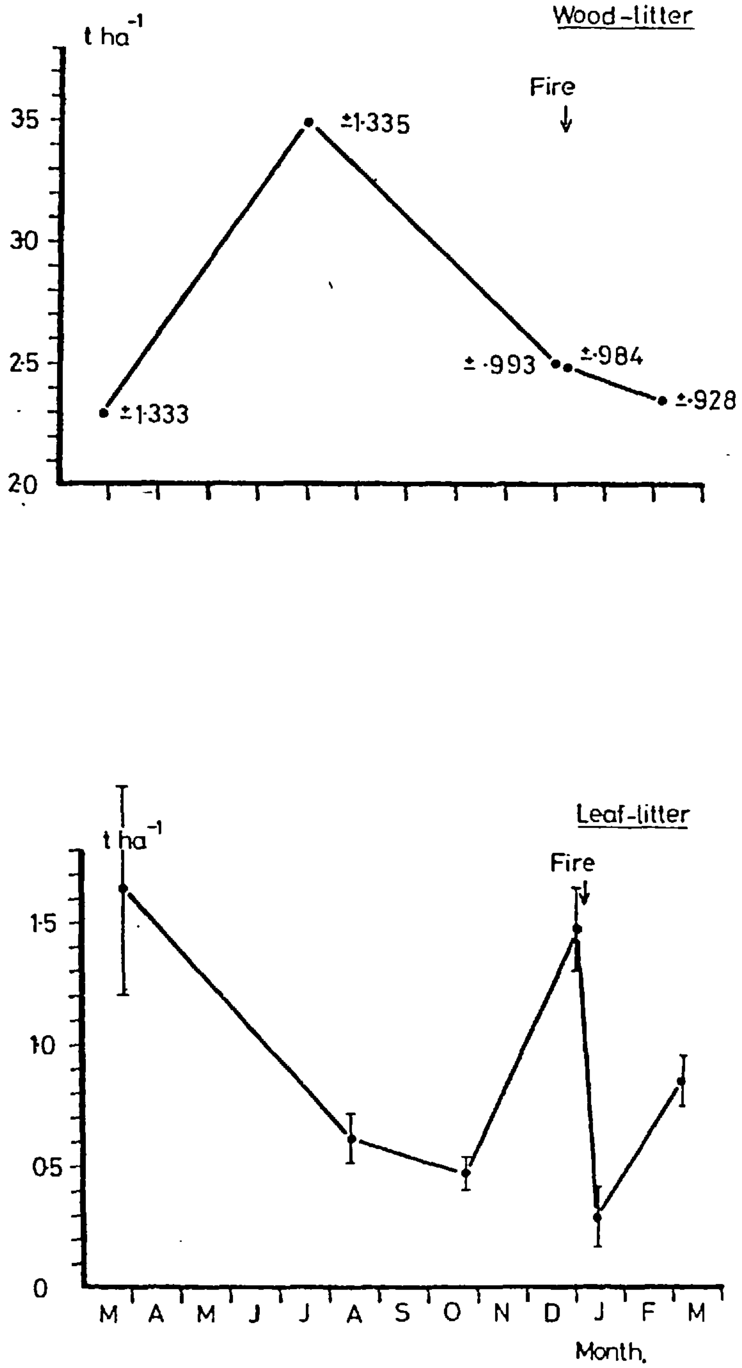


FIGURE 2.2.1 The standing crops of wood litter (including standing dead items) and leaf litter, ± 95% c.l.

TABLE 2.2.7 Comparison of calculated leaf decomposition data from various W. African localities. (Adapted from John, 1973).

| LOCALITY | LEAF DECOMPOSITION CONSTANT (% $a^{-1}$) (k) | LEAF DECOMPOSITION RATE (YEARS FOR DECAY) ($\frac{1}{k}$) | SOURCE |
|---|---|---|---|
| Kade, Ghana | 250 % $a^{-1}$ | 0.4 years | John (1973) |
| Ibadan, Nigeria | 250 | 0.4 | Madge (1965) |
| Olokemiji, 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 | 264.3 | 0.379 | Present study |

Note: Expressions of decomposition vary between authors and may cause some confusion. In this thesis I follow the work of Nye (1961) who called the ratio litter production : litter accumulation the decomposition constant (k). Madge (1965), and Olson (1963) also used this ratio but the latter author called k the decomposition rate. Conversely, John (1973) expressed decomposition in terms of the ratio litter accumulation : litter production (i.e. $\frac{1}{k}$), which is equal to the mean years for decay (of a leaf, twig etc.). In this work I will call this ratio ($\frac{1}{k}$), the decomposition rate. It should also be noted that the decomposition constant, k, is not equivalent to that calculated by Jenny (1950).

# SECTION 2.3

# DECOMPOSITION OF WOOD AND LEAVES WITH SPECIAL REFERENCE TO TERMITES

## 2.3.1 INTRODUCTION

The previous sections on litter fall and standing crop of litter provide a basis for discussing the role of termites as decomposers of plant material. The rates of wood and leaf decomposition were measured directly and the effect of termites estimated by exclusion experiments.

Five factors need to be taken into account in examining the impact of termites on litter decomposition. These are 1) size of food item, 2) presentation and disturbance of items, 3) species of food used, 4) seasonal changes in activity, 5) state of fungal decay of food at presentation.

Some of these have been examined by earlier authors, for example:-

1) Size of food item. In a selection of bait sizes in timber "graveyard" tests Usher and Ocloo (1974) found that 15 x 10 x 2.5 cm blocks were most heavily attacked. In my experiments two classes were used, twigs < 2.0 cm diameter and logs > 2.0 cm diameter.

2) Presentation and disturbance of items. Deeply buried samples were most heavily attacked among various presentations tried by Usher and Ocloo (loc. cit.). Naturally fallen litter seldom penetrates the soil and only scattered surface items were considered in my work. To minimise disturbance, wood samples were checked only every six weeks.

3) Species of food used. Small et al. (1960), Williams (1973) and many other authors, have found that the palatability of wood to termites

varies enormously with the species of wood used. Haverty and Nutting (1975b) have shown that this can lead to wood selection by termites in the field. In the present study items were collected indiscriminately from trees in an attempt to simulate litter fall from various species.

4) Seasonal changes in activity. Hopkins (1966), in S. Nigeria, found that wood samples offered in the dry season decayed to 50% faster than samples offered in the wet season. In my study only one set of natural wood baits was presented and left for one calendar year (1975). Seasonality of termite activity was assessed in a separate experiment (Section 2.4).

5) State of fungal decay of food at presentation. The state of fungal decay of wood may affect its palatability to termites. Kovoor (1964b) found that *Microcerotermes edentatus* (Wasmann), prefers to feed on decayed wood and Esenther et al. (1961) record similar results for *Reticulitermes* spp. Williams (1965) found that *Pinus caribaea* heartwood was toxic to *Coptotermes niger* (Snyder) unless attacked by a fungus, *Lentinus pallidus*. Usher (1975) found that *Ancistrotermes* spp. and *Pseudacanthotermes militaris* preferentially attacked decaying wood while *Microtermes* spp. and *Macrotermes* spp. did not. In the present study all wood was fresh at presentation but observations during the year showed that it was rapidly attacked by fungi, especially during the rainy season. The method therefore assumes that wood litter falling from the trees was relatively fresh and, in general, this was the case.

## 2.3.2 METHODS

### 2.3.2.1 Wood

Two 10 x 10 m decomposition quadrats were marked in blocks 1 - 8 by random choice of map squares not already containing quadrats (Fig. 1.4.2). All quadrats were cleared of wood litter. On 7 January 1975

10 kg of paint-marked air-dry logs ($>2$ cm diameter, mainly 4-10 cm) were scattered over each quadrat and 5 kg of twigs ($<2$ cm diameter) placed under two 1 $m^2$ pieces of chicken wire pegged to the ground. The total of 15 kg 100 $m^2$ placed on each quadrat was similar to the mean standing crop of wood litter on the study area (excluding standing dead items) of 17.31 kg 100 $m^2$ (Section 2.2). Hence there was no possibility of making the decomposition quadrats unnaturally attractive to termites. The wood samples were collected from living trees, air-dried, and sampled for dry weight estimation. The wood samples were reweighed every six weeks for one year on a 10 kg top-loading Salter spring balance. Termites feeding on the samples were noted. Samples for dry weight estimation were taken from surrounding wood litter. All samples were removed before the bush fire in 1976.

At the same time three 10 kg log samples and three 5 kg twig samples were set aside for decomposition measurements with the exclusion of termites. Three methods were considered:

1) Litter bags with a fine mesh. These have been used for leaves by Crossley et al.(1962) Madge(1969)&Wood(1971 , 1974). Anderson (1973) considered that litter bags slow down microbial decay and prevent litter from following normal decay patterns. In addition, termites would quickly eat through litter bags. This method was therefore rejected.

2) Insecticidal application to the substrate beneath the samples. A non-residual insecticide would not prevent the temporary and intermittent attacks of termites. A residual insecticide would be quickly leached and require renewal. Other decomposers may also be affected (e.g. Fox 1967). This method was also rejected.

3) Suspension of the samples off the ground. This method also has limitations:- certain soil organisms would be unable to reach the

samples, and the drier surroundings of the samples could slow down microbial and fungal decay. However, tropical savanna soils do not harbour the numbers and species of animals to be found in temperate soils, (Greenslade et al. 1968), and of those that do occur, termites have been found to be the most important decomposers (Nye 1961, Hopkins 1966). Flying insects such as bark beetles (Scolytidae) and boring beetles (Bostrychoidea) were able to reach the samples. Fungal and microbial decay was quite marked in the rainy season. This method, although not entirely satisfactory (as with any exclusion experiment), was chosen as the one to be used.

#### 2.3.2.2 Leaves

Observations during 1974 suggested that leaf litter was not attacked by termites to the same extent as wood. However, some termites, particularly Macrotermes bellicosus, produced widespread foraging galleries over leaf litter mainly during the rainy season in late May - early September when leaf litter standing crop was high and wood litter standing crop was low (Fig. 2.2.1). Three 160 g samples (148 g dry wt.) were placed in each of the 16 decomposition quadrats under three 1 $m^2$ pieces of chicken wire pegged to the ground. Exclusion methods were unnecessary since sufficient unattacked samples remained at the end of the study period. Samples were examined weekly for termite attack from June to October. The amount removed by termites was calculated from the differences between final weights of attacked and unattacked samples.

### 2.3.3 RESULTS

#### 2.3.3.1 Wood

Results for the decomposition of log and twig samples are given in Tables 2.3.1, 2.3.2 and Figure 2.3.1. Termite mud which accumulated in the samples was removed prior to the final weighings. It could not be removed in the field without damaging the wood and this factor constitutes a slight error in intermediate results. More significant errors resulted from dry weight estimations; samples taken from the litter led on several occasions to inconsistent rises or falls in the % decomposed. These results have been bracketed in Tables 2.3.1 and 2.3.2 and omitted from Figure 2.3.1. Particularly erroneous results occurred in the suspended twig samples at weeks 36, 42 and 48 (Table 2.3.3). However, only the original and final weights are used in calculations and these are reliable since the samples themselves were sub-sampled for dry weight.

A summary of the decomposition results is given in Table 2.3.4. Calculation of a mean value for total decomposition must include a correction for the different annual fall of log and twig litter.

Hence:

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

where k = decomposition constant (expressed as % decomposed per year).

A = annual litter production, (Section 2.1).

$$\therefore \quad \text{Mean } k = \left(47.86 \times \frac{681.825}{1390.756}\right) + \left(53.98 \times \frac{708.931}{1390.756}\right) = \underline{50.98\%\ a^{-1}}$$

This figure agrees remarkably well with the decomposition constant calculated from litter fall and standing crop of 49.31% $a^{-1}$, (Section 2.2). It may also be noted that Usher (1975) recorded a weight loss of 12.68% in 16 weeks in wood blocks protected from soil arthropods in Ghana. The data suggest a possible loss of 20.30% after a year, similar to the results for my suspended samples (Table 2.3.4).

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

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

equal to: $\left( 681.825 \times \frac{25.66}{47.86} \right) + \left( 708.931 \times \frac{35.78}{53.98} \right)$

equal to: 365.668 kg of logs + 469.906 kg of twigs = $\underline{\underline{835.464 \text{ kg ha}^{-1}\text{a}^{-1}}}$

With a mean calorific equivalent of wood of 5.4634 kcal $g^{-1}$ (Table 2.1.5) the total wood consumed by termites is equivalent to: 4,564,474 kcal $ha^{-1}$ $a^{-1}$.

The role of the various termite species in the consumption of this litter is indicated by presence records for termites on logs and twigs given in Table 2.3.5. The data are not detailed enough to calculate quantities removed per species, further work on this subject being described in Section 2.4. However, the data show no significant difference between species attacking logs and those attacking twigs. The ranked recorded species totals for logs and twigs give a 100% correlation.

TABLE 2 3.1 THE DECOMPOSITION OF 16 SAMPLES OF LOGS ( >2 cm diam.) (Sample weights in kg.)

| WEEK | 0 | 6 | 12 | 18 | 24 | 30 | 36 | 42 | 48 | 52 | 52 (After cleaning) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| DATE | 7/1/75 | 19/2/75 | 2/4/75 | 20/5/75 | 25/6/75 | 6/8/75 | 17/9/75 | 29/10/75 | 6/12/75 | 7/1/76 | 7/1/76 |
| 1 Bb | 10 | 8.84 | 8.61 | 10.36 | 9.4 | 9.56 | 9.17 | 7.06 | 6.35 | 5.43 | 4.82 |
| 2 Bc | 10 | 8.33 | 8.04 | 9.22 | 8.45 | 8.62 | 8.53 | 7.19 | 5.76 | 4.15 | 3.47 |
| 3 Be | 10 | 8.16 | 7.69 | 8.65 | 8.25 | 8.07 | 8.00 | 6.62 | 5.04 | 4.59 | 4.00 |
| 4 Bf | 10 | 8.75 | 8.64 | 10.08 | 9.47 | 9.88 | 8.18 | 6.55 | 5.80 | 5.37 | 4.70 |
| 5 Dc | 10 | 8.55 | 8.21 | 9.50 | 8.95 | 9.71 | 9.33 | 7.44 | 6.95 | 4.65 | 4.40 |
| 6 Dg | 10 | 8.47 | 8.32 | 9.70 | 9.05 | 8.34 | 8.33 | 6.25 | 4.44 | 3.91 | 3.81 |
| 7 Ef | 10 | 8.89 | 8.75 | 9.95 | 9.34 | 9.83 | 9.90 | 8.33 | 6.71 | 6.17 | 6.10 |
| 8 Fc | 10 | 8.42 | 8.37 | 9.96 | 8.84 | 9.39 | 9.40 | 7.40 | 5.92 | 5.39 | 5.10 |
| 9 Gd | 10 | 8.20 | 8.02 | 9.01 | 8.52 | 8.75 | 8.52 | 7.36 | 6.50 | 6.00 | 5.81 |
| 10 Gh | 10 | 6.53 | 6.47 | 7.10 | 6.62 | 6.46 | 6.40 | 5.38 | 4.65 | 4.25 | 4.10 |
| 11 Ha | 10 | 7.70 | 7.48 | 8.30 | 7.90 | 8.15 | 8.20 | 6.60 | 5.26 | 4.32 | 4.10 |
| 12 Ie | 10 | 7.90 | 7.57 | 8.22 | 7.82 | 8.50 | 8.45 | 7.67 | 6.45 | 5.95 | 5.84 |
| 13 Jc | 10 | 8.20 | 8.01 | 9.12 | 8.50 | 8.55 | 8.36 | 6.60 | 5.25 | 4.85 | 4.70 |
| 14 Jf | 10 | 8.13 | 7.85 | 8.99 | 8.26 | 8.12 | 7.95 | 7.02 | 5.95 | 5.51 | 5.50 |
| 15 Ld | 10 | 7.95 | 7.50 | 8.65 | 8.22 | 7.70 | 7.13 | 5.44 | 4.72 | 4.30 | 3.95 |
| 16 Le | 10 | 8.30 | 8.24 | 9.16 | 8.80 | 9.02 | 9.00 | 7.26 | 5.85 | 5.60 | 5.55 |
| Mean | 10 | 8.21 | 7.99 | 9.12 | 8.52 | 8.67 | 8.43 | 6.89 | 5.73 | 5.03 | 4.75 |
| ±95% conf. limits | 0 | 0.27 | 0.28 | 0.41 | 0.35 | 0.44 | 0.42 | 0.38 | 0.38 | 0.36 | 0.40 |
| % Dry matter | 86.5 | 90.237 | 97.338 | 84.811 | 88.362 | 75.188 | 66.252 | 87.142 | 87.73 | 94.919 | 94.919 |
| Mean dry wt. | 8.65 | 7.41 | 7.78 | 7.73 | 7.53 | 6.52 | 5.59 | 6.00 | 5.03 | 4.77 | 4.51 |
| % Decomposed | 0 | (14.34) | 10.06 | 10.64 | 12.95 | 24.62 | 35.38 | (30.64) | 41.85 | 44.86 | 47.86 |
| ±95% conf. limits | 0 | 2.82 | 3.15 | 4.02 | 3.58 | 3.82 | 3.22 | 3.83 | 3.85 | 3.95 | 4.39 |

TABLE 2.3.2 THE DECOMPOSITION OF 16 SAMPLES OF TWIGS (< 2 cm diam.) (Sample weights in kg.)

| WEEK | | 0 | 6 | 12 | 18 | 24 | 30 | 36 | 42 | 48 | 52 | 52 (After cleaning) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DATE | 7/1/75 | 19/2/75 | 2/4/75 | 20/5/75 | 25/6/75 | 6/8/75 | 17/9/75 | 29/10/75 | 6/12/75 | 7/1/76 | 7/1/76 |
| 1 | Bb | 5 | 4.74 | 4.61 | 5.81 | 5.08 | 4.88 | 4.53 | 3.49 | 3.25 | 2.72 | 2.53 |
| 2 | Bc | 5 | 3.91 | 3.68 | 4.46 | 3.78 | 3.51 | 3.30 | 2.71 | 2.20 | 1.19 | 1.11 |
| 3 | Be | 5 | 4.35 | 4.34 | 5.48 | 4.80 | 4.94 | 4.71 | 3.12 | 2.52 | 2.25 | 2.00 |
| 4 | Bf | 5 | 3.80 | 3.71 | 4.35 | 4.00 | 3.95 | 3.59 | 2.54 | 1.70 | 1.51 | 1.37 |
| 5 | Dc | 5 | 4.54 | 4.48 | 5.60 | 4.86 | 5.19 | 4.34 | 3.25 | 2.07 | 1.81 | 1.61 |
| 6 | Dg | 5 | 4.53 | 4.48 | 5.18 | 4.65 | 4.62 | 4.67 | 3.22 | 2.62 | 2.56 | 2.26 |
| 7 | Ef | 5 | 4.69 | 4.69 | 5.64 | 5.21 | 5.32 | 5.15 | 4.40 | 2.93 | 2.34 | 2.07 |
| 8 | Fc | 5 | 4.85 | 4.81 | 5.94 | 5.27 | 4.41 | 4.19 | 3.35 | 2.69 | 2.36 | 2.06 |
| 9 | Gd | 5 | 4.50 | 4.41 | 5.31 | 4.85 | 4.83 | 4.68 | 3.85 | 2.99 | 2.82 | 2.54 |
| 10 | Gh | 5 | 4.43 | 4.32 | 5.18 | 4.72 | 4.85 | 4.80 | 3.95 | 3.40 | 3.12 | 2.91 |
| 11 | Ha | 5 | 4.28 | 4.20 | 4.94 | 4.39 | 4.72 | 4.73 | 3.41 | 2.49 | 2.02 | 2.88 |
| 12 | Ie | 5 | 4.90 | 4.90 | 5.58 | 5.04 | 5.30 | 5.33 | 4.20 | 4.04 | 3.32 | 3.20 |
| 13 | Jc | 5 | 4.24 | 4.18 | 4.95 | 4.46 | 4.72 | 4.22 | 3.21 | 2.31 | 2.08 | 1.95 |
| 14 | Jf | 5 | 4.80 | 4.80 | 5.82 | 5.29 | 5.03 | 4.74 | 3.94 | 3.00 | 2.83 | 2.44 |
| 15 | Ld | 5 | 4.92 | 4.97 | 5.94 | 5.21 | 4.90 | 3.34 | 2.12 | 1.55 | 1.18 | 1.09 |
| 16 | Le | 5 | 3.82 | 3.82 | 4.38 | 3.80 | 3.95 | 3.63 | 2.90 | 2.01 | 1.95 | 1.79 |
| Mean | | 5 | 4.46 | 4.40 | 5.29 | 4.71 | 4.70 | 4.37 | 3.35 | 2.61 | 2.25 | 2.11 |
| ±95% conf. limits | | 0 | 0.18 | 0.20 | 0.27 | 0.25 | 0.25 | 0.30 | 0.30 | 0.32 | 0.31 | 0.31 |
| % Dry matter | | 89.5 | 94.747 | 96.170 | 79.697 | 78.214 | 72.947 | 70.277 | 80.675 | 88.36 | 97.713 | 97.713 |
| Mean dry wt. | | 4.48 | 4.23 | 4.23 | 4.22 | 3.68 | 3.43 | 3.07 | 2.70 | 2.31 | 2.20 | 2.06 |
| % Decomposed | | 0 | 5.68 | 5.68 | 5.89 | 17.77 | 23.47 | 31.45 | 39.67 | 48.52 | 50.93 | 53.98 |
| ±95% conf. limits | | | 3.81 | 4.29 | 4.80 | 4.37 | 4.07 | 4.71 | 5.40 | 6.31 | 6.76 | 6.76 |

TABLE 2.3.3 THE DECOMPOSITION OF TERMITE EXCLUDED SAMPLES OF LOGS AND TWIGS (Sample weights in kg.)

LOGS

| WEEK | 0 | 6 | 12 | 18 | 24 | 30 | 36 | 42 | 48 | 52 |
|---|---|---|---|---|---|---|---|---|---|---|
| | 7/1/75 | 19/2/75 | 2/4/75 | 20/5/75 | 25/6/75 | 6/8/75 | 17/9/75 | 20/10/75 | 6/12/75 | 7/1/76 |
| 1 | 10 | 8.97 | 8.80 | 9.91 | 9.50 | 10.20 | 9.96 | 8.40 | 7.75 | 7.17 |
| 2 | 10 | 8.87 | 8.40 | 9.43 | 9.05 | 9.60 | 9.44 | 8.20 | 7.66 | 7.00 |
| 3 | 10 | 9.32 | 8.90 | 9.66 | 9.32 | 9.80 | 9.81 | 8.30 | 7.74 | 7.10 |
| Mean | 10 | 9.053 | 8.70 | 9.67 | 9.29 | 9.87 | 9.74 | 8.30 | 7.72 | 7.09 |
| ±95% conf. limits | 0 | 0.587 | 0.657 | 0.596 | 0.563 | 0.759 | 0.665 | 0.248 | 0.123 | 0.212 |
| % Dry | 86.5 | 90.237 | 97.338 | 84.811 | 88.362 | 75.188 | 66.252 | 87.142 | 87.73 | 94.919 |
| Mean Dry | 8.65 | 8.17 | 8.47 | 8.20 | 8.21 | 7.42 | 6.45 | 7.23 | 6.77 | 6.73 |
| % Decomposed | 0 | (5.55) | 2.10 | 5.19 | 5.10 | 14.21 | (25.40) | 16.38 | 21.70 | 22.20 |
| ±95% conf. limits | | 6.12 | 7.40 | 5.85 | 5.75 | 6.60 | 5.09 | 2.50 | 1.243 | 2.33 |

TWIGS

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | 5.0 | 4.98 | 5.60 | 5.15 | 5.43 | 5.25 | 4.50 | 4.40 | 4.10 |
| 2 | 5 | 4.85 | 4.85 | 5.60 | 5.16 | 5.48 | 5.25 | 4.50 | 4.26 | 4.00 |
| 3 | 5 | 4.94 | 4.94 | 5.50 | 5.05 | 5.35 | 5.16 | 4.35 | 4.10 | 3.80 |
| Mean | 5 | 4.93 | 4.925 | 5.57 | 5.12 | 5.42 | 5.22 | 4.45 | 4.25 | 3.97 |
| ±95% conf. limits | 0 | 0.188 | 0.165 | 0.143 | 0.151 | 0.163 | 0.129 | 0.215 | 0.373 | 0.379 |
| % Dry | 93.47 | 93.47 | 93.47 | 79.697 | 78.214 | 72.947 | 70.277 | 80.675 | 88.36 | 96.254 |
| Mean Dry | 4.67 | 4.61 | 4.60 | 4.45 | 4.01 | 3.95 | 3.67 | 3.59 | 3.76 | 3.82 |
| % Decomposed | 0 | 1.28 | 1.50 | 4.71 | 14.13 | 15.42 | (21.41) | (23.13) | (19.49) | 18.20 |
| ±95% conf. limits | 0 | 3.75 | 3.31 | 2.45 | 2.53 | 2.55 | 1.94 | 3.72 | 7.056 | 7.822 |

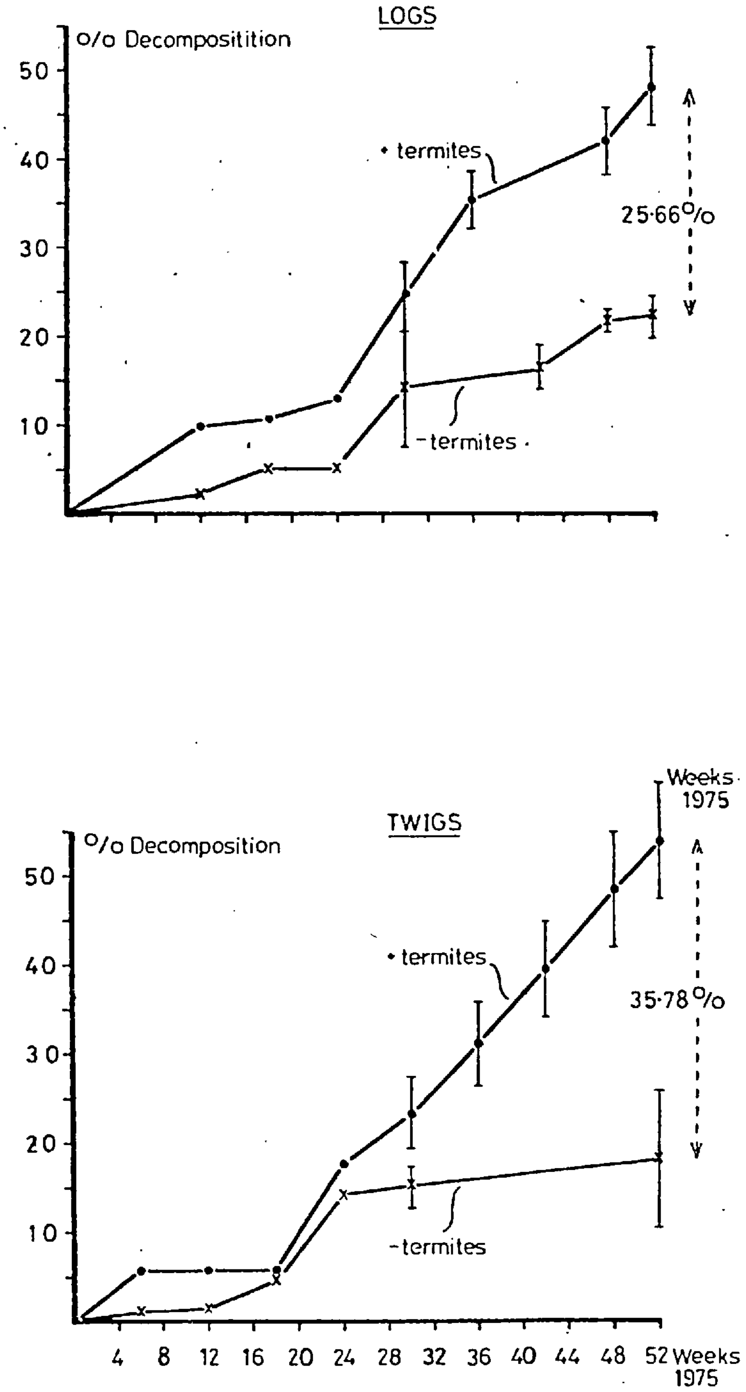


FIGURE 2.3.1 The decomposition of logs ( > 2.0 cm diameter) and twigs ( < 2.0 cm diameter) during 1975), ± 95% c.l.

## TABLE 2.3.4 SUMMARY OF THE DECOMPOSITION DATA WITH CALCULATED AMOUNTS REMOVED BY TERMITES

| Items | Decomposition rate in years $(\frac{1}{K})$ | Decomposition constant (k) |
|---|---|---|
| 1) Logs on ground | 2.09 | 47.86% $a^{-1}$ |
| 2) Twigs on ground | 1.85 | 53.98% |
| 3) Logs suspended | 4.50 | 22.20% |
| 4) Twigs suspended | 5.49 | 18.20% |
| 5) Termites on logs (1-3) | 3.90 | 25.66% |
| 6) Termites on twigs (2-4) | 2.79 | 35.78% |

TABLE 2.3.5 THE SPECIES OF TERMITES RECORDED AT THE 6-WEEKLY CHECKS OF LOG AND TWIG SAMPLES WITH SUMMATIONS OF RECORDS/SPECIES AND THEIR RANKS

| SPECIES OF TERMITE | NO. OF DECOMPOSITION QUADRATS UPON WHICH EACH SPECIES WAS RECORDED ON EACH DATE (MAX 16) TWIGS ONLY | | | | | | | | | TOTAL | RANK |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 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 | | |
| Microtermes spp. | 0 | 0 | 7 | 4 | 8 | 6 | 3 | 1 | 1 | 30 | 4 |
| Ancistrotermes cavithorax | 10 | 9 | 16 | 15 | 12 | 14 | 15 | 16 | 11 | 118 | 1 |
| Odontotermes spp. | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 8 | 5 |
| Macrotermes bellicosus | 2 | 3 | 3 | 2 | 4 | 4 | 3 | 6 | 4 | 31 | 3 |
| Macrotermes subhyalinus | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 7 |
| Microcerotermes | 3 | 2 | 8 | 7 | 5 | 9 | 4 | 3 | 0 | 41 | 2 |
| Amitermes | | | | 1 | | 1 | 1 | | | 3 | 6 |
| Basidentitermes | | | | | | | | | | 0 | 9 |
| Trinervitermes | | | | | | | | | | 0 | 9 |
| Fulleritermes | | | | | | | | | | 0 | 9 |

| SPECIES OF TERMITE | NO. OF DECOMPOSITION QUADRATS UPON WHICH EACH SPECIES WAS RECORDED ON EACH DATE (MAX 16) LOGS ONLY | | | | | | | | | TOTAL | RANK |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 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 | | |
| Microtermes spp. | 0 | 0 | 10 | 4 | 3 | 7 | 4 | 5 | 2 | 35 | 4 |
| Ancistrotermes cavithorax | 6 | 10 | 15 | 15 | 15 | 14 | 12 | 15 | 12 | 114 | 1 |
| Odontotermes spp. | 2 | 3 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 11 | 5 |
| Macrotermes bellicosus | 1 | 6 | 4 | 6 | 3 | 5 | 7 | 8 | 7 | 47 | 3 |
| Macrotermes subhyalinus | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 7 |
| Microcerotermes | 7 | 8 | 9 | 4 | 3 | 5 | 3 | 13 | 4 | 56 | 2 |
| Amitermes | | | 1 | 2 | 1 | 1 | 1 | | | 6 | 6 |
| Basidentitermes | | | | 1 | | | | | | 1 | 9 |
| Trinervitermes | | | | | | 1 | | | | 1 | 9 |
| Fulleritermes | | | | | | 1 | | | | 1 | 9 |

### 2.3.3.2 Leaves

Results for the attack of leaf litter samples are given in Table 2.3.6 and calculations of decomposition due to termites and other factors in Table 2.3.7. During the study period, leaves decomposed by 66.30%; 5.90% was due to termites (M. bellicosus 5.49%, others (mainly Odontotermes spp) 0.41%) and 60.40% due to leaching, microbial and fungal decay etc. The method assumes that the difference between the mean weights of attacked and unattacked samples represents the amount removed by termites. Samples Bf1 and Ha1 were ignored in the calculations because they were attacked by M. bellicosus and another species, their respective roles being inseparable.

Since the decomposition rate of leaves was not followed throughout the year, the calculated decomposition rate of 0.379 a (264.25% $a^{-1}$) (Section 2.2) cannot be checked. To calculate the weight of leaves removed by termites per hectare during the period of study, the standing crop of leaves at the start of the experiment is estimated from Figure 2.2.1 as about 1.160 t $ha^{-1}$. Decomposition at 66.30% during the period gives an expected value at the end of the experiment of 0.391 t $ha^{-1}$. The measured value was similar, being 0.474 t $ha^{-1}$ (st. crop of leaves on 23.10.1975, Table 2.2.5). Termites took 5.90%, equivalent to 68.44 kg $ha^{-1}$; 5.49% by M. bellicosus equivalent to 63.684 kg $ha^{-1}$; 0.41% by other termites, equivalent to 4.756 kg $ha^{-1}$.

The calorific equivalent of leaves was 4.7077 kcal $g^{-1}$ (Table 2.1.5) so the above weights are equivalent to: M. bellicosus 299,805 kcal $ha^{-1}$, other termites 22,390 kcal $ha^{-1}$. These will be regarded as annual figures. Table 2.3.6 indicates that most of the consumption by "other termites" was due to Odontotermes spp. and will therefore be assigned to these species in future calculations.

The total litter taken by termites can now be calculated as:- wood: 835.464 kg $ha^{-1}a^{-1}$ (60.073% of wood fall); leaves: 68.44 kg $ha^{-1}a^{-1}$ (2.867% of leaf fall); total: 903.904 kg $ha^{-1}a^{-1}$ (23.925% of total litter fall). The total is equivalent to 4,886,669 kcal $ha^{-1}$ $a^{-1}$ (25.942% of total fall calorific equivalent).

TABLE 2.3.6 THE TERMITE SPECIES RECORDED FROM WEEKLY CHECKS OF 48 LEAF SAMPLES (29.5.75 - 16.10.75)

| SAMPLE NO. | SAMPLE WEIGHT gms. | | 5.6.75 | 12.6.75 | 19.6.75 | 25.6.75 | 3.7.75 | 10.7.75 | 17.7.75 | 24.7.75 | 31.7.75 | 7.8.75 | 14.8.75 | 21.8.75 | 28.8.75 | 4.9.75 | 11.9.75 | 18.9.75 | 25.9.75 | 2.10.75 | 9.10.75 | 16.10.75 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ORIGINAL | FINAL | | | | | | | | | | | | | | | | | | | | |
| Bb 1 | 148 | 51 | | | | | | | 1 | | | | | | | | | | | | | |
| 2 | 148 | 31 | | | | | | | 1 | | | | | | | | | | | | | |
| 3 | 148 | 41 | 2 | | | | | | | | 2 | 3 | | | | | | | | | | |
| Bc 1 | 148 | 45 | | 3 | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 60 | 1 | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 36 | | | | 1 | | | | | | | | | | | | | | | | |
| Be 1 | 148 | 87 | | | | | | | | | | 2 | | | | | | | | | | |
| 2 | 148 | 52 | | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 60 | 1 | | | | | | | 1 | | | | | | | | | | | | |
| Bf 1 | 148 | 46 | | | 2 | | | | | | | 1 | | | | | | | | | | |
| 2 | 148 | 55 | | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 59 | | | | | | | | | | | | | | | | | | | | |
| Dc 1 | 148 | 33 | | | | | | | | | | | | | | 1 | | | | | | |
| 2 | 148 | 55 | 4 | 2 | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 53 | | | | | | | | | | | | | | | | | | | | |
| Dg 1 | 148 | 38 | | | | | | | | | | | | 1 | | | | | | | | |
| 2 | 148 | 48 | | | | 1 | | | | | | | | | | | | | | | | |
| 3 | 148 | 37 | | | | | | | | | 1 | | | | | | | | | | | |
| Ef 1 | 148 | 71 | | | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 59 | | | 2 | | | | | | | | | | | | | | | | | |
| 3 | 148 | 80 | | | | 1 | | | | | | | | | | | | | | | | |
| Fc 1 | 148 | 37 | | | | | | | | | | | 1 | | | | | | | | | |
| 2 | 148 | 56 | | | | | | | | | | 1 | | 1 | | | | | | | | |
| 3 | 148 | 62 | 4 | 5 | | | | | | | | | | | | | | | | | | |
| Gd 1 | 148 | 74 | | | | | | | 1 | | | | | | | | | | | | | |
| 2 | 148 | 85 | | | | | | | | 1 | | | | | | | | | | | | |
| 3 | 148 | 53 | | | | | | | | 1 | | | | | | | | | | | | |
| Gh 1 | 148 | 70 | | 3 | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 63 | | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 69 | | | | 1 | | | | | | | | | | | | | | | | |
| Ha 1 | 148 | 38 | | | 2 | 1 | | | | | | 2 | | | | | | | | | | |
| 2 | 148 | 41 | | | | 1 | | | | | | | | | | | | | | | | |
| 3 | 148 | 43 | | | | 2 | | | | | | | | | | | | | | | | |
| Ie 1 | 148 | 67 | | | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 80 | | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 27 | | | | | | | | | | | | | 1 | | | | | | | |
| Jc 1 | 148 | 38 | | | | | | | 1 | | | | | | | | | 1 | | | | |
| 2 | 148 | 64 | | | | 1 | | | | | | | | | | | | | | | | |
| 3 | 148 | 52 | | | | | | | | | | | | | | | | | | | | |
| Jf 1 | 148 | 34 | | | | | | | | | 1 | | | | | | | | | | | |
| 2 | 148 | 57 | | | | | | 1 | | | | | | | | | | | | | | |
| 3 | 148 | 40 | | | | | | | | | | | | | | | | | | | | |
| Ld 1 | 148 | 34 | | | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 68 | | | | | | | | | | | | | | | | | | | | |
| 3 | 148 | 44 | | | 4 | | | | | | | | | | | | | | | | | |
| Le 1 | 148 | 68 | | | | | | | | | | | | | | | | | | | | |
| 2 | 148 | 70 | | | 3 | | | | | | | | | | | | | | | | | |
| 3 | 148 | 41 | | | | | 4 | | | | | | | | | | | | | | | |

CODE:
1 : *Macrotermes bellicosus*
2 : *Odontotermes pauperans* or *O. smeathmani*
3 : *Ancistrotermes cavithorax*
4 : *Microtermes spp.*
5 : *Macrotermes subhyalinus*

## TABLE 2.3.7 SUMMARY OF LEAF DECOMPOSITION DATA WITH CALCULATIONS OF THE AMOUNTS REMOVED BY TERMITES

| | | |
|---|---|---|
| 1) SAMPLES NOT ATTACKED BY TERMITES | Be 2, Bf 2 & 3, Dc 3, Ef 1, Gh 2, Ie 1 & 2, Jc 3, Jd 3, Ld 1 & 2, Le 1 = 13 x 148 gms. | 1924 gms. |
| 2) SAMPLES ATTACKED BY *Macrotermes bellicosus* | Bb 1 & 2, Bc 2 & 3, Be 3, Dc 1, Dg 1,2 & 3, Ef 3, Fc 1 & 2, Gd 1,2 & 3, Gh 3, Ha 2, Ie 3, Jc 1 & 2, Jf 1 & 2 = 22 x 148 gms. | 3526 gms. |
| 3) SAMPLES ATTACKED BY SPP. OF TERMITES OTHER THAN *M. bellicosus* | Bb 3, Bc 1, Be 1, Dc 2, Ef 2, Fc 3, Gh 1, Ha 3, Ld 3, Le 2, Le 3 = 11 x 148 gms. | 1728 gms. |
| 4) SAMPLES ATTACKED BY *M. bellicosus* & other termites. (Ignored in the calculations) | Bf 1, Ha 1, = 2 x 148 gms. | 296 gms. |
| 5) TOTAL SAMPLES OFFERED | = 48 x 148 gms. | 7104 gms. |
| 6) TOTAL OFFERED MINUS 4) | = 43 x 148 | 6364 gms. |

| | UNATTACKED SAMPLES (1) | SAMPLES ATTACKED BY *M. bellicosus* (2) | SAMPLES ATTACKED BY OTHER SPECIES (3) | TOTALS |
|---|---|---|---|---|
| WEIGHT OF LEAVES PUT OUT | 1924 gms.<br>(13 samples) | 3256 gms.<br>(22 samples) | 1628 gms.<br>(11 samples) | 6808 gms. |
| WEIGHT OF LEAVES TAKEN IN | 762 gms. | 916 gms. | 617 gms. | 2295 gms. |
| WEIGHT OF LEAVES LOST | 1162 gms. | 2340 gms. | 1011 gms. | 4513 gms. |
| WEIGHT OF LEAVES LOST AND ASSUMED LOST TO LEACHING ETC. | 1162 gms.<br>(89.38 gms/sample) | 1966.46 gms.<br>(89.38 x 22) | 983.235<br>(89.38 x 11) | 4111.705 |
| WEIGHT OF LEAVES REMOVED BY TERMITES | 0 | 373.54 gms. | 27.765 gms. | 401.295 |
| % OF TOTAL REMOVED BY TERMITES | | 5.49 %<br>(*M. bellicosus*) | 0.41 %<br>(Others) | 5.90 % |
| % REMOVED BY OTHER FACTORS | | | | 60.40 % |
| OVERALL DECOMPOSITION | | | | 66.30 % |

## 2.3.4 DISCUSSION

The important role of termites as components of the tropical soil fauna has been reviewed by Wood and Sands (in press). Table 2.3.8 is adapted from their work to summarise the quantitative relationship between termite consumption and total annual litter production, as depicted in the more complete recent publications. In S. Guinea savanna, Nigeria, and derived savanna, Ivory Coast, similar consumption values of about a third of annual litter production are reported. The data from Malaysian rain forest are only concerned with leaf litter but also give a value of 30%. Nutting, Haverty and LaFage (unpubl. data) calculate that 92% of wood fall is consumed by termites in shrub grassland in Arizona.

As Wood (1976) has pointed out, the large termite population in the savanna at Mokwa results in consumption of significant quantities of fresh plant litter prior to its degradation by saprophytic micro-organisms. Wood-feeding termites have been seen to remove 60.1% of the annual wood fall and 2.9% of the annual leaf fall, most of this being relatively fresh, undecayed litter. This is quite dissimilar to decomposition processes in temperate regions where arthropod and other soil fauna tend to consume litter only after some degree of decay by fungi and micro-organisms.

This topic will be more fully discussed in Section 2.5, following presentation of data on partition of resources between termite species, given in Section 2.4.

## TABLE 2.3.8 CONSUMPTION BY TERMITES, WITH CALORIFIC EQUIVALENTS, IN SOME TROPICAL AND SUB-TROPICAL ECOSYSTEMS

(Revised from Wood and Sands, in press)

| | | Annual litter production | | Annual consumption by termites | | % of litter consumed by termites | | Authority |
|---|---|---|---|---|---|---|---|---|
| | | g $m^{-2}$ $yr^{-1}$ | kcal $m^{-2}yr^{-1}$ | g $m^{-2}$ $yr^{-1}$ | kcal $m^{-2}$ $yr^{-1}$ | by weight | by kcals | |
| Sahel Savanna<br>Senegal | TOTAL | 160 | | 12.5 | | 7.8 | | Lepage 1974<br>Bille 1973a, b. |
| S. Guinea Savanna<br>Nigeria | WOOD | 139 | 760 | 83.5 | 456 | 60.1 | 60.1 | Present study |
| | LEAVES | 239 | 1124 | 6.8 | 32 | 2.9 | 2.9 | Present study. |
| | GRASS | 155 | | 98 | | 63.2 | | Wood & Ohiagu (unp.) |
| | TOTAL | 533 | | 188.3 | | 35.3 | | |
| Derived Savanna<br>Ivory Coast | TOTAL | 480 | | 135 | | 28.1 | | Josens (1972a) |
| Rain forest<br>Malaysia | LEAVES | 630 | 2835 | 189 | 8505 | 30.0 | 30.0 | Matsumoto 1976 |
| | OTHER | 430 | | | | | | Abe & Matsumoto 1974 |
| | TOTAL | 1060 | | | | | | Ogawa 1974 |
| Shrub grassland<br>Arizona | WOOD | 45 | | 41.4 | | 92.0 | | Nutting, Haverty & LaFage (unp.) |

# SECTION 2.4

# CONSUMPTION BY WOOD-FEEDING TERMITES

## 2.4.1 INTRODUCTION

Termites eat plant material, either living or in various stages of decay down to the last residues of humus. The range of feeding habits has been reviewed by Adamson (1943), Harris (1961), Noirot and Noirot-Timothée (1969), Lee and Wood (1971) and more recently by Wood (in press).

Grassé and Noirot (1959) regard wood feeding as the primitive habit and most lower termites (all families except Termitidae) are wood feeders. Other habits are also known in the group; *Anacanthotermes* (Hodotermitidae) eats dung (Harris 1970) while *Hodotermes* (Hodotermitidae) eats grass (Coaton 1958), as may *Schedorhinotermes derosus* (Rhinotermitidae) (Watson 1969). *Mastotermes darwiniensis* (Mastotermitidae) and *Psammotermes hybostoma* (Rhinotermitidae) are more or less polyphagous herbivores (Gay and Calaby 1970, Harris 1970).

The higher termites (Termitidae) are grouped into four subfamilies, the Termitinae, Apicotermitinae, Nasutitermitinae and Macrotermitinae (Sands 1972b). The Termitinae include soil feeders (e.g. *Cubitermes*, *Pericapritermes*, *Thoracotermes*), wood feeders (e.g. *Termes*, *Cephalotermes*) many of which show a preference for rotten wood, and dung feeders (e.g. *Microcerotermes serratus*, *Amitermes heterognathus*, Ferrar and Watson 1970). Two specialised coprophagous termites from Australia, *Incolitermes* and *Ahamitermes*, are obligate inquilines in *Coptotermes* nests, feeding on faecal nest material (Gay and Calaby 1970).

The Apicotermitinae (Grassé and Noirot 1954) are a group of soil feeders which may take very rotten wood (e.g. Collins, in press) and include the soldierless termites (Sands 1972b).

The Nasutitermitinae have a variety of diets, from sound wood (some *Nasutitermes* spp.) to grass (*Trinervitermes*) and soil (*Eutermellus*). *Hospitalitermes* feeds on lichens and algae (Kalshoven 1958).

The Macrotermitinae also have representatives of a variety of diets. Species of *Macrotermes* may feed on grass (*M. subhyalinus*, Lepage 1974), wood (*M. bellicosus*) or leaves (*M. carbonarius*, Matsumoto 1976). Macrotermitinae do not occur in Australasia or the Americas and are unique amongst termites in building their faeces into combs within the nest. Symbiotic fungi (*Termitomyces* spp.) grow on the combs and, after a period of breakdown the faeces are re-ingested by the termites. Species from other groups are known to prefer rotten wood with a high proportion of fungal mycelium (Kovoor 1964, Esenther et al. 1961, Sands 1969).

The literature on methodology of consumption measurement is as diverse as the feeding habits themselves and a brief review follows.

Many primitive wood feeders of the Kalotermitidae and Rhinotermitidae nest within the logs and trees on which they feed and are difficult to study in the field (Ratcliffe et al. 1952, Greaves 1962, Kalshoven 1930). However, they can be cultured in the laboratory (Light and Weesner 1947, Becker 1969) and of the 21 laboratory studies reviewed by Wood (in press), 17 are concerned with the lower termites (e.g. Haverty and Nutting, 1974, Seifert 1962, Becker 1967). The wide range of results for wood feeders (2.0 - 90.8 mg (d.wt.) $g^{-1}$ (fr.wt. termites) $day^{-1}$), reflects differences in species, wood palatability and culture methods (Wood loc. cit.). Relating these data to the field may be complex and should involve seasonal corrections (Haverty and Nutting 1975). Results obtained from non-breeding colonies are particularly questionable since workers normally feed growing larvae as well as themselves (Wood, in press). Conversely, the controlled laboratory environment may yield useful information on food preferences (McMahon 1966) and the effects of environment on consumption (Haverty and Nutting 1974).

The consumption of subterranean termites that feed entirely in the soil, is the most difficult to quantify. To date there have been no reports of direct estimates. Population studies using soil cores have met with limited success (Strickland 1944, Bodine and Ueckert 1975, Lepage 1972, 1974, Josens 1971, 1972, Wood, Johnson and Ohiagu in press) and Wood and Sands (in press) have used soil core data and assumed energy requirements to calculate consumption. Hébrant (1970) used respiration data and population estimates to calculate consumption of Cubitermes exiguus Mathot.

A number of termites forage without the use of covered runways (Table 2.4.1). In general they forage at night or in the early morning and evening, but some also in day time in overcast conditions. Many are grass feeders and the open-foraging habit may have resulted from the mechanical and energetic impracticality of building runways on standing grass. Genera such as Trinervitermes, Hodotermes, Microhodotermes and Drepanotermes climb grasses, cut pieces off and carry them back to the nest, (Sands 1961, Nel and Hewitt 1969, Gay and Calaby 1970). Nel and Hewitt (1969) have made direct observational estimates of consumption by Hodotermes mossambicus but obtained no population estimates. Ohiagu (1976) and Ohiagu and Wood (1975) combined direct observation of consumption with population estimates to obtain a

TABLE 2.4.1 Termites that habitually forage without covered runways

| SUB-FAMILY | GENUS/SPECIES | LOCALITY | FOOD | FORAGING HABITS | REFERENCES |
|---|---|---|---|---|---|
| HODOTERMITINAE | *Hodotermes* | S. and E.Africa | Grass | Daytime (winter), night mornings, evenings (summer) | Coaton 1958, Nel 1968 |
| | *Microhodotermes* | N. and S.Africa | Grass, leaves, twigs | Similar to *Hodotermes* | Harris 1970, Coaton 1958 |
| | *Anacanthotermes* | Asia and N.Africa | Grass & dung | Night and early morning | Harris 1970 |
| RHINOTERMITINAE | *Schedorhinotermes derosus* (Hill) | Australia | Wood, grass | Nocturnal | Watson 1969 |
| TERMITINAE | *Drepanotermes rubriceps* (Froggatt) | Australia | Grass, some wood | Night or cloudy days | Gay and Calaby 1970 |
| NASUTITERMITINAE | *Nasutitermes* spp. | N.Australia | Grass | Nocturnal | Gay and Calaby 1970 |
| | *Hospitalitermes* | Indo-Malaya | Wood, lichen | Evening, night, morning, cloudy days | Roonwall 1970, John 1925, Kalshoven 1958 |
| | *Lacessitermes* | Indo-Malaya | Wood | Evening, night, morning | Roonwall 1970, John 1925 |
| | *Syntermes* | S.America | Grass | ? | Emerson 1945 |
| | *Tenuirostritermes* | N.America | Grass, seeds | Usually nocturnal | Nutting 1970, Weesner 1970, Banks & Snyder 1920 |
| | *Trinervitermes* 7 spp. | India | Grass | ? | Roonwall 1970 |
| | *Trinervitermes* spp. | Africa | Grass | Evening, night, morning, cloudy days | Sands 1961 |

consumption estimate of 28 mg $g^{-1}$ $day^{-1}$ for Trinervitermes geminatus. Food is consumed in situ as well as beingcarried back to the nest (Kalshoven 1958, Sands 1961), and Ohiagu (loc. cit.) allowed for this by weighing outgoing and incoming workers.

Different problems are presented by suface-feeding species that forage under covered runways since direct observation is precluded. Lepage (1972) measured the length of occupied Macrotermes subhyalinus runways along 5 m line transects and weighed litter under runways and in places where no foraging had occurred. From population data he calculated a consumption rate of 29.1 mg $g^{-1}$ $day^{-1}$.

Matsumoto (~~1974~~, 1976) estimated consumption of leaves by four species of termites in Malaysian rain forest by following photometrically the decline in leaf area of samples put out. He had no termite-excluded samples and his results will include errors due to consumption by millipedes and other saprophages. Ogawa (1974) recorded leaf fall of 6.3 t $ha^{-1}$ $a^{-1}$ and Matsumoto (1976) estimated termite consumption at 30% (1.89 t $ha^{-1}$ $a^{-1}$). Assuming this to be the only food taken by the four species concerned (total biomass 34.61 kg $ha^{-1}$, live weight, Matsumoto loc. cit.) the consumption rate can be calculated as 149.61 mg $g^{-1}$ $day^{-1}$.

"Baiting" has become a common method for studying the habits of surface wood feeders under field conditions. The method consists of providing wood, wood-based or man-made products for termites to feed upon. Three basic types of study have been carried out: 1) palatability tests on building and engineering materials, 2) population estimates, 3) consumption measurements.

1) Palatability tests involve systematic presentation ("graveyard tests"), usually of timber samples, in such a way as to make them

easily and equally available to the termites. Williams (1973) has reviewed field and laboratory methods for testing termite resistance and Usher and Ocloo (1974) have investigated bait shape, size and presentation for maximum attack. Experiments have included assays for insecticides, timber preservatives, plastics and materials exposed to termite attack by virtue of their location, (e.g. underground cables, Beal et al. 1973), or their nature, (e.g. telegraph poles, Usher and Barnacle 1974). Such experiments are designed to attract termites to the test site, often with a pre-baiting period before the tests are begun, (Gay et al. 1957, Butterworth and MacNulty 1966, Williams 1973, Hrdý 1967). Hence, estimates of the termite populations and their consumption on these sites are not realistic.

2) Wood, Johnson and Ohiagu (in press) have used soil coring to estimate termite populations in crops and woodland at Mokwa, Nigeria. Since this method was laborious and time-consuming, softwood baits were used in parallel studies in an attempt to find correlations between bait attack and soil populations (Johnson, pers. comm.). Significant correlations were suggested between % bait discovery and population estimates within specific crops, but there was considerable variation in the intercepts and slopes of correlations for the various crops used. Discrepancies in bait attack may be associated with differences in food availability (Wood, pers. comm.).

3) Two attempts have been made to measure consumption by termites in the field by using baiting. As said, the Macrotermitinae use their faeces to build combs upon which specific fungi grow. Fresh faeces are deposited on the outer edge of the comb while old faeces plus fungal mycelium are consumed from the inner edge (Kalshoven 1936). Josens (1971) used sawdust baits impregnated with soot to mark the faeces on the comb. From the position of the soot after a known period, the turnover rate of the combs was calculated. Annual pro-

duction of faeces was then estimated from biomass and turnover rate and this figure was used as a consumption estimate, assuming no assimilation during the first passage through the gut. This is clearly a serious assumption and the method suffers from three other disadvantages:- 1) seasonal variation is not accounted for, 2) in at least one species of the Macrotermitinae (*M. bellicosus*, Section 3.4), not all the combs are utilised, 3) the area was pre-baited prior to use of the soot baits, making it unnaturally attractive to the termites. Josen's (1971) result of 594 mg $g^{-1}$ $day^{-1}$ for four species of Macrotermitinae is four times higher than the maximum recorded for *M. bellicosus* (Section 2.4.4.1), mainly because Josen's population figures were undoubtedly low (Wood, in press).

Haverty and Nutting (1975a) estimated consumption of the subterranean wood feeder *Heterotermes aureus* Snyder in Arizona by a simulation method. They used toilet roll baits to study foraging activity in relation to temperature and were able to account for seasonal variations. Consumption was calculated from daily turnover of foragers, laboratory consumption of various woods at various temperatures (Haverty and Nutting 1974) and daily field temperature and rainfall records. They assumed that foragers constantly move to and from food and that they move at a rate recorded for *Amitermes hastatus* by Skaife (1955). The authors state that certain parameters require refinement and that the model might be expected to give an over-estimate of consumption; 70.32 mg $g^{-1}$ $day^{-1}$ was recorded for consumption of *Acacia greggii* (Haverty and Nutting 1975a). Lafage (1976) has recently recorded an average consumption of 56.78 mg $g^{-1}$ $day^{-1}$ for *Marginitermes hubbardi* (Banks) in the Sonoran Desert, Arizona.

In Section 2.3 I have described the methods used to obtain figures for annual consumption of wood and leaves by termites and discussed the factors considered in the experimental design. It was not possible to quantify the role of each species in wood removal without seriously disturbing the wood samples. In this section I will show how the relative proportions of wood removal by each species have been estimated and give results for the application of these proportions to the total wood consumption figures for termites given in Section 2.3.

### 2.4.2 METHODS

The total annual consumption of wood litter by all wood feeding termites has been estimated as 835.464 kg $ha^{-1}$ $a^{-1}$ (Section 2.3). Quantification of the amount removed by each species was done by means of softwood baits arranged in a grid pattern on four plots of 32 x 80m, chosen randomly, but subject to the constraint that other plot positions were given priority (Fig. 1.4.2). Because of this, they were not evenly stratified throughout blocks 1-8 but gave a reasonable coverage of the study area as a whole. Each plot was marked in a 4 m grid using wire pegs with aluminium foil flags, to give eight rows of 20 pegs per plot, a total of 640. In January 1975 and at the beginning of every second month thereafter, a pre-weighed (approximately 35 g dry weight) softwood bait 15 x 2.5 x 2.5 cm was placed near each peg. Between 07.00 h and 10.00 h on every second day after bait placement, all the baits were examined for termite attack by quickly lifting the bait, recording any termite species present, and replacing the bait. Records from each bait were kept on prepared sheets (Table 2.4.2). After 28 days (14 checks), the baits were removed, brushed clean, dried and re-weighed. By collating records of termite attack (Table 2.4.3) and records of weight loss from individual baits, the proportion of the total wood loss attributable to each species was calculated. When more than one species attacked a bait, the proportion assigned to each species was the estimate derived from baits attacked by a single species only. This assumed that species foraged independently of each other and that they have no differential preferences for untouched or previously attacked baits.

The checks every two days disturbed the termites to some extent but it is assumed that all species were disturbed equally. The extent to which disturbance reduced consumption was examined by placing four inter-rows of baits between the experimental baits on two plots, (total of 160) in July 1975, and leaving them unchecked until the final collection.

It was considered that the use of softwood might confer disproportionate advantage on one or other of the major species. To check this possibility, four inter-rows of hardwood baits were put on plots 3 and 4, (total of 160), in May 1975; these were checked in the usual way.

The weight of softwood baits put out averaged 23.1 kg $ha^{-1}$. This was less than 1% of the total standing crop of dead wood of 2.821 t $ha^{-1}$ (Section 2.2) and is assumed to have had no effect on the distribution of the termite populations.

## 2.4.3 RESULTS

### 2.4.3.1 Calculation of Consumption by Termites

A total of 53,760 checks were made on 3,840 baits, far too many records to be presented in full, although available if required. An example of the 48 hour checks from one baiting plot is given in Table 2.4.2 and an example of the cumulative results,(for Area 2 in July 1974), given in Table 2.4.3. Unattacked baits were used as controls for correcting for weight losses caused by agents other than termites.

The complete data for weight of wood removed from the baits / species / month / baiting plot are given in Table 2.4.4 together with calculations of the relative proportion removed by each species over the whole period from each plot and from all plots. The 95% confidence limits for the mean of each species in each month are noticeably high, mainly because only four plots were used and 't' (with 3 d.f.) is therefore equal to 3.182. However, it was necessary to use large plots in order to eliminate variation between them (see below) and time and labour precluded the use of more than four plots of this size. The data are summarised in the form of pie diagrams in Figure 2.4.1.

Table 2.4.5 gives an analysis of variance of the total consumption per species per plot. The variance ratio between plots is 0.39 at 3 and 21 D.F. and is not significant, indicating the homogeneity of the baiting plots. The variance ratio between species is 11.74 at 7 and 21 D.F. and is highly significant ($p < 0.001$). In Table 2.4.6 the mean consumptions of the species are analysed by t-tests. The variation in consumption by each species in the four plots was high but, as stated, time and labour precluded further work and I shall accept a probability level of 10% as indicating a significant difference for between-species means. Hence, there are four sets of species with similar feeding levels. Microtermes spp. consumed the largest proportion (35.79%). *Macrotermes bellicosus*, *Ancistrotermes cavithorax* and *Odontotermes* spp. also took large amounts, (21.17%, 18.81% and 14.49% respectively), with no significant differences between them. At a lower level, *Microcerotermes* sp. and *Macrotermes subhyalinus* took 4.81% and 4.40% with no significant difference between them. Finally, *Amitermes evuncifer* and *Trinervitermes* sp. took 0.28% and 0.09%, also with no significant difference.

The amount of wood litter removed annually by each species (CWsp) can be calculated from the expression:

$$CWsp = CWt \, . \, \frac{\overline{CB}sp}{\overline{CB}t}$$

where $CW_t$ = consumption of wood litter by all termites, equal to 835.464 kg $ha^{-1}$ $a^{-1}$ (Section 3.3).

$\overline{CB}sp$ = mean total consumption of baits per species.

$\overline{CB}_t$ = mean total consumption of baits by all species (equal to 2334.55 g, Table 2.4.4).

Table 2.4.7 gives the results calculated for each species. Estimates of leaf litter consumption have been brought forward and the total consumption of wood and leaf litter by each species has been calculated.

TABLE 2.4.2 An example of a 48 hour bait check sheet. Key as in Table 2.4.3 except, ? = baits previously attacked but now abandoned.

| BAITING PLOT : TWO DATE : 12/7/1975 SHEET ONE | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H |
| 1 | | | | | | | M | |
| 2 | A | | | | M | | | A |
| 3 | | | | A | M | | | |
| 4 | | | | | | M | | |
| 5 | | | | | | | | |
| 6 | M | M | | M | | | | M |
| 7 | A,M | | | | | | | |
| 8 | M | | | | | | | |
| 9 | | | | | | Ms | | |
| 10 | | | | | | | | A |
| 11 | ? | M | ? | M | M | | | |
| 12 | A | | | | | | | |
| 13 | | | | | | Ms | | |
| 14 | | M | | | | | | |
| 15 | | | | | | | M | |
| 16 | | | A | A | | | | |
| 17 | | | ? | | | A | | ? |
| 18 | | Ms | | | | ? | | M |
| 19 | | | Mb | | | | M | M |
| 20 | M | Mb | | | | | | |

TABLE 2.4.3 An example of the cumulative results of bait discovery on one area in one month. Key : A = *Ancistrotermes*, M = *Microtermes*, Mc = *Microcerotermes*, Mb = *Macrotermes bellicosus*, Ms = *Macrotermes sybhyalinus* O = *Odontotermes*, T = *Trinervitermes*

BAITING PLOT : TWO DATE : JULY OVERALL SHEET TWO

| | A | B | C | D | E | F | G | H |
|---|---|---|---|---|---|---|---|---|
| 1 | CONTROL | | | Mb | O | A | | Mb,A |
| 2 | A,M | | M | | M | A | | A,M |
| 3 | | | | A,M | M | | | M |
| 4 | | CONTROL | M | | M | M | | M |
| 5 | M | | M | | | | | M |
| 6 | M,A | M | M | M | | M | | M |
| 7 | M,A | M | CONTROL | | A | | A | M |
| 8 | M | M,A | | | | | | M |
| 9 | | | A | A | | Ms,A | | A |
| 10 | | | A | CONTROL | | | | A,M |
| 11 | M | M | Ms | M | M | A | | |
| 12 | Mc,A | M | | | CONTROL | | | |
| 13 | A,M | | | | Ms,M | Ms | O | A |
| 14 | | M,A | M,O | | | | | A,M |
| 15 | | | | | T | CONTROL | M | |
| 16 | | | A,M | A | | | | CONTROL |
| 17 | M | M | M,Ms | O,M | | A | M | A |
| 18 | | Ms | | | | Mb,Ms,A | CONTROL | M |
| 19 | M | A,M | A,Mb | M | | M | A,M | M |
| 20 | M | Mb | | | | | Mb | Mb |

TABLE 2.4.4 The weight of wood removed from the baits/species/month/baiting plot. The relative proportion taken by each species is the ratio of consumption/species to the total consumed by all species, expressed as a %.

| SPECIES | BAITING PLOT | CONSUMPTION FROM BAITS g | | | | | | TOTAL CONSUMPTION BY EACH SPECIES g | RELATIVE PROPORTION TAKEN BY EACH SPECIES (as % of TOTALS) |
|---|---|---|---|---|---|---|---|---|---|
| | | JANUARY | MARCH | MAY | JULY | SEPTEMBER | NOVEMBER | | |
| Microtermes | 1 | 0 | 10.358 | 442.896 | 154.929 | 319.154 | 75.798 | 1003.135 | 36.110 |
| | 2 | 0.993 | 30.265 | 375.614 | 299.798 | 316.187 | 29.711 | 1052.568 | 47.722 |
| | 3 | 0.223 | 2.107 | 269.883 | 226.030 | 210.678 | 36.880 | 745.801 | 35.484 |
| | 4 | 6.659 | 0 | 166.313 | 156.937 | 182.453 | 44.694 | 557.056 | 24.727 |
| | MEAN<br>±95% c.l. | 1.97<br>±5.02 | 10.68<br>±21.95 | 313.68<br>±193.05 | 209.42<br>±109.34 | 257.12<br>±112.76 | 46.77<br>±32.29 | 639.64<br>±368.26 | 35.966 |
| Ancistrotermes | 1 | 58.002 | 43.310 | 136.890 | 263.136 | 62.773 | 8.473 | 572.584 | 20.612 |
| | 2 | 4.956 | 12.588 | 92.386 | 93.583 | 43.080 | 8.129 | 254.722 | 11.549 |
| | 3 | 21.598 | 39.301 | 86.277 | 96.072 | 60.242 | 7.548 | 311.038 | 14.799 |
| | 4 | 18.975 | 67.171 | 396.171 | 55.180 | 71.621 | 8.663 | 617.781 | 27.423 |
| | MEAN<br>±95% c.l. | 25.88<br>±36.00 | 40.59<br>±35.57 | 177.93<br>±234.25 | 126.99<br>±147.44 | 59.43<br>±19.00 | 8.20<br>±0.78 | 439.03<br>±290.68 | 18.806 |
| Odontotermes | 1 | 111.346 | 29.514 | 7.110 | 32.194 | 14.835 | 113.589 | 308.588 | 11.108 |
| | 2 | 36.313 | 8.727 | 28.536 | 4.985 | 26.601 | 137.107 | 242.269 | 10.984 |
| | 3 | 50.137 | 28.892 | 32.511 | 9.024 | 19.923 | 5.461 | 145.948 | 6.944 |
| | 4 | 144.182 | 57.735 | 181.575 | 15.141 | 53.475 | 203.682 | 655.790 | 29.110 |
| | MEAN<br>±95% c.l. | 85.49<br>±81.03 | 31.22<br>±32.05 | 62.43<br>±127.61 | 15.34<br>±19.07 | 28.71<br>±27.36 | 114.96<br>±131.05 | 338.15<br>±353.26 | 14.485 |
| Macrotermes bellicosus | 1 | 173.764 | 0 | 146.331 | 184.419 | 48.773 | 157.731 | 711.018 | 25.595 |
| | 2 | 0.424 | 0 | 5.950 | 69.887 | 50.184 | 225.478 | 351.923 | 15.956 |
| | 3 | 103.041 | 17.891 | 125.441 | 99.023 | 93.150 | 268.544 | 707.090 | 33.642 |
| | 4 | 24.574 | 21.327 | 20.294 | 126.060 | 0 | 14.195 | 206.450 | 9.164 |
| | MEAN<br>±95% c.l. | 75.45<br>±125.42 | 9.80<br>±18.15 | 74.50<br>±113.96 | 119.85<br>±77.61 | 48.03<br>±60.57 | 166.49<br>±177.08 | 494.12<br>±406.02 | 21.166 |
| Macrotermes subhyalinus | 1 | 12.517 | 0 | 0 | 19.427 | 0 | 0 | 31.944 | 1.150 |
| | 2 | 97.783 | 22.319 | 0 | 40.832 | 5.248 | 44.515 | 210.697 | 9.553 |
| | 3 | 51.915 | 12.971 | 2.778 | 5.732 | 21.961 | 52.196 | 147.553 | 7.020 |
| | 4 | 0 | 4.422 | 0 | 2.808 | 13.243 | 0.058 | 20.531 | 0.911 |
| | MEAN<br>±95% c.l. | 40.55<br>±70.17 | 9.93<br>±15.69 | 0.69<br>±2.21 | 17.20<br>±27.59 | 10.11<br>±15.26 | 24.19<br>±44.67 | 102.68<br>±146.49 | 4.398 |
| Microcerotermes | 1 | 28.217 | 56.854 | 14.354 | 12.317 | 13.875 | 17.950 | 143.567 | 5.168 |
| | 2 | 22.008 | 65.104 | 0 | 0 | 0 | 4.854 | 91.966 | 4.170 |
| | 3 | 5.326 | 8.664 | 0 | 0 | 0 | 7.664 | 21.654 | 1.030 |
| | 4 | 46.479 | 70.122 | 24.722 | 10.972 | 9.608 | 29.772 | 191.675 | 8.508 |
| | MEAN<br>±95% c.l. | 25.51<br>±27.04 | 50.19<br>±44.89 | 9.77<br>±19.17 | 5.82<br>±10.73 | 5.87<br>±11.14 | 15.06<br>±17.99 | 112.22<br>±115.86 | 4.807 |
| Trinervitermes | 1 | 0.579 | 0 | 0 | 0 | 2.786 | 0 | 3.365 | 0.121 |
| | 2 | 0 | 0 | 0 | 0.149 | 0 | 1.345 | 1.494 | 0.068 |
| | 3 | 0 | 0 | 0 | 0.088 | 0 | 0 | 0.088 | 0.004 |
| | 4 | 0 | 0 | 0 | 0.960 | 0 | 2.569 | 3.529 | 0.157 |
| | MEAN<br>±95% c.l. | 0.14<br>±0.46 | 0 | 0 | 0.30<br>±0.71 | 0.70<br>±2.22 | 0.98<br>±1.97 | 2.12<br>±2.61 | 0.091 |
| Amitermes | 1 | 0 | 0 | 0 | 0 | 3.770 | 0 | 3.770 | 0.136 |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 3 | 0 | 0 | 22.616 | 0 | 0 | 0 | 22.616 | 1.076 |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | MEAN<br>±95% c.l. | 0 | 0 | 5.65<br>±17.99 | 0 | 0.94<br>±3.00 | 0 | 6.60<br>±17.23 | 0.283 |

| PLOT | | TOTAL CONSUMPTION BY ALL SPECIES g | | | | | | TOTALS g | |
|---|---|---|---|---|---|---|---|---|---|
| | | JANUARY | MARCH | MAY | JULY | SEPTEMBER | NOVEMBER | | |
| ONE | | 384.424 | 140.038 | 747.581 | 666.422 | 465.966 | 373.542 | 2777.973 | 100% |
| TWO | | 162.477 | 139.003 | 502.486 | 509.235 | 441.300 | 451.139 | 2205.640 | 100% |
| THREE | | 232.240 | 109.825 | 539.506 | 435.970 | 405.954 | 378.295 | 2101.790 | 100% |
| FOUR | | 240.870 | 220.776 | 789.074 | 368.058 | 330.398 | 303.632 | 2252.808 | 100% |
| | MEAN<br>±95% c.l. | 255.00<br>±148.20 | 152.41<br>±75.86 | 644.66<br>±230.04 | 494.92<br>±203.72 | 410.90<br>±93.95 | 376.65<br>±95.87 | 2334.55<br>±480.91 | 100% |

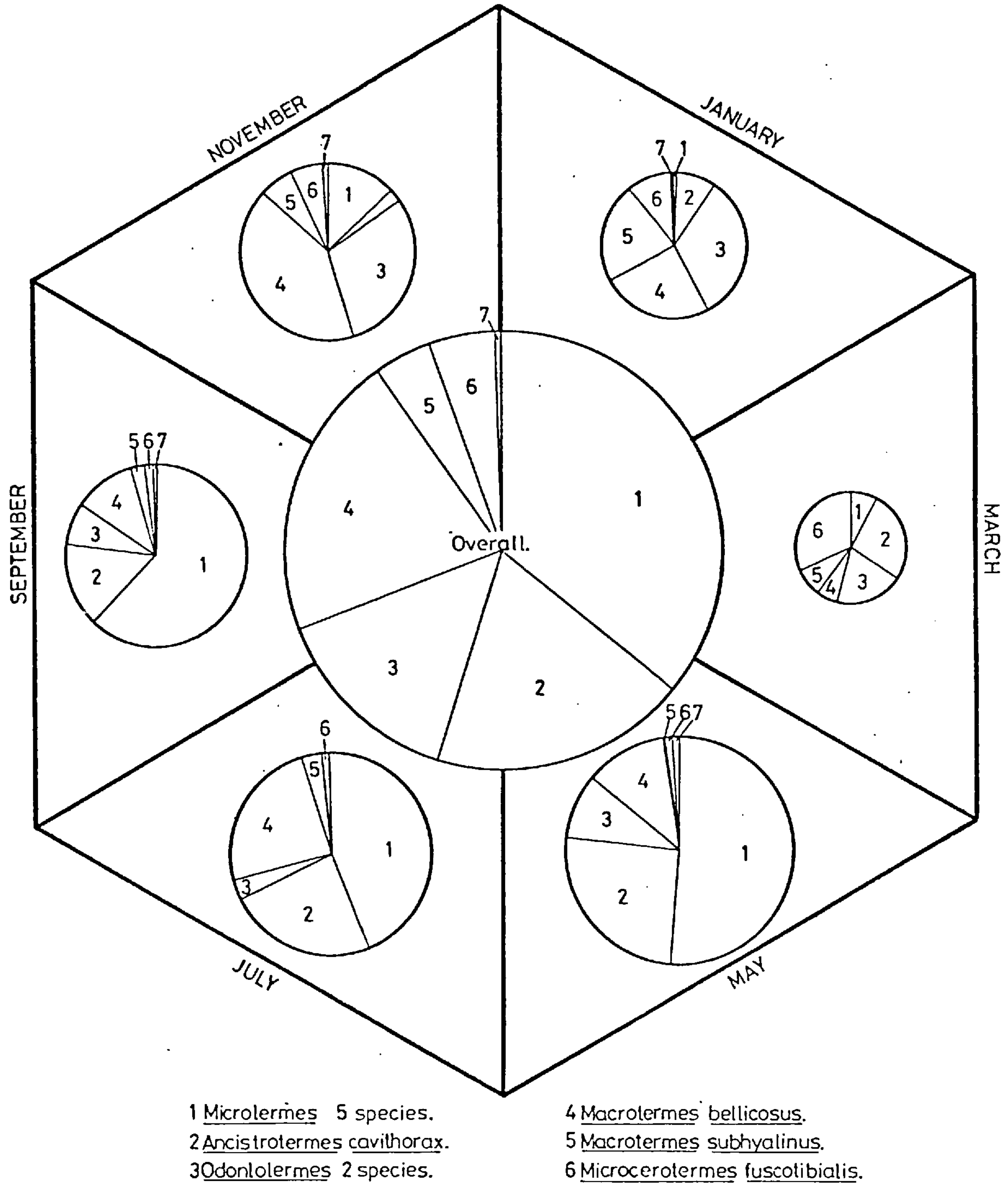


FIGURE 2.4.1 Bait consumption data represented by pie diagrams. The area of each pie represents the total wood removed and the segments represent the amount consumed by each species of termite.

TABLE 2.4.5 Analysis of variance between baiting areas and between species of termites

| SPECIES | TOTAL CONSUMPTION g | | | | MEAN CONSUMPTION |
|---|---|---|---|---|---|
| | PLOT 1 | PLOT 2 | PLOT 3 | PLOT 4 | |
| *Microtermes* | 1003.14 | 1052.57 | 745.80 | 557.06 | 839.64 g |
| *Macrotermes bellicosus* | 711.02 | 351.92 | 707.09 | 206.45 | 494.12 |
| *Ancistrotermes* | 572.58 | 254.72 | 311.04 | 617.78 | 439.03 |
| *Odontotermes* | 308.59 | 242.27 | 145.95 | 655.79 | 338.15 |
| *Microcerotermes* | 143.57 | 91.97 | 21.65 | 191.68 | 112.22 |
| *Macrotermes subhyalinus* | 31.94 | 210.70 | 147.55 | 20.53 | 102.68 |
| *Amitermes* | 3.77 | 0 | 22.62 | 0 | 6.60 |
| *Trinervitermes* | 3.37 | 1.49 | 0.09 | 3.53 | 2.12 |
| MEAN CONSUMPTION PER PLOT g | 347.25 | 275.71 | 262.72 | 281.60 | |

| SOURCE OF VARIATION | Degrees of freedom | Sum of squares | Mean square |
|---|---|---|---|
| Between areas | 3 | 34263.13 | 11421.04 (MA) |
| Between species | 7 | 2392643.98 | 341806.28 (MS) |
| Residual | 21 | 611587.92 | 29123.23 ($S^2$) |
| Total | 31 | 3038495.03 | |

VARIANCE RATIOS F 1) $\frac{MA}{S^2}$ = 0.39 @ 3 & 21 d.f., not. sig.

2) $\frac{MS}{S^2}$ = 11.74 @ 7 & 21 d.f., sig. @ .001

TABLE 2.4.6 t-test analysis of mean consumption per baiting area for each species of wood-litter feeding termite species

| SPECIES | MEAN CONSUMPTION PLOT $^{-1}$g | S | $S^2$ | n | d.f. | t | SIGNIFICANCE LEVEL |
|---|---|---|---|---|---|---|---|
| Microtermes | 839.64 | 231.47 | 53576.28 | 4 | 6 | 2.01 | 0.1 |
| Macrotermes bellicosus | 494.12 | 255.20 | 65125.57 | 4 | 6 | 0.35 | n.s. |
| Ancistro-termes | 439.03 | 182.70 | 33379.59 | 4 | 6 | 0.70 | n.s. |
| Odontotermes | 338.15 | 222.04 | 49300.93 | 4 | 6 | 1.93 | 0.1 |
| Microcero-termes | 112.22 | 72.82 | 5303.23 | 4 | 6 | 0.16 | n.s. |
| Macrotermes subhyalinus | 102.68 | 92.08 | 8478.14 | 4 | 6 | 2.707 | 0.1 |
| Amitermes | 6.60 | 10.83 | 117.26 | 4 | 6 | 0.82 | n.s. |
| Trinervi-termes | 2.12 | 1.64 | 2.69 | 4 | 6 | | |

NOTE:- The least significant difference for consumption means of each species can be calculated from:-

$$LSD = st\sqrt{\frac{2}{f}}$$

where s is calculated as the square root of the error mean square (Table 2.4.5), t from Student's t tables @ DF in $s^2$, f = number of replicates. (Bliss 1967, p252).

Hence for p = 0.05

$$LSD = 170.655 \cdot 2.080\sqrt{\frac{2}{4}} = \underline{250.996}\ g$$

for p = 0.10

$$LSD = 170.655 \cdot 1.721\sqrt{\frac{2}{4}} = \underline{207.675}\ g$$

## TABLE 2.4.7 ESTIMATED CONSUMPTION OF WOOD AND LEAF LITTER BY TERMITES, WITH CALORIFIC EQUIVALENTS

| SPECIES | PROPORTION TAKEN $(\overline{CBsp} \div \overline{CBt} \times 100)$ | 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 (1) kcal $ha^{-1}a^{-1}$ |
|---|---|---|---|---|---|
| *Microtermes* 5 spp. | 35.966 | 300.483 | ~0 | 300.483 | 1,641,659 |
| *Ancistrotermes cavithorax* | 18.806 | 157.117 | ~0 | 157.117 | 858,393 |
| *Odontotermes* 2 spp. | 14.485 | 121.017 | 4.756 | 125.773 | 683,554 |
| *Macrotermes bellicosus* | 21.166 | 176.834 | 63.684 | 240.518 | 1,265,920 |
| *Macrotermes subhyalinus* | 4.398 | 36.744 | ~0 | 36.744 | 200,747 |
| *Microcerotermes* sp. | 4.807 | 40.161 | 0 | 40.161 | 219,416 |
| *Amitermes evuncifer* | 0.282 | 2.356 | 0 | 2.356 | 12,872 |
| *Trinervitermes* sp. | 0.090 | 0.752 | 0 | 0.752 | 4,108 |
| Totals | 100 | (2) 835.464 $(CW_t)$ | (2) 68.440 | 903.904 | 4,886,669 |

(1) Calorific equivalent of wood (Section 2.1) : 5.4634 kcal $g^{-1}$
Calorific equivalent of leaves (Section 2.1) : 4.7077 kcal $g^{-1}$

(2) From Section 2.3

### 2.4.3.2 Assessment of Assumptions used in the Baiting Experiments

The methods involved in the baiting experiments have included some assumptions which can be examined in more detail.

1) The assumption that species forage independently of each other and remove similar proportions of wood from multi-species and single-species attacked baits.

Table 2.4.8 is an analysis of bait attack. Monthly bait discovery data are divided into baits discovered by only one species and baits discovered by more than one species. In Table 2.4.9 the ranked totals for single-attack and multi-attack are tested for correlation using the Spearman rank correlation test. In all cases the correlations are significant at the 99% level. In addition, it has been found (Figure 2.4.2) that overall bait discovery and wood consumption are directly correlated ($p < 0.001$). I therefore consider this assumption to be justified.

2) The assumption that all species find fresh wood baits equally palatable.

*Amitermes* spp. undoubtedly preferred rotting wood but was uncommon on the study area. Table 2.4.10 shows bait discovery data for four common species and genera, *Microtermes*, *Ancistrotermes*, *Macrotermes bellicosus* and *Odontotermes* during two months of high foraging activity, May and July. Substantial rainfall in these months (160 and 174 mm) promoted fungal attack of baits. For a species preferring decomposing wood an increase in rate of attack during the latter half of the month might be expected. As Table 2.4.10 shows, this was not the case. Discovery and attack of baits was fastest in the early part of the month. In a survey of wood litter over eight 100 m$^2$ plots in

April 1975, less than 5% of items were found to show any obvious signs of rotting (Collins, R.A. Johnson, C.E. Ohiagu and T.G. Wood, unpubl. data). A preference for rotting wood would therefore be a severe disadvantage in this area and inconsistent with the obvious importance of Macrotermitinae in this ecosystem.

3) The assumption that the size of bait used did not predispose disproportionate attack by one or more species.

Table 2.3.5 (Section 2.3) shows the species recorded on the decomposing wood samples on 16 10 x 10 m quadrats. The totals of the records have been ranked and a perfect correlation found between log and twig records. This strongly suggests that preferences for large or small items do not vary appreciably between the species at Mokwa.

4) The assumption that the use of softwood does not predispose disproportionate attack by one or more species.

Table 2.4.11 gives the results for the hardwood test made in May 1975 and described in Section 2.4.2. Consumption per species for the hard and soft wood have been ranked and tested for correlation by the Spearman method. For plots 3 and 4 separately the correlation is poor but for the two areas summed it is 100%. This is not a quantitative test and the relative consumptions of softwood : hardwood were about 3 : 1 for Odontotermes, 1 : 1 for Microcerotermes and 2.2 : 1 for the other species. Therefore, the assumption appears to be justified for all the major species except perhaps Odontotermes spp.

5) The assumption that bait checking did not disproportionately disturb the termite species feeding on them.

Table 2.4.12 gives results for the disturbance test described in Section 2.4.2. The mean consumption per bait dropped by a mean of 25.85% from controls to experimental baits, clearly showing that checking disturbed the termites. It has already been stated that this was the reason that the baiting method was developed. Since it was impossible to estimate whether one species was disturbed more than another without checking the baits to see which species were feeding, this assumption remains untested.

TABLE 2.4.8 Analysis of bait attack. Monthly data are divided into baits attacked by one species only and baits attacked by more than one species.

| JANUARY 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| Microtermes | 0 | 1 | 1 | 2 | 4 | 2 | 1 | 0 | 0 | 3 | 7 | 1.09 |
| Ancistrotermes | 11 | 4 | 9 | 4 | 28 | 6 | 2 | 3 | 5 | 16 | 54 | 8.44 |
| Odontotermes | 11 | 9 | 14 | 13 | 47 | 6 | 1 | 3 | 4 | 14 | 61 | 9.53 |
| M.bellicosus | 7 | 1 | 10 | 2 | 20 | 1 | 1 | 2 | 2 | 6 | 26 | 4.06 |
| M.subhyalinus | 1 | 9 | 4 | . | 14 | . | 3 | 1 | 1 | 5 | 19 | 2.97 |
| Microcerotermes | 8 | 11 | 6 | 12 | 37 | 3 | 3 | 1 | 6 | 13 | 50 | 7.81 |
| Trinervitermes | 1 | . | . | . | 1 | 1 | . | . | . | 1 | 2 | 0.31 |
| Amitermes | . | . | . | . | . | . | . | . | . | . | . | . |
| TOTALS | 39 | 35 | 44 | 33 | 151 | 19 | 11 | 10 | 18 | 57 | | |

| MARCH 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| Microtermes | 1 | 1 | 1 | . | 3 | 1 | . | 2 | . | 3 | 6 | 0.94 |
| Ancistrotermes | 13 | 3 | 7 | 14 | 37 | 5 | 2 | 1 | 6 | 14 | 51 | 7.97 |
| Odontotermes | 6 | 2 | 10 | 9 | 27 | 2 | . | 1 | 1 | 4 | 30 | 4.69 |
| M.bellicosus | . | . | 5 | 3 | 8 | . | . | . | 2 | 2 | 10 | 1.56 |
| M.subhyalinus | . | 2 | 2 | 1 | 5 | . | 1 | . | . | 1 | 6 | 0.94 |
| Microcerotermes | 11 | 9 | 3 | 16 | 39 | 5 | 3 | . | 4 | 12 | 51 | 7.97 |
| Trinervitermes | . | . | . | . | . | . | . | . | . | . | . | . |
| Amitermes | . | . | . | . | . | . | . | . | . | . | . | . |
| TOTALS | 31 | 17 | 28 | 43 | 119 | 13 | 6 | 4 | 13 | 36 | | |

| MAY 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| Microtermes | 36 | 40 | 34 | 16 | 126 | 67 | 46 | 48 | 67 | 228 | 354 | 55.31 |
| Ancistrotermes | 20 | 17 | 15 | 30 | 82 | 56 | 42 | 41 | 74 | 213 | 295 | 46.09 |
| Odontotermes | 4 | 11 | 9 | 8 | 32 | 18 | 9 | 14 | 26 | 67 | 9 | 15.47 |
| M.bellicosus | 10 | 1 | 5 | 3 | 19 | 31 | 2 | 20 | 12 | 65 | 84 | 13.13 |
| M.subhyalinus | . | . | 1 | . | 1 | 2 | 4 | 2 | 1 | 9 | 10 | 1.56 |
| Microcerotermes | 4 | 1 | . | 3 | 8 | 2 | 9 | 4 | 8 | 23 | 31 | 4.84 |
| Trinervitermes | . | . | . | . | . | . | . | . | . | . | . | 0.0 |
| Amitermes | . | . | 1 | . | 1 | . | . | . | . | . | 2 | 0.31 |
| TOTALS | 74 | 70 | 65 | 60 | 269 | 176 | 112 | 129 | 188 | 605 | | |

TABLE 2.4.8 (cont'd.)

| JULY 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| *Microtermes* | 18 | 36 | 22 | 27 | 103 | 39 | 17 | 27 | 23 | 106 | 209 | 32.66 |
| *Ancistrotermes* | 20 | 13 | 21 | 8 | 62 | 38 | 18 | 23 | 17 | 96 | 158 | 24.69 |
| *Odontotermes* | 5 | 2 | 4 | 5 | 16 | 11 | 2 | 7 | 16 | 36 | 52 | 8.13 |
| *M.bellicosus* | 11 | 4 | 8 | 9 | 32 | 14 | 3 | 3 | 10 | 30 | 62 | 9.69 |
| *M.subhyalinus* | 1 | 3 | 2 | 1 | 7 | 1 | 4 | 4 | 0 | 9 | 16 | 2.50 |
| *Microcerotermes* | 4 | . | . | 4 | 8 | 3 | 1 | 1 | 2 | 7 | 15 | 2.34 |
| *Trinervitermes* | . | 1 | 1 | 1 | 3 | 3 | . | 5 | 1 | 9 | 12 | 1.88 |
| *Amitermes* | . | . | . | . | . | 2 | . | 1 | . | 3 | 3 | 0.47 |
| TOTALS | 59 | 59 | 58 | 55 | 231 | 111 | 45 | 71 | 69 | 296 | | |

| SEPTEMBER 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| *Microtermes* | 43 | 36 | 34 | 47 | 160 | 15 | 15 | 24 | 13 | 67 | 227 | 35.47 |
| *Ancistrotermes* | 11 | 8 | 12 | 16 | 47 | 14 | 5 | 13 | 5 | 37 | 84 | 13.13 |
| *Odontotermes* | 3 | 8 | 2 | 14 | 27 | 3 | 6 | 7 | 6 | 22 | 49 | 7.66 |
| *M.bellicosus* | 7 | 9 | 4 | 0 | 20 | 4 | 5 | 6 | 2 | 17 | 37 | 5.78 |
| *M.subhyalinus* | 0 | 1 | 1 | 4 | 6 | 0 | 2 | 5 | 0 | 7 | 13 | 2.03 |
| *Microcerotermes* | 2 | . | . | 2 | 4 | 1 | . | . | 1 | 2 | 6 | 0.94 |
| *Trinervitermes* | 1 | . | . | . | 1 | 1 | . | . | . | 1 | 2 | 0.31 |
| *Amitermes* | 1 | . | . | . | 1 | 2 | . | 1 | 1 | 4 | 5 | 0.78 |
| TOTALS | 68 | 62 | 53 | 83 | 266 | 40 | 33 | 56 | 28 | 157 | | |

| NOVEMBER 1975 | SINGLE-ATTACK | | | | | MULTI-ATTACK | | | | | TOTAL ATTACK | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | TOTAL | 1 | 2 | 3 | 4 | TOTAL | No. | %640 |
| *Microtermes* | 23 | 21 | 11 | 16 | 71 | 13 | 13 | 10 | 9 | 45 | 116 | 18.13 |
| *Ancistrotermes* | 2 | 3 | 3 | 2 | 10 | 5 | 6 | 2 | 5 | 18 | 28 | 4.38 |
| *Odontotermes* | 17 | 14 | 7 | 26 | 64 | 5 | 2 | 6 | 4 | 17 | 81 | 12.66 |
| *M.bellicosus* | 9 | 7 | 14 | 1 | 31 | 1 | 4 | 8 | . | 13 | 44 | 6.88 |
| *M.subhyalinus* | . | 6 | 5 | 1 | 12 | . | 2 | 2 | 1 | 5 | 17 | 2.66 |
| *Microcerotermes* | 10 | 7 | 5 | 15 | 37 | 12 | 6 | 8 | 12 | 38 | 75 | 11.72 |
| *Trinervitermes* | . | 1 | . | 1 | 2 | . | . | . | . | . | 2 | 0.31 |
| *Amitermes* | . | . | . | . | . | . | . | . | . | . | | |
| TOTALS | 61 | 59 | 45 | 62 | 227 | 36 | 33 | 36 | 31 | 136 | | |

TABLE 2.4.9 Spearman rank correlation test between total single species attacked baits and total multi-species attacked baits

JANUARY 1975

| SPECIES | No. BAITS ATTACKED BY ONE SPECIES | RANK | No. BAITS ATTACKED BY ONE SPECIES | RANK |
|---|---|---|---|---|
| *Microtermes* | 4 | 6 | 3 | 6 |
| *Ancistrotermes* | 28 | 3 | 16 | 1 |
| *Odontotermes* | 47 | 1 | 14 | 2 |
| *M. bellicosus* | 20 | 4 | 6 | 4 |
| *M. subhyalinus* | 14 | 5 | 5 | 5 |
| *Microcerotermes* | 37 | 2 | 13 | 3 |
| *Trinervitermes* | 1 | 7 | 1 | 7 |
| *Amitermes* | 0 | 8 | 0 | 8 |

$r_s = 0.93$

$p = < .01$

MARCH

| | | | | |
|---|---|---|---|---|
| *Microtermes* | 3 | 6 | 3 | 4 |
| *Ancistrotermes* | 37 | 2 | 14 | 1 |
| *Odontotermes* | 27 | 3 | 4 | 3 |
| *M. bellicosus* | 8 | 4 | 2 | 5 |
| *M. subhyalinus* | 5 | 5 | 1 | 6 |
| *Microcerotermes* | 39 | 1 | 12 | 2 |
| *Trinervitermes* | 0 | 7.5 | 0 | 7.5 |
| *Amitermes* | 0 | 7.5 | 0 | 7.5 |

$r_s = 0.90$

$p = < .01$

MAY

| | | | | |
|---|---|---|---|---|
| *Microtermes* | 126 | 1 | 228 | 1 |
| *Ancistrotermes* | 82 | 2 | 213 | 2 |
| *Odontotermes* | 32 | 3 | 67 | 3 |
| *M. bellicosus* | 19 | 4 | 65 | 4 |
| *M. subhyalinus* | 1 | 6.5 | 9 | 6 |
| *Microcerotermes* | 8 | 5 | 23 | 5 |
| *Trinervitermes* | 0 | 8 | 0 | 7.5 |
| *Amitermes* | 1 | 6.5 | 0 | 7.5 |

$r_s = 0.98$

$p = < .01$

JULY

| | | | | |
|---|---|---|---|---|
| Microtermes | 103 | 1 | 106 | 1 |
| Ancistrotermes | 62 | 2 | 96 | 2 |
| Odontotermes | 16 | 4 | 36 | 3 |
| M. bellicosus | 32 | 3 | 30 | 4 |
| M. subhyalinus | 7 | 6 | 9 | 5.5 |
| Microcerotermes | 8 | 5 | 7 | 7 |
| Trinervitermes | 3 | 7 | 9 | 5.5 |
| Amitermes | 0 | 8 | 3 | 8 |

$r_s = 0.90$

$p = <.01$

SEPTEMBER

| | | | | |
|---|---|---|---|---|
| Microtermes | 160 | 1 | 67 | 1 |
| Ancistrotermes | 47 | 2 | 37 | 2 |
| Odontotermes | 27 | 3 | 22 | 3 |
| M. bellicosus | 20 | 4 | 17 | 4 |
| M. subhyalinus | 6 | 5 | 7 | 5 |
| Microcerotermes | 4 | 6 | 2 | 7 |
| Trinervitermes | 1 | 7.5 | 1 | 8 |
| Amitermes | 1 | 7.5 | 4 | 6 |

$r_s = 0.96$

$p = <.01$

NOVEMBER

| | | | | |
|---|---|---|---|---|
| Microtermes | 71 | 1 | 45 | 1 |
| Ancistrotermes | 10 | 6 | 18 | 3 |
| Odontotermes | 64 | 2 | 17 | 4 |
| M. bellicosus | 31 | 4 | 13 | 5 |
| M. subhyalinus | 12 | 5 | 5 | 6 |
| Microcerotermes | 37 | 3 | 38 | 2 |
| Trinervitermes | 2 | 7 | 0 | 7.5 |
| Amitermes | 0 | 8 | 0 | 7.5 |

$r_s = 0.84$

$p = <.01$

TABLE 2.4.9 (cont'd.)

TABLE 2.4.10 The number of baits being attacked by four major wood-feeding species or groups of species at the 48 hour checks during two months of high activity - May and July

MAY

| SPECIES | NUMBER OF BAITS BEING ATTACKED AT THE CHECK ON DAY: | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 4 | 6 | 8 | 10 | 12 | 14 | 16 | 18 | 20 | 22 | 24 | 26 | 28 |
| *Microtermes* | 77 | 126 | 148 | 159 | 146 | 153 | 172 | 176 | 172 | 171 | 185 | 179 | 179 | 166 |
| *Ancistrotermes* | 46 | 73 | 61 | 70 | 75 | 88 | 104 | 120 | 141 | 155 | 157 | 166 | 169 | 176 |
| *Macrotermes bellicosus* | 9 | 10 | 11 | 8 | 9 | 12 | 18 | 20 | 18 | 18 | 12 | 15 | 15 | 16 |
| *Odontotermes* | 5 | 3 | 12 | 8 | 9 | 11 | 10 | 11 | 15 | 12 | 15 | 14 | 12 | 9 |

JULY

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Microtermes* | 31 | 49 | 59 | 62 | 65 | 75 | 86 | 89 | 102 | 94 | 104 | 95 | 99 | 92 |
| *Ancistrotermes* | 9 | 20 | 39 | 53 | 52 | 51 | 52 | 53 | 52 | 54 | 57 | 56 | 68 | 52 |
| *Macrotermes bellicosus* | 13 | 15 | 14 | 15 | 15 | 11 | 12 | 8 | 9 | 9 | 9 | 5 | 3 | 5 |
| *Odontotermes* | 2 | 5 | 8 | 8 | 7 | 5 | 9 | 9 | 9 | 2 | 3 | 1 | 2 | 3 |

TABLE 2.4.11 Spearman rank correlation test of species specific consumption of hardwood and softwood baits

PLOT 3

| SPECIES | CONSUMPTION OF HARD-WOOD g | RANK | CONSUMPTION OF SOFT-WOOD g | RANK | d | $d^2$ |
|---|---|---|---|---|---|---|
| *Microtermes* | 65.67 | 2 | 269.883 | 1 | +1 | 1 |
| *Ancistrotermes* | 108.322 | 1 | 86.277 | 3 | -2 | 4 |
| *Odontotermes* | 39.868 | 4 | 32.511 | 4 | 0 | 0 |
| *M. bellicosus* | 41.935 | 3 | 125.441 | 2 | +1 | 1 |
| *M. subhyalinus* | 0 | 5.5 | 2.778 | 5 | +.5 | .25 |
| *Microcerotermes* | 0 | 5.5 | 0 | 6 | -.5 | .25 |

PLOT 4

| | | | | | | |
|---|---|---|---|---|---|---|
| *Microtermes* | 138.036 | 1 | 166.313 | 3 | -2 | 4 |
| *Ancistrotermes* | 103.958 | 2 | 396.171 | 1 | +1 | 1 |
| *Odontotermes* | 27.283 | 3 | 181.575 | 2 | +1 | 1 |
| *M. bellicosus* | 19.782 | 4 | 20.294 | 5 | -1 | 1 |
| *M. subhyalinus* | 0 | 6 | 0 | 6 | 0 | 0 |
| *Microcerotermes* | 19.503 | 5 | 24.722 | 4 | +1 | 1 |

PLOTS 3 AND 4

| | | | | | | |
|---|---|---|---|---|---|---|
| *Microtermes* | 203.706 | 2 | 436.196 | 2 | 0 | 0 |
| *Ancistrotermes* | 212.280 | 1 | 482.448 | 1 | 0 | 0 |
| *Odontotermes* | 67.151 | 3 | 214.086 | 3 | 0 | 0 |
| *M. bellicosus* | 61.717 | 4 | 145.735 | 4 | 0 | 0 |
| *M. subhyalinus* | 0 | 6 | 2.778 | 6 | 0 | 0 |
| *Microcerotermes* | 19.503 | 5 | 24.722 | 5 | 0 | 0 |

PLOT 3 : $r_s = 0.8142$

PLOT 4 : $r_s = 0.7714$

PLOTS 3 & 4 : $r_s = 1.0000$

TABLE 2.4.12 Differences in consumption between checked and unchecked baits

| | UNCHECKED BAITS | | CHECKED BAITS | | % DROP IN CONSUMPTION BAIT$^{-1}$ | | |
|---|---|---|---|---|---|---|---|
| | PLOT ONE | PLOT TWO | PLOT ONE | PLOT TWO | PLOT ONE | PLOT TWO | MEAN |
| MEAN CONSUMPTION PER BAIT OFFERED g | 5.917 | 4.084 | 4.165 | 3.183 | 29.6 | 22.1 | 25.85 |

## 2.4.4 DISCUSSION

### 2.4.4.1 Consumption Estimates in Relation to Feeding Habits

Wood and leaf litter are not the only food sources used by termites and the consumption data recorded in Table 2.4.7 must be considered in relation to feeding habits. All the species feed on fresh, dead, plant material with the exception of *Amitermes evuncifer* which prefers rotten wood and is a relatively rare species.

Bark is regularly consumed by all the Macrotermitinae except *Microtermes*. During the dry season tree trunks and branches are covered with soil sheets under which the termites feed. Stem-flow prevents this in the rainy season. *Microtermes* did not forage in the dry season and took no bark. *Odontotermes* and *Ancistrotermes* were common bark feeders but, although no measurements were made, the amount removed appeared small in comparison to wood litter removed.

Rotting roots may be important for *Amitermes*, and *Microcerotermes* undoubtedly takes considerable quantities. *Microtermes* may take small roots, particularly in the dry season.

The estimated consumption for *Microtermes* (300.483 kg $ha^{-1}$ $a^{-1}$) may thus be a close approximation, since only small roots are omitted. *Ancistrotermes* and *Odontotermes* lack bark consumption data so their estimates (157.117 kg $ha^{-1}$ $a^{-1}$ and 125.773 kg $ha^{-1}$ $a^{-1}$) are probably slightly low. *Macrotermes bellicosus* also takes bark but the result (240.518 kg $ha^{-1}$ $a^{-1}$) is checked elsewhere. The biomass of *M. bellicosus* on the study area has been estimated as 4.720 kg $ha^{-1}$ and the consumption (expressed in mg (dry wt) of food eaten per g (wet wt) of termites per day) can be calculated as 139.608 mg $g^{-1}$ $day^{-1}$. In Section 3.2.3.7, calculations based on food store standing crop and turnover rate (1 week) give an estimated consumption of

139.297 mg $g^{-1}$ $day^{-1}$. In Section 3.3, estimations of consumption by isolated colonies give a mean maximum consumption of 126.032 mg $g^{-1}$ $day^{-1}$. These estimates are further discussed in Section 4,

The results for *Macrotermes subhyalinus* and *Trinervitermes* are of no value as total consumption estimates since both species consume large quantities of grass.

*Microcerotermes* and *Amitermes* feed extensively underground and these estimates are also only a portion of their annual consumption.

### 2.4.4.2 Seasonality of Foraging

Figures 2.4.2 and 2.4.3 give monthly results for consumption and bait discovery (sums of all plots) for all species together and for six major species separately. Correlations between bait discovery and consumption were highly significant for *Microtermes* and *Ancistrotermes* but not significant for the other termites considered. Whereas *Microtermes* and *Ancistrotermes* tend to enter a log from beneath and hollow it out, *Odontotermes* and *Macrotermes* normally cover the food item with mud sheeting and consume it from the outside. Hence activity of these latter species is more susceptible to disruption by heavy rain storms. This accounts for their low level of persistence on baits in the rainy season and the lack of positive correlation between bait discovery and consumption, (Table 2.4.13).

Foraging of *Microtermes* is highly seasonal with a very low level of activity in the dry season and peak activity in May at the beginning of the rains (for 1975 rainfall see Table 1.1.1). This is in agreement with Sands (1972a). As Bodot (1967b) agrees, *Ancistrotermes* is similar but with more dry season activity. Foraging by *Macrotermes bellicosus* and *Odontotermes* is far less seasonal. Foraging occurs all year round with a suggestion of slightly greater activity in May-

July and November. Bodot (*loc. cit*) records similar results for *M. bellicosus* in the Ivory Coast. The data for *Macrotermes sybhyalinus* are scanty but the suggestion of all-year foraging with a peak in the dry season was confirmed by general observation. *Microcerotermes* (Termitinae) is exceptional in having a distinct foraging peak in the dry season despite a downward migration of the soil population at this time (Wood *et al*. unpubl. data).

Bouillon (1970) suggested that seasonality in foraging is more evident in the higher latitudes with greater climatic variability. Bodot (1967b) found that foraging in *Ancistrotermes cavithorax* was significantly correlated with rainfall but that foraging in *Macrotermes bellicosus* was not. She concluded that foraging is probably affected by an interplay of the internal nest environment and the external climatic factors.

My own data suggest that two indistinct types of foraging pattern occur in the Macrotermitinae. In one group (*Microtermes*, *Ancistrotermes*) foraging is at a very low level throughout the dry season while in the other group (*Macrotermes*, *Odontotermes*) foraging, although showing some seasonality, occurs at a more constant level all year round. The reasons for this difference can only be surmised but the former pair has smaller individuals than the latter and may be more susceptible to dehydration.

There are also differences in nest size, compactness and complexity between the two groups. *Microtermes* and *Ancistrotermes* are polycalic and have a diffuse system of subterranean fungus combs 5-10 cm across linked by runways in the soil. *Odontotermes smeathmani* and *O. pauperans* on the other hand construct a sizeable subterranean comb of about 30 cm diameter while *Macrotermes bellicosus* and *M.*

*subhyalinus* have complex nests with a single agglomeration of fungus combs, (up to 3 m across in *M. bellicosus*). The nest of *M. bellicosus* is further discussed in Section 3.1 but it can be said that the massive mound offers considerable resistance to the extremes of the external climate and the high respiratory rate of the fungus combs helps to maintain the nest temperature and humidity at optimal levels. Becker (1969) has shown that at least in *Heterotermes indicola*, (Rhinotermitidae), the humidity of wood strongly affects its palatability. The position of the food stores in *M. bellicosus* nests (on top of the fungus combs) is ideal for humidifying the food to a suitable level. Hence, this species collects very dry forage in part of the dry season but may be able to make it more palatable, prior to consumption, by the absorption of metabolic water from the faeces. However, even *M. bellicosus* has a low foraging level in March and there are suggestions (Section 3.4) that feeding on the fungus combs may in some cases be important at this time. *Microtermes* appears to survive the whole dry period by this method and fungus comb chambers are normally empty towards the end of that season (R.A. Johnson, pers. comm.).

At Mokwa, therefore, although low rainfall appears to limit foraging to some extent in most species of Macrotermitinae, those with advanced nests are well protected from the external environment and are able to feed at a more constant level. Some dependance on the fungus combs as a reserve food source may be of importance in all Macrotermitinae but they are more heavily utilised by species with polycalic nests. *Macrotermes subhyalinus*, with large individuals and a complex, compact nest system is exceptionally resilient and has a peak of foraging activity in the dry season when plenty of grass litter, (the main food source for this species), is available.

Similarly, Microcerotermes (Termitinae) forages on wood litter mainly in the dry season but, as previously stated, the genus feeds extensively on roots. Although it is able to consume surface litter at a higher level in the dry season when Microtermes and Ancistrotermes are largely absent, this may not be a true indication of its absolute feeding levels.

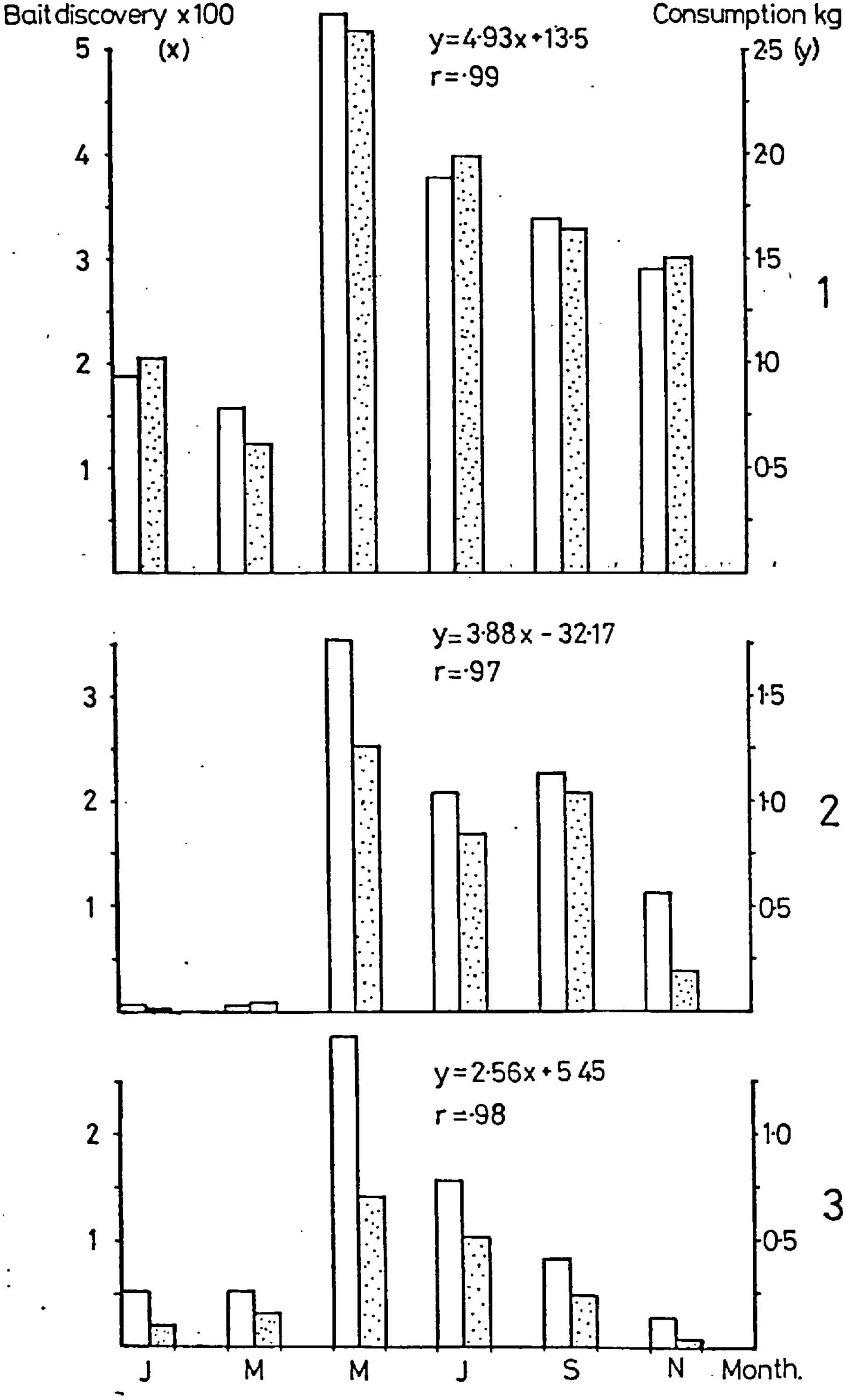


FIGURE 2.4.2 Monthly bait discovery and bait consumption data for 1) all termites 2) _Microtermes_ spp. 3) _Ancistrotermes cavithorax_.

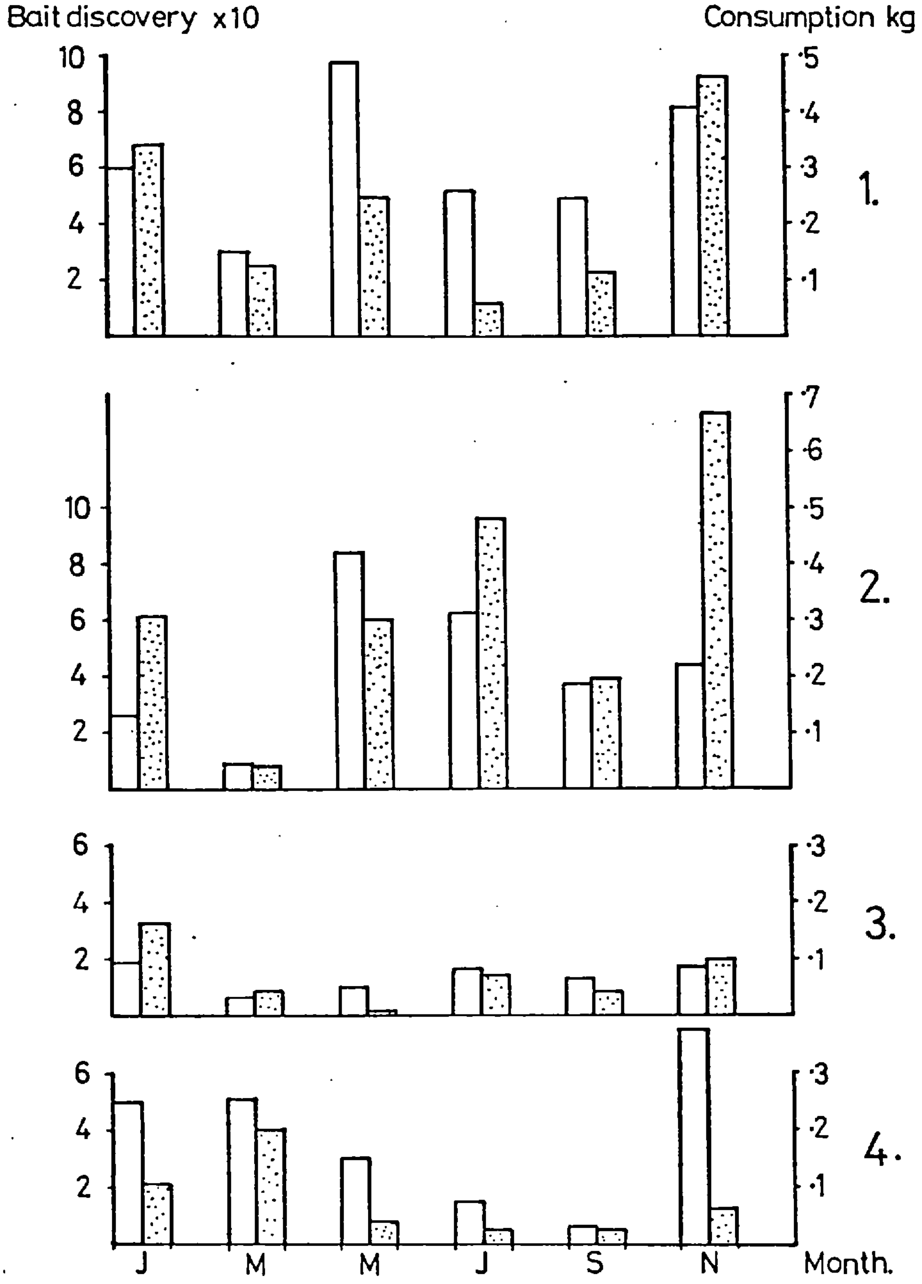


FIGURE 2.4.3 Monthly bait discovery and bait consumption data for 1) Odontotermes spp. 2) Macrotermes bellicosus 3) Macrotermes subhyalinus 4) Microcerotermes sp.

TABLE 2.4.13 The amount of wood consumed per bait discovered by each species during each month. Note that while *M. bellicosus* was less persistent on baits in the rainy season, this species was consuming large quantities of leaf litter (Section 2.3.3.2).

| | J | M | M | J | S | N |
|---|---|---|---|---|---|---|
| *Microtermes* | 1.13 | 7.12 | 3.86 | 3.99 | 4.53 | 1.64 |
| *Ancistrotermes* | 1.92 | 3.06 | 2.41 | 3.22 | 2.83 | 1.13 |
| *Odontotermes* | 5.70 | 4.16 | 2.55 | 1.18 | 2.34 | 5.68 |
| *Macrotermes bellicosus* | 11.61 | 4.36 | 3.55 | 7.73 | 5.19 | 15.13 |
| *Macrotermes subhyalinus* | 8.84 | 6.62 | 0.28 | 4.30 | 3.12 | 5.69 |
| *Microcerotermes* | 2.04 | 3.94 | 1.30 | 1.55 | 3.92 | 0.80 |
| *Amitermes* | | | 22.6 | | 0.95 | |
| *Trinervitermes* | 0.30 | | | 0.10 | 1.40 | 1.98 |
| All species | 5.70 | 3.86 | 4.82 | 5.22 | 4.86 | 1.95 |

# SECTION 2.5

# DISCUSSION AND CONCLUSIONS

## 2.5.1 k-VALUES

Olson (1963) examined 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 W.Africa south of the Sahara Desert, increases with proximity to the equator (cf. Section 2.1.3.2). In tropical forests, Olson (loc. cit) calculated k-values ranging from 4.0 to 1.0, while in various parts of the U.S.A., values ranged from 0.25 to 0.0156. He calculated k-values in terms of total carbon, in some cases using values for carbon content from Jenny (1950). Carbon content has not been empirically determined here but is assumed to be related to the calorific equivalent by a constant factor. Hence, k-values of a comparable nature can be calculated from the calorific equivalents and in this study the ratio of litter production : accumulation (k) is equal to 0.958 (95.8% $a^{-1}$). Calorific values have been summarised in Table 2.4.4. The value excludes data on grass production but in general agrees with Olson's (loc. cit.) data, being higher than temperate values but lower than rain forest values.

## 2.5.2 MAJOR DETERMINANTS OF THE DECOMPOSITION CONSTANT (k)

The factors which are known to affect decomposition rates are numerous, but before considering which are most important at Mokwa, it is necessary to briefly review present knowledge.

Climatic factors are undoubtedly important and may act in direct (e.g. leaching), or indirect ways (e.g. effects on litter fauna and flora). Although Madge (1965) found no relationship between k-values and rainfall or temperature for a few tropical data, Williams and Gray (1974) considered that temperature is a major controlling factor. Jenny et al. (1949) in the Americas, and Wood (1974) in Australia, both found that rainfall and temperature were major factors in decomposition rates. Van der Drift (1963) found that drought retarded litter decomposition and attributed this to reduced soil fauna. Rainfall is known to leach water-soluble matter from leaves even while they are still on the trees. Nye (1961) found that almost 30% of the annual addition of nutrients to the floor of a Ghanaian rain forest was contained in the rain-wash.

The biochemical constitution of the litter is also of considerable importance and is receiving an increasing amount of attention (Janzen 1975). Broadfoot and Pierre (1939) found that decomposition was faster in temperate leaves of high base content than of low. The carbon : nitrogen ratio of litter affects decomposition via the fauna and flora, which use the carbon as an energy source and assimilate nitrogen into cell proteins and other compounds. A high nitrogen content thus facilitates growth of decomposer organisms and rapid turnover of substrates. Tropical forest litter in Ghana has been found to have a higher nitrogen content than that of temperate forests (Nye 1961), but more data are required from other forests. Jenny (1950) stressed the importance of nitrogen fixation, especially in leguminous trees, (a prominent group in rain forest and at Mokwa, Section 1.3), in his consideration of the high nitrogen content of some S.American soils. Effects of nitrogen content on decomposition are most marked in the early stages and Williams and Gray (1974) suggest that in the later stages nitrogen may be less easily available, possibly being contained in complex nitrogenous organic compounds or associated with protective polyphenols such as tannins.

Polyphenols are complex polymeric phenolic compounds, such as lignins and tannins, which appear to be relatively inert as far as plant degradative processes are concerned (Walker 1975). Lignins are basic components of cell walls and the structural parts of plants, but the role of tannins is poorly understood. Polyphenols may be present in plants at 5-15% (d.w.) and there is increasing evidence of their importance in controlling decomposition rates, (Williams and Gray 1974, Janzen 1975). Coulson <u>et al</u>. (1960) found that more polyphenols were produced in the leaves of a plant grown on nutrient-poor mor than in the leaves of the same plant grown on nutrient-rich mull. This indicated a relationship between soil, leaf composition and litter decomposition since, in general, litter breakdown is slow on mor soils. There are however, a number of soil micro-organisms which are capable of breaking down polyphenols in plant litter. Lignin, for example, is broken down into coniferyl alcohol, ferulic acid and other products, which are subsequently oxidised via the catechol pathways described by Walker (1974). He also notes that initial microbial attack on wood and lignin is thought to be due to fungi which are divided into two groups: the white-rots and the brown-rots. The white-rots are able to utilise both lignin and cellulose as a carbon source while the brown-rots preferentially attack only the cellulose components.

Burges (1967) has described a generalised decomposition pathway based mainly on temperate region data. Some microflora develop even before the litter falls. After fall, saprophytic micro-organisms colonise the litter and, following a period of initial breakdown, invertebrates comminute and ingest the litter and incorporate it into the soil. Microbes colonise faeces and litter, resulting in further degradation, release of humic acids and formation of humus.

The initial colonisation by micro-organisms on the fallen litter appears to be a very important process which, until it reaches a certain stage, largely precludes the activities of invertebrates. Fittkau and Klinge (1973) consider that a similar process occurs in Amazonian rain forest. They contend that the action of fungi, in concentrating limited food resources, permits a high proportion of soil fauna and hence a consumer food chain based almost entirely on dead organic matter.

### 2.5.3 TERMITES AND DECOMPOSITION PROCESSES IN SOUTHERN GUINEA SAVANNA

How does this scheme compare with the results which have been described from S.Guinea savanna at Mokwa? The data for Mokwa have been given in terms of biomass and energetic equivalents in Figure 2.5.1. About 24% of the annual wood and leaf litter production was consumed by termites, partitioned into 60% of wood fall and 3% of leaf fall. Conversely, estimates of removal by fire show that 49% of annual leaf fall was burnt and only 0.9% of wood fall. Hence, of the litter fall available for biotic decomposition (i.e. excluding burnt litter), termites removed about 34.5%. It has also been seen that 95.2% of the total consumption of litter by termites is attributable to members of the subfamily Macrotermitinae, which feed predominantly on relatively fresh, undecayed litter (Table 2.4.7). Hence, in the savannas, litter removal by the Macrotermitinae largely replaces the typical temperate decomposition pathways, (fungal rot followed by invertebrate and microbial degradation), and results in a rapid turnover of plant litter.

The symbiosis of Macrotermitinae with basidiomycete fungi of the genus Termitomyces, is perhaps the factor that permits them to feed predominantly on fresh wood. Termitomyces appear to be white-rots, (M.J. Swift pers. comm.), capable of digesting polyphenolic compounds such as lignin, and releasing the nutrients required for growth of the termites.

It is of interest to speculate as to how the ability to feed on fresh litter may have affected the distribution of Macrotermitinae. Using data from various sources, including my collection from the Cameroon rain-forest (Collins, submitted), Wood (1976) has pointed out the general trend of decreasing number of fresh litter feeders (mainly Macrotermitinae) and increasing number of rotten wood and soil feeders, with proximity to the equator. In the savanna regions, with a long dry spell, the action of fungi as litter decomposers, is undoubtedly curtailed. The Macrotermitinae, perhaps by virtue of their fungus gardens, appear to have become to some extent independent of this bottle-neck. Hence it may be suggested that in the more equatorial regions where rainfall is higher and less seasonal, fungal decay plays a greater part, wood rots and is humified more quickly, and the rotten wood and soil feeders are able to become more prevalent.

This simple picture is complicated by the occurrence of high populations of soil feeders in isolated pockets of soils of high organic matter content, scattered over the savannas. Examples may be found along the alluvial flood plains of the River Niger. The typical red and yellow soils of the savannas ("lateritic" soils) are very low in clays of the montmorillonite and illite types, which are known to maintain high humus levels by chemical and physical interactions (Allison 1973). Leprun and Roy-Noël (1976) have found that, on Cape

Verde, M. bellicosus is confined to ferruginous soils and ferrollitic ironstones with kaolinite clays, but no montmorillonites. It may therefore be tentatively concluded that, in general, the Macrotermitinae are predominant in the savannas where fungal activity is restricted by rainfall and seasonality and "lateritic" soils are prevalent, but that in comparatively rare savanna soils with high content of montmorillonite and illite clays, organic matter content of the soil may build up, resulting in ingress of more soil-feeding species.

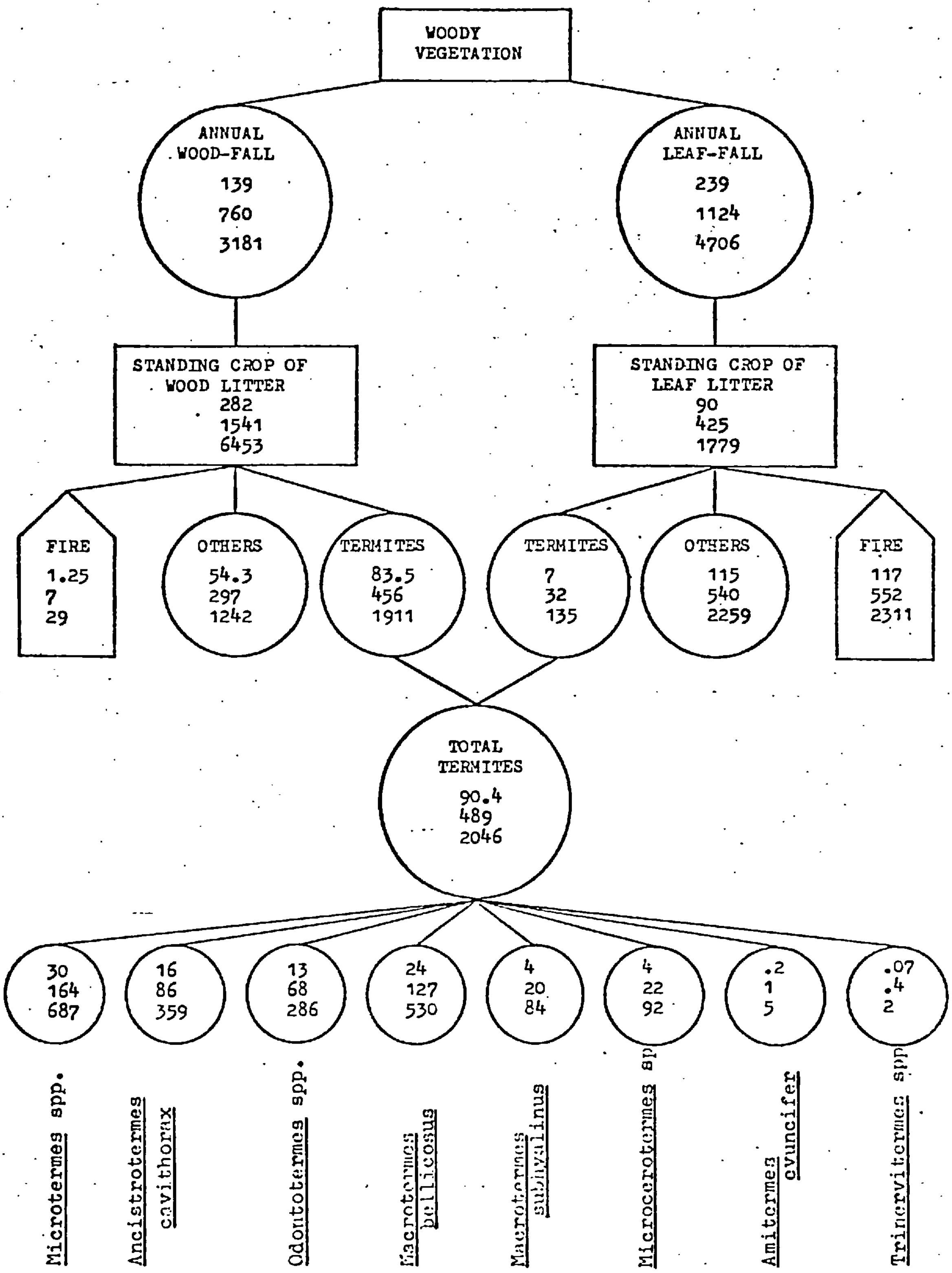


FIGURE 2.5.1 Flow diagram summarising data from Section Two. In each compartment the upper figure is the biomass (g $m^{-2}$, d.w.), the centre figure is the calorific equivalent (kcal $m^{-2}$), and the lower figure is the joule equivalent (kj $m^{-2}$). The text should be consulted for more precise values. Estimates of standing crops are in boxes, flux values in circles (flux $a^{-1}$), and energy losses to fire in cones (loss $a^{-1}$).

# SECTION THREE

## THE NEST STRUCTURE, POPULATIONS AND ENERGETICS OF MACROTERMES BELLICOSUS

The quantitative role of the Macrotermitinae as decomposers of plant litter has been examined and it has been suggested that their associations with fungi of the genus *Termitomyces* may be the feature that allows them to feed predominantly on fresh litter.

In Section Three, the energetics of one species of the Macrotermitinae, *Macrotermes bellicosus*, is studied in detail and the function and effects of the symbiosis examined more closely.

## SECTION 3.1

## THE NEST OF MACROTERMES BELLICOSUS

### 3.1.1 INTRODUCTION

The nests of most termites are completely enclosed except during periods of building, foraging and flights of alates (Noirot 1970), thus giving protection from predators and extremes of climatic variability.

Many primitive termites from the Kalotermitidae, Termopsinae and Rhinotermitidae maintain a simple nest within the food source, often a log or tree (e.g. Nutting 1965, 1966), building activity being limited to the erection of partitions and sealing of holes. Even so, *Copiotermes acinaciformis*, with unusually large colonies of up to two million individuals, can maintain a nest temperature 13-20°C higher than that of the tree in which it lives (Greaves 1964).

The majority of the more advanced Termitidae build concentrated nests with a definite architectural plan. These may be hypogeal, epigeal or arboreal and built by addition to, or reorganisation of, the environment of the royal pair, (Noirot 1970). Building materials vary between species and since excreta are often a basic component, the feeding habits may be reflected in the nest materials (Harris 1961). Excreta may be the main component as in *Cephalotermes rectangularis*, where carton is the principal material; a secondary component, as in *Psammotermes* nests which are built of sand bound with faeces; or not used in the mound fabric at all, as in the Macrotermitinae.

Grassé (1949) divided the termite nest and peripheral structures into four regions and although some homologies between species are unclear and the system may be over-simplified, it is useful in describing most nest types.

1) The endoecie: the central nest area where the royal pair live and the brood is raised. It may contain food stores (e.g. *Macrotermes*, *Trinervitermes*, *Hodotermes*) and fungus combs (Macrotermitinae). There may be a distinct innermost region round the royal pair known as the nursery, habitacle or hive.

2) The periecie: the system of galleries communicating with food sources; it may be extended into a protective wall around the endoecie to form a mound (epigeal species) or a thin shell (hypogeal species).

3) The exoecie: a system of cavities external to the paraecie and endoecie. They generally take the form of chimneys (e.g. Weir 1973) and although they are normally closed at the nest end, they have been found opening directly into nest chambers (Coaton 1947) and may be opened in response to the nest environment (Howse 1970).

4) The paraecie: an open space found between many subterranean nests and the soil (e.g. *Apicotermes* spp. Bouillon 1970). In epigeal nests there may be a space between the mound wall and the habitacle, regarded by Noirot (1970) as homologous to the paraecie, (e.g. *Macrotermes bellicosus*, Grassé and Noirot 1961; *Macrotermes gilvus*, Kalshoven 1956).

The nests and associated structures built by termites have been reviewed at length by Emerson (1938), Grassé (1949), Bouillon and Mathot (1965) and Noirot (1970), while Lee and Wood (1971) report further studies on nest micro-structure. With the exception of *Sphaerotermes* (Grassé and Noirot 1948), the Macrotermitinae build two types of nest (Noirot 1970). In one group of genera the endoecie is excavated within the soil (e.g. *Microtermes*, *Ancistrotermes*), or within soil dumps (some *Odontotermes*, Grassé and Noirot 1950), and the fungus comb chambers may be scattered (*Microtermes*), or clumped (some *Odontotermes*). An exoecie may be present as in *Protermes minutus* (Grassé 1944-1945) and several species of *Odontotermes* (Coaton 1947, Fuller 1915, Grassé and Noirot 1950, Escherich 1911).

In the second group, the *Acanthotermes* - *Macrotermes* line (see Krishna 1970), the nest is begun in a similar fashion, in an underground cavity excavated by the royal pair (Grassé and Noirot 1958), but increases in size by construction of a habitacle of various types. The royal cell is entirely constructed. Nest growth may be by enlargement or construction of new calies (*Acanthotermes acanthothorax*, Grassé and Noirot 1951). An exoecie may be present (e.g. *Macrotermes subhyalinus*, Weir 1973).

The nest structure of *Macrotermes bellicosus* has already been extensively studied by many authors (Smeathman 1781; Grasse 1944-1945; Kutter 1943; Grassé and Noirot 1951, 1955, 1958, 1961; Luscher 1955, 1956, 1961; Ruelle 1964, 1970; Noirot, Noirot-Timothée and Bodot in Noirot 1970) and Ruelle (1970) considers the nest architecture in this species to be the most elaborate of all the *Macrotermes*.

Harris (1956) notes that *M. subhyalinus* (as *M. bellicosus*) builds nests with many styles of architecture under different regimes of soil and climate, and Grassé and Noirot (1961) note similar variation for *M. bellicosus* (as *B. natalensis*). Harris (*loc. cit.*) considered this to be due to modification of behaviour patterns under the influence of local conditions. I have examined the structure of over 30 nests of *M. bellicosus* from the Kulfo soils in the immediate vicinity of my study area. It was surprising to find that two types of nest occurred, both under the same conditions of soil, climate and drainage, with no clear pattern of distribution to distinguish them. Substantial collections have been made from both types of nest and, as yet, no distinct morphological characteristics to distinguish the termites have been found. Both are M. bellicosus as described by Ruelle (1970). A similar case has been reported by Matsumoto (1976) from Malaysian rainforest, where Dicuspiditermes nemorosus (Haviland) builds two types of nest.

### 3.1.2 MACROTERMES BELLICOSUS NESTS

#### 3.1.2.1 M. bellicosus Nest with a Spiral Base Plate.

This was by far the most common type of nest found in the Mokwa area; similar nests were prevalent as far east as Bida (9°4'N, 6°0'E) and south to Jebba (9°8'N, 4°51'E). Similar mounds also occur on lateritic soils at Yankari (9°53'N, 10°22'E), but their internal structure was not examined. The mound is of the "cathedral" type (see Frontispiece and Grassé and Noirot 1961, pl.I.), being conical with vertical flutings round the periphery, some of which separate from the main cone to produce secondary spires (Figure 3.1.1). Smaller, often solid, spires may originate from gound level around the base of the mound. The largest mounds are 6-7m high and 3-4m wide. The main spires are hollow with a large central cavity and occasional smaller galleries extending into the walls, most numerous in areas of building. Mound wall thickness varies with colony age - old colonies have thicker walls, and with position in the mound - spire summits are thinnest and may be shell-like and brittle during building. Building occurs at any time of year, depending on the requirements of the colony, but the most active time is at the end of the dry season in March/April, (cf. Bodot 1967a, Pomeroy 1976).

The position of the habitacle differs from that portrayed by Noirot (1970), Grassé and Noirot (1961) and Harris (1956) in being below the level of the soil. Most of the habitacle consists of a fragile network of earthen supports within which the fungus combs are contained. In larger colonies the combs are laid down in several fairly distinct layers. The habitacle has a vertical empty core, like the Ivory Coast nest of Grassé and Noirot (1961, pl.III). The space invariably lies immediately below the large central gallery of the main spire. Above the fungus combs are foodstores of moist chewed food in rounded masses, often pierced with small unlined galleries, and the home of many termitophiles, especially Dipterous larvae. The entire habitacle is surrounded by a thin mud sheet known as the idiothéque (Grassé and Noirot 1958), usually fairly complete in small colonies but becoming increasingly perforated and broken in older ones. Between the fungus combs and base-plate, lamellae of compact earth form layers of low wide galleries, interconnecting by narrow passages and generally full of larvae.

The queen cell is a hard, thick-walled, clay structure, elliptical in profile and ovoid in plan, lying immediately above the larval galleries or supported at a slightly higher level, and generally offset from the horizontal centre of the nest, (see also van Ryn 1973, Grassé 1937, Grassé and Noirot 1961 pl.V). The cell periphery is pierced by a series of passages, too small for the king or queen to get out. One cell examined contained two queens of equal size, a rare event probably resulting from an error in tandem formation.

The base-plate is probably unique among the constructions of social insects. It consists in plan view of a perfectly circular plate, up to 3.5m across, made of solid clay-rich earth and supported centrally by a pillar approximately a quarter of the width of the plate. The plate rests on top of the pillar but is not physically bonded to it.

Very small cones protruding from the underside of the plate fit into cavities on the surface of the pillar. The cones, although very reduced in size, are probably analogous to the supporting cones described by Grassé and Noirot (1961) and seen in the second type of nest at Mokwa (Section 3.1.3). In the spiral base-plate nest the cones have no great supporting function, the plate lying flush on the pillar. The underside of the base-plate, from the edge of the pillar to the plate periphery, bears a number of clay vanes hanging downwards to a depth of up to 10cm in large mounds and encircling the plate in a series of spirals (Plate 6,7 ). The spiral occasionally stops and a new one begins, but 3-4 complete spirals are common. The vane is stalactitic in cross-section, being perhaps 2.5cm thick at its attachment to the base-plate, 1mm thick and extremely fragile at the fine edge, which is irregularly wavy. The spirals are generally coated with a white layer of mineral salts, thicker in older mounds, absent in very young ones. The spiral base-plate type nest was first found in this area of Nigeria by Dr. P.E. Howse of Southampton University.

The central supporting pillar is a solid earth cylinder, longer than wide and containing a high clay fraction. It does not have a coating of mineral salts. Because of the structure of pillar and plate, the cellar in this type of nest is very large (Figure 3.3.1, Plate 5 ). At the sides of the pillar wide galleries (up to 20cm in large mounds) extend vertically downwards to a depth of 2-3m. Most of the building repairs are done by minor workers and in cases of extreme damage where the cellar has been exposed, columns of minor workers have been watched going down these galleries and returning with spherules of wet mud, presumably gathered from the moist sub-soil near the water-table. Between these galleries, (which are part of the periecie) domed solid earth pillars extend upwards from the floor of the cellar. These may have been left behind as the cellar was extended or may be built from unwanted soil brought up from the deep galleries.

The entire habitacle is surrounded by an air-space (the paraecie), traversed by fragile earth bridges leading to the main galleries of the mound spires and to slit-like openings in the underground walls which are the entrances to the system of foraging galleries, part of the periecie. The galleries may extend some considerable distance underground before surfacing. An isolated medium sized mound (1.5-2.5m high) was found to have a regular foraging circle of 15m radius, with further extensions at some points.

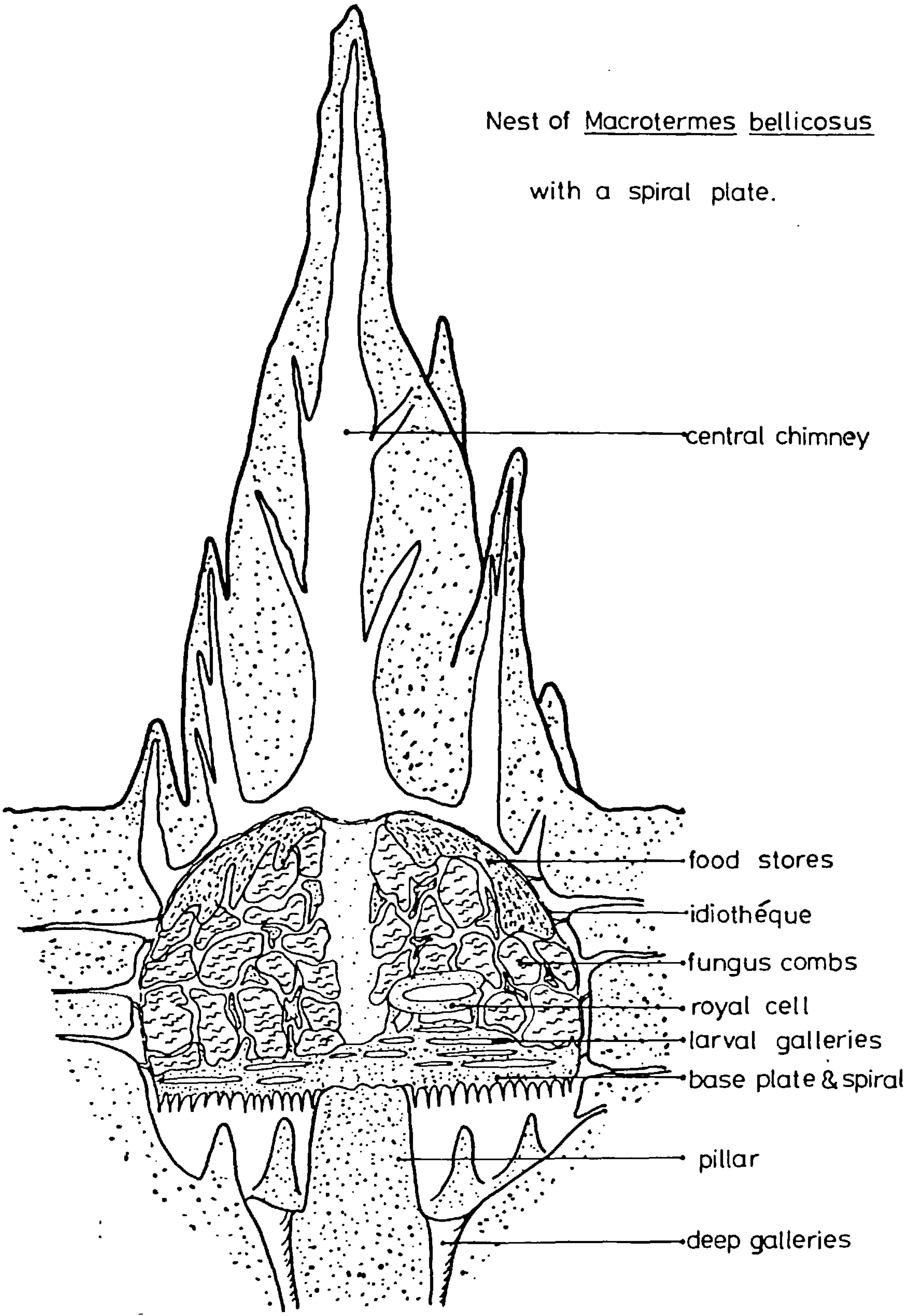


FIGURE 3.1.1 Vertical section of the nest of *Macrotermes bellicosus* with a spiral plate.

### 3.1.2.2 Macrotermes bellicosus Nest without a Spiral Base Plate.

The structure of this nest is essentially the same as that from the Ivory Coast described by Noirot (1970) and Grassé and Noirot (1961 pl.III, as B. natalensis) except that here again, the habitacle is normally below ground level (Plate 3 ). The mounds and colonies are smaller than in the spiral plate type. The mound is more rounded, with less distinct flutings and no "spires", (Figure 3.3.2). The central mound gallery is less distinct and the walls more reticulated with smaller galleries. The endoecie consists similarly of fungus combs, food stores, larval galleries, royal cell and idiothéque, all resting on a base-plate. A central chimney runs through the combs. There is no sign of a spiral on the plate or of a pillar. The plate is supported on cone-like pillars, up to 10-15cm long, which extend from the underside of the plate and rest with the points on the floor of the cellar. The cave is not extensive, the widest found being little more than 1m across. Since less soil is removed from below the habitacle in this type of nest, it is perhaps not surprising that the mound is relatively small. The habitacle is surrounded by an air space (the paraecie), as in the spiral plate nest, with earth bridges leading to the chimneys and foraging galleries.

In some regions of Africa the mound walls have large openings which connect with the cellar (Uganda : Lüscher 1955, 1956, Harris 1956; Zaire : Grassé and Noirot 1958, Ruelle 1962, 1964). I have also seen such holes in non-plate nests on sandy alluvial soils on the Niger flood-plainat Raba, Nigeria. They are caused by rain erosion and are generally sealed off at the earliest opportunity (Noirot 1970). While the holes are present, the cellar is sealed off and becomes an exoecie (Grassé and Noirot 1958). No such holes were found in mounds on the Kulfo soils.

These limited observations were all that could be fitted into the available time, and to understand the relationship between the two nest types fully would require much more intensive study. If built by the same species, the factors responsible for the difference could be environmental or physiological. The lack of any obvious environmental correlation suggests that perhaps some deficiency in the development of the population in a young colony might be responsible. A lower metabolic rate in an ailing colony might tip the balance towards the simpler structure, either through lowered heat production or fewer constructing castes capable of elaborate building. It remains to be seen whether biochemical or detailed morphological studies would indicate a specific separation of the two forms.

The ontogeny of the plateless nest of M. bellicosus has been described by Grassé and Noirot (1958). The spiral plate nest may follow the same basic pattern and no fundamental differences need be postulated. The development of the plate simply requires a more extreme lateral development associated with an extension of the cellar and loss of the supporting cones.

Nest of Macrotermes bellicosus without a spiral plate.

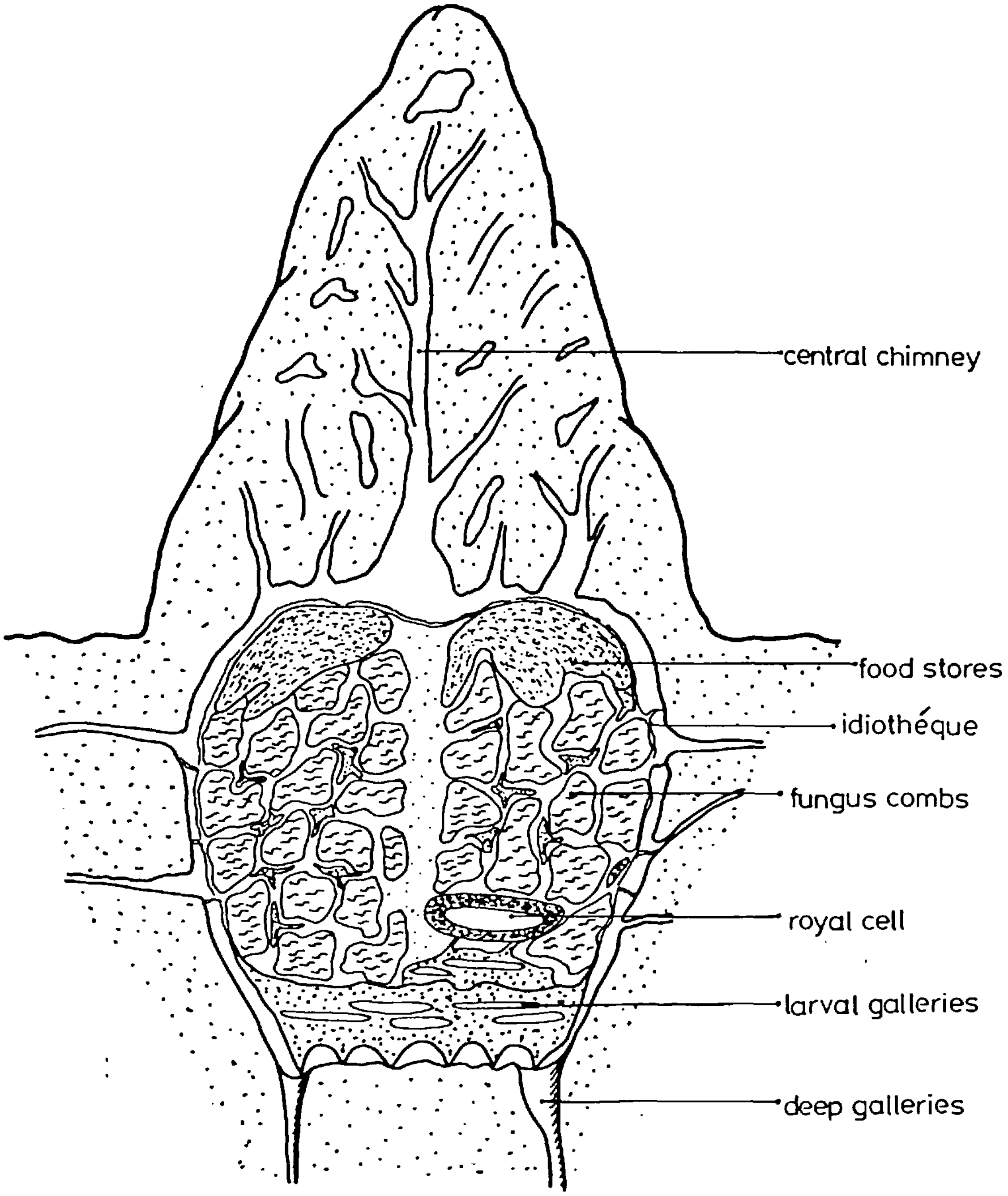


FIGURE 3.1.2 Vertical section of the nest of *Macrotermes bellicosus* without a spiral plate.

### 3.1.3 Nest structure and microclimatic stability.

In this section, only the more common spiral plate nests are considered. Noirot (1970) and Lee and Wood (1971) have reviewed the data on the microclimate of termite nests. In many cases, no more than a dampening of diurnal fluctuations is achieved, e.g. *Cubitermes fungifaber*, *Thoracotermes macrothorax*, *Procubitermes arboricola* (Noirot 1970, Collins submitted) but in others the nest temperature may be constantly higher than the environment, e.g. *Cephalotermes rectangularis*(Noirot 1970; Collins submitted;) *Nasutitermes exitiosus*,(Day 1938; Holdaway and Gay 1948;) *Coptotermes* spp.(Greaves 1964).

*M. bellicosus* nests have been closely scrutinised (Lüscher 1955, 1956, 1961; Grassé and Noirot 1958; Harris 1956) and Ruelle (1962, 1964) in particular has demonstrated the constancy of temperature within the habitacle at around 30°C. The source of heat is at least in part the termites themselves. Holdaway and Gay (1948) demonstrated a marked drop in temperature following application of arsenic to a nest of *Nasutitermes exitiosus* and Greaves (1964) associated the highest temperatures in *Coptotermes frenchi* and *C. lacteus* colonies with the presence of alates. Lüscher (1951) considered the fungus combs to be of prime importance in heat production in nests of the Macrotermitinae but this was contested by Noirot (1970) who quoted Geyer's (1951) findings of little difference between the temperature in fungus comb chambers of *Odontotermes badius* and soil at the same depth. My own work on the respiratory rate of termites and fungus combs (Section 3.4) shows quite clearly that the heat output from the fungus gardens of a colony of *M. bellicosus* of any given size is generally far in excess of that from the termites.

Lüscher (1955, 1956, 1961) also described two types of nest of M. bellicosus (Ivory Coast and Uganda types) whose galleries allowed circulation of the atmosphere by convection currents. Grassé and Noirot (1958) criticised his conclusions on points of nest structure and temperatures. Ruelle (1962, 1964) studied the nest structure and found that the interconnecting passages favoured air flow. Loos (1964) used microanemometers to confirm the existence of convection currents but found them to be variable in character, depending on wind speed and direction outside the mound.

I have done temperature studies of five M. bellicosus nests of the spiral plate type. All measurements were taken using a 24-probe Grant thermistor temperature recorder set to record automatically every hour. Probes were protected by passing the leads through 1cm diameter aluminium tubes of various lengths, supporting the probe itself in a rubber bung in the end of a V-shaped notch at the end of the tube (Figure 3.1.3). All probes were left in place for two days prior to recording in order to give the termites time to effect repairs following insertion of the probes.

Table 3.1.1 shows results of central nest temperatures in five nests. The average mean temperature was 30.96°C with a range of means from 30.67°C to 31.22°C. Unless this is purely fortuitous, then the fact that such close means were found in nests of all sizes demonstrates very clearly that the termites actively regulate the nest temperature by some method. Results of a more detailed examination of nests 3 and 4 are shown in Figures 3.1.4 and 3.1.5. Probes positioned at various distances up the mound reveal a gradient of temperatures that decrease and fluctuate more widely with distance from the fungus combs. Undoubtedly, therefore, there would be a general movement of heat from nest to air via the mound wall. To postulate constant air currents or heat flow would, however, be erroneous, since during the hottest part of some days the air is hotter than the habitacle. Convection currents may be fairly constant during cooler hours and particularly at night. The position of the chimney through the combs strongly suggests that this may function as a vent for hot air, channeling it up from the fungus combs into the mound.

The habitacle is below ground level and heat may also be lost to the soil. Figure 3.1.6 shows the results from a series of probes placed in the soil at various distances from the habitacle of nest 2. A temperature gradient exists and may be of a more constant nature than that up the mound. Gas exchange via the foraging galleries may also be important.

The function of the spiral plate is suggested by the mineral salts on its underside. These look like deposits resulting from continuous evaporation, which would produce a cooling effect on the much-increased surface area of the underside of the habitacle. The spiral plate nests grow larger than those without the spiral plate and I consider that the plate allows the densely populated habitacle to enlarge without overheating or other deleterious micro-environmental affects. The extended cellar may assist efficient circulation of air.

One curious fact regarding mound development and microclimatic relationships remains. Despite a positive linear correlation between mound width and height (Table 3.1.2, $r = 0.935$, $p = < .001$), measurements of the internal basal diameter of the main central gallery of six mounds showed that the width of the main chimney increases with mound size up to a mound height of about 3.5m, but decreases in mounds larger than this (Table 3.1.3). It has also been found that in older colonies, the central area of the fungus combs consists of old combs with a low respiratory rate (Section 3.4 and 3.5). The suggestion is that although the habitacle increases in size to accommodate the expanding comb system, heat production may not be increasing at the same rate. The soil must be removed from habitacle to mound (no soil "dumps" have ever been found) and in order to maintain microclimatic stability, it must be carefully deployed. I would suggest that as well as generally enlarging the mound, the termites narrow the main gallery, thus partially counter-balancing the greater heat-dispersing properties of the growing mound and the reduced heat output of the accumulation of old combs.

To conclude, there is evidence that as a result of highly sensitive building behaviour, M. bellicosus colonies are able to build nests of various sizes, all of which maintain a fairly constant mean temperature of 30-31°C in the nest centre. Why this temperature is optimal is uncertain. Mukerji (1970) has shown that larval development rate is dependent upon temperature so this could be an important aspect. Dr. M.J. Swift (pers. comm.) has recently shown that cultures of the fungus Termitomyces sp., from the nests of M. bellicosus, grow fastest between 28° and 30°C. These are unusually high temperatures for optimal growth of a fungus, suggesting a degree of co-adaptation between fungus and termites. It will be seen later that the fungi are of great importance to the nutrition of the termites as well as being the main source of heat in the nest, and it appears likely that the fungus-termite association has had considerable influence on nest-building behaviour and the evolution of the complex structures found in this species.

It should be noted that in the remainder of this thesis, any reference to M. bellicosus mounds or colonies refers to the spiral plate type nest unless otherwise stated.

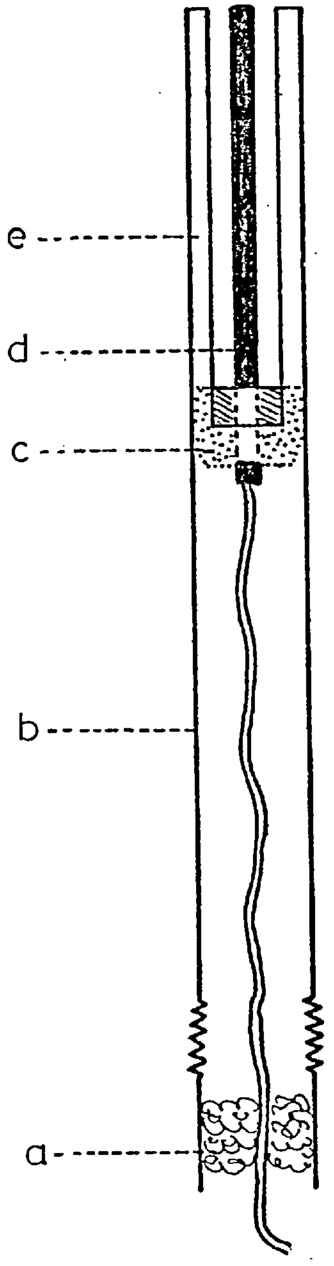


FIGURE 3.1.3 Diagram of the design of protected thermistor probes used in temperature studies of nests of <u>Macrotermes bellicosus</u>.

Key: a = cotton wool plug, b = aluminium tube, c = rubber bung, d = thermistor probe, e = protective wings.

TABLE 3.1.1 Mean and ranges of temperatures in the habitacle of five different-sized *Macrotermes bellicosus* mounds.

| MOUND NUMBER | DATES OF STUDY | NUMBER OF DAYS | MOUND HEIGHT m | MEAN TEMPERATURE IN HABITACLE °C | RANGE OF TEMPERATURES °C |
|---|---|---|---|---|---|
| 1 | 13-15/3/76 | 3 | 3.8 | 31.22 | 27.7-33.7<br>(7°) |
| 2 | 12-16/7/75 | 4 | 3.4 | 30.98 | 30-31.8<br>(1.8°) |
| 3 | 3-9/7/76 | 6 | 2.6 | 30.87 | 30.2-31.3<br>(1.1°) |
| 4 | 18-23/6/74 | 6 | 1.6 | 30.67 | 29.8-31.7<br>(1.9°) |
| 5 | 24-31/5/74 | 7 | 1.1 | 31.05 | 28.8-32.1<br>(3.3°) |
|  |  |  |  | $\bar{x}$: 30.96 |  |

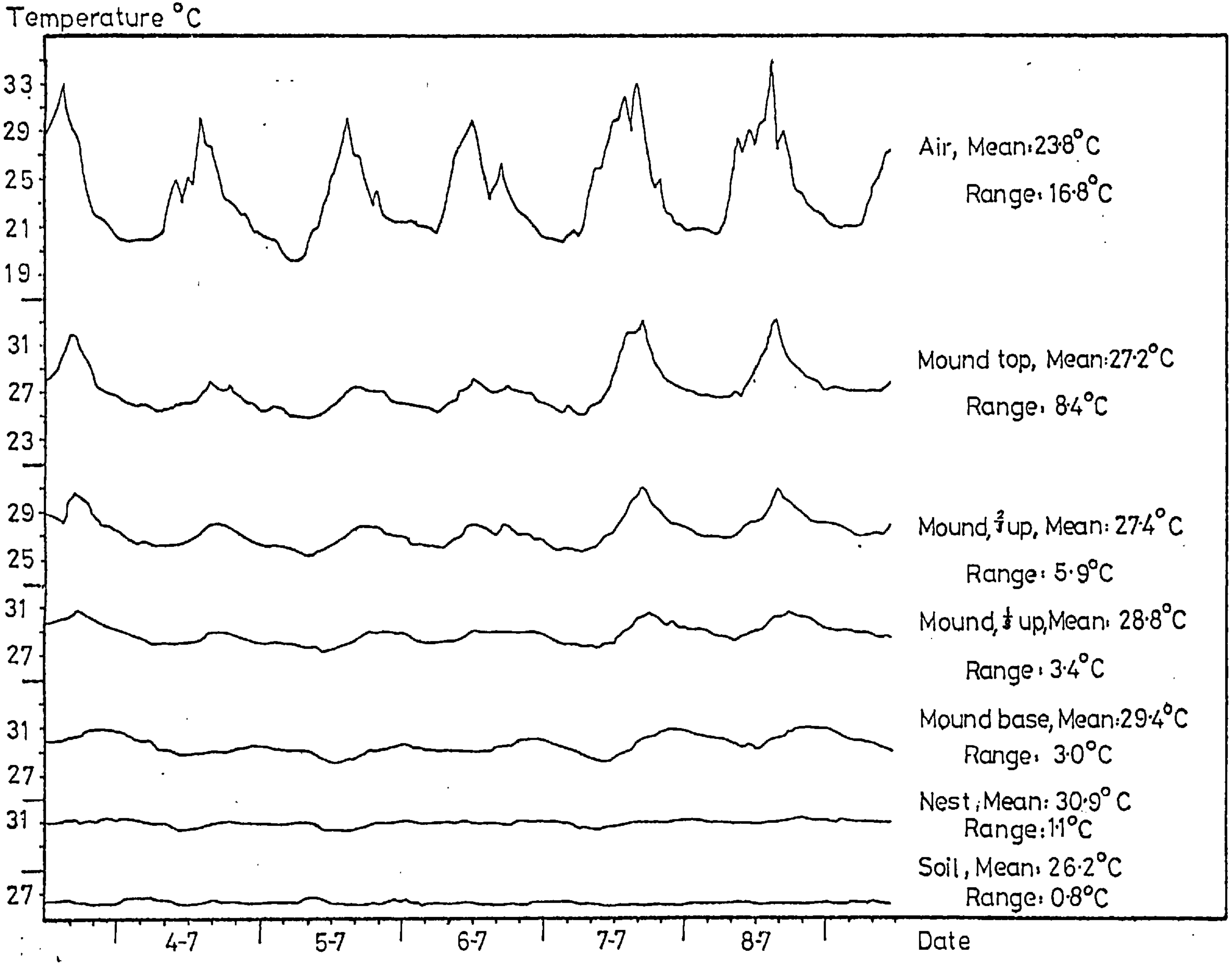


FIGURE 3.1.4 Results of a six-day study of temperatures in air, soil and various parts of a mound of *Macrotermes bellicosus* of 2.6 m height.

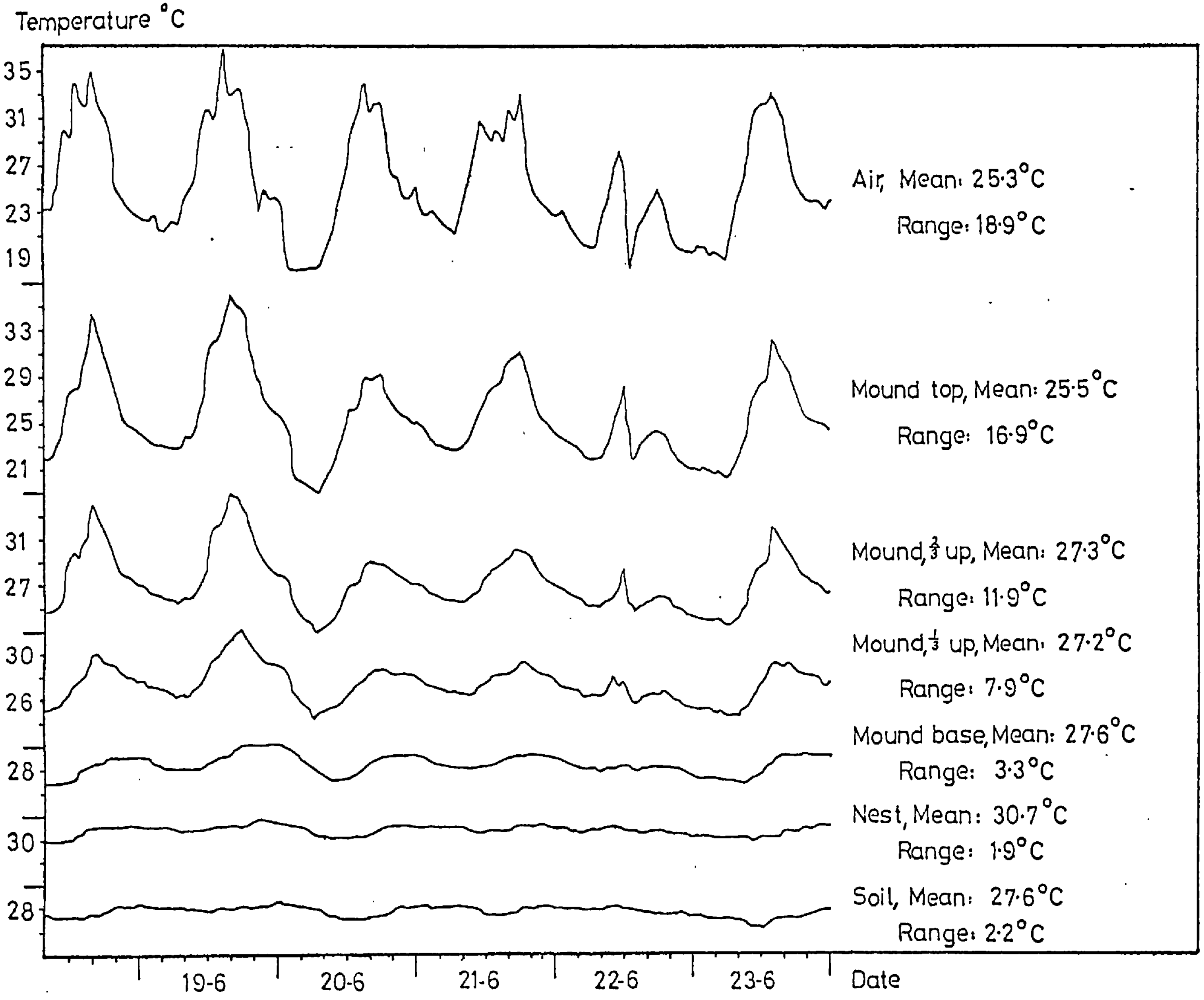


FIGURE 3.1.5 Results of a six-day study of temperatures in air, soil and various parts of a mound of *Macrotermes bellicosus* of 1.6 m height.

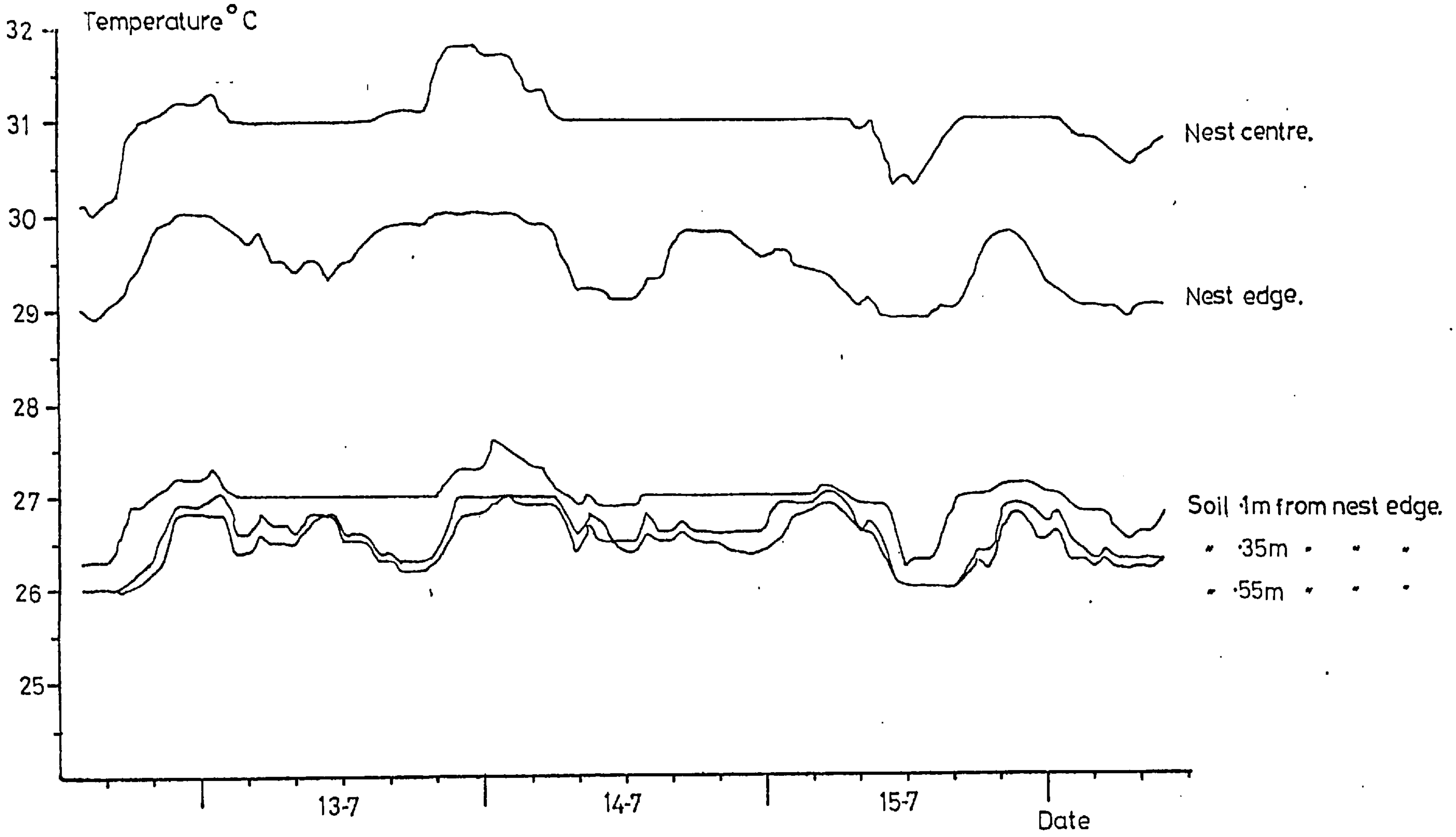


FIGURE 3.1.6 Results of a four-day study of the temperature profiles in the habitacle of a large (3.5 m) mound of *Macrotermes bellicosus* with results from probes in the soil at various distances from the edge of the mound.

TABLE 3.1.2 The heights and widths of 83 mounds of *Macrotermes bellicosus*. The two variables are linearly related by the equation:

Height = 1.7442. width - 0.5781, r = 0.9354, $p < 0.001$

There is some departure from this formula in mounds with height < 0.5m.

| NO. | HEIGHT m | WIDTH m | NO. | HEIGHT m | WIDTH m | NO. | HEIGHT m | WIDTH m |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.90 | 1.30 | 29 | 0.35 | 0.65 | 57 | 0.27 | 0.60 |
| 2 | 0.55 | 0.80 | 30 | 0.40 | 0.85 | 58 | 0.70 | 0.80 |
| 3 | 1.25 | 1.00 | 31 | 0.55 | 1.05 | 59 | 0.11 | 0.15 |
| 4 | 0.65 | 0.70 | 32 | 1.20 | 0.60 | 60 | 0.45 | 0.70 |
| 5 | 2.20 | 1.60 | 33 | 1.00 | 1.05 | 61 | 0.24 | 0.60 |
| 6 | 1.65 | 1.40 | 34 | 0.15 | 0.45 | 62 | 0.70 | 0.90 |
| 7 | 0.65 | 0.75 | 35 | 0.30 | 0.20 | 63 | 0.50 | 0.55 |
| 8 | 0.50 | 0.50 | 36 | 1.30 | 1.10 | 64 | 0.35 | 0.65 |
| 9 | 0.40 | 0.60 | 37 | 0.40 | 0.75 | 65 | 0.00 | 0.00 |
| 10 | 0.05 | 0.10 | 38 | 0.35 | 0.60 | 66 | 0.15 | 0.20 |
| 11 | 0.20 | 0.30 | 39 | 0.40 | 0.35 | 67 | 0.36 | 0.38 |
| 12 | 0.50 | 0.40 | 40 | 0.35 | 1.00 | 68 | 0.49 | 0.52 |
| 13 | 0.40 | 0.55 | 41 | 0.40 | 1.10 | 69 | 0.60 | 0.60 |
| 14 | 0.50 | 0.90 | 42 | 0.85 | 1.22 | 70 | 0.70 | 0.80 |
| 15 | 0.20 | 0.60 | 43 | 0.45 | 0.50 | 71 | 0.90 | 0.76 |
| 16 | 0.30 | 0.60 | 44 | 1.80 | 1.00 | 72 | 0.95 | 0.90 |
| 17 | 0.20 | 0.55 | 45 | 0.42 | 0.50 | 73 | 1.30 | 1.00 |
| 18 | 0.80 | 0.80 | 46 | 0.35 | 0.60 | 74 | 1.45 | 1.15 |
| 19 | 0.25 | 0.40 | 47 | 0.27 | 0.58 | 75 | 1.50 | 1.20 |
| 20 | 0.85 | 1.00 | 48 | 0.27 | 0.50 | 76 | 1.85 | 1.26 |
| 21 | 2.05 | 1.35 | 49 | 0.33 | 0.50 | 77 | 2.58 | 1.68 |
| 22 | 0.35 | 0.70 | 50 | 0.95 | 0.63 | 78 | 2.67 | 1.56 |
| 23 | 2.01 | 1.60 | 51 | 0.24 | 0.70 | 79 | 3.00 | 1.66 |
| 24 | 0.20 | 0.50 | 52 | 0.09 | 0.18 | 80 | 3.50 | 1.80 |
| 25 | 0.50 | 0.85 | 53 | 0.15 | 0.55 | 81 | 3.55 | 2.34 |
| 26 | 0.25 | 0.40 | 54 | 0.65 | 1.00 | 82 | 4.40 | 3.00 |
| 27 | 0.90 | 0.70 | 55 | 0.27 | 0.60 | 83 | 5.79 | 2.86 |
| 28 | 4.60 | 3.10 | 56 | 0.32 | 0.45 |  |  |  |

TABLE 3.1.3 The diameter of the main chimney of nine different-sized *Macrotermes bellicosus* mounds.

| MOUND NO. | HEIGHT | WIDTH | MAIN CHIMNEY BASAL WIDTH |
|---|---|---|---|
| 1 | 1.3m | - | .20m |
| 2 | 1.45 | 1.15m | .17 |
| 3 | 1.7 | 1.20 | .25 |
| 4 | 2.58 | 1.68 | .22 |
| 5 | 2.67 | 1.56 | .40 |
| 6 | 3.50 | 1.80 | .46 |
| 7 | 4.40 | 3.0 | .34 |
| 8 | 5.50 | 2.70 | .37 |
| 9 | 5.79 | 2.86 | .30 |

# SECTION 3.2

## POPULATIONS OF MACROTERMES BELLICOSUS

### 3.2.1 INTRODUCTION

The difficulties involved in quantitative sampling of termite populations have been discussed at length by Lee and Wood (1971) and Sands (1972). As with consumption studies (Section 2.4), population studies require a variety of techniques suited to the habits and habitats of the termites.

Methods of estimating populations of subterranean species include soil coring (Harris 1963, Salt 1952, Strickland 1944, 1945, Bodine and Ueckert 1975, Wood 1976) and digging of pits (Sands 1965a, Kemp 1955) or trenches (Hartwig 1966). Epigeal nesting species have been more intensively studied due to the relative ease with which nests can be collected and occupants counted (Sands 1972). Methods generally include estimation of mound density in sample quadrats or over the whole, or a large part of, the study area (Sands 1965b, Bouillon and Mathot 1964, Bodot 1967b, Maldague 1964, Wood and Lee 1971, Pomeroy 1976, Wiegert 1970, Matsumoto 1976). Such data, combined with a number of population counts from part colonies (Sands 1965b) or whole colonies (Matsumoto 1976, Maldague 1964, Bouillon and Mathot 1964, Wiegert 1970) have been used to estimate population density and biomass per unit area. Prediction of the total population from individual colony counts generally involves the use of a linear regression between some measure of mound size and mound population (e.g. Matsumoto 1976, Ohiagu 1976, Lepage 1972, 1974, Josens 1972a, Wiegert 1970). This procedure should be used cautiously in the light of Bodot's (1966) discovery that caste population of Cubitermes severus varies considerably with colony age and Kalshoven's (1930) findings that senile Neotermes tectonae colonies have very low populations in very large nests.

### 3.2.2 METHODS

The distribution of living M. bellicosus colonies on the study area was plotted in March 1974, February 1975 and February 1976 by taking co-ordinates from two corners of the map square in which each mound occurred. The height of each mound was recorded every year and the basal width in 1975 and 1976. In 1975 all the unoccupied mounds were also recorded. These were easily distinguished from the inhabited ones by their heavily eroded and perforated walls.

During the course of the two year study, a total of 19 spiral plate colonies were sacrificed for total population estimates. Nests of all sizes were chosen from within one mile of the study area. Height, mean of two widths, basal circumference and mean of two arcs at right angles over the top of the mound were recorded. In all cases a trench was dug to the side of the habitacle and the wall breached to allow access. At this stage major soldiers swarmed out of the mound and were collected by hand. In small colonies, the entire endoecie could then be removed by lifting the spiral plate from the pillar. This was wrapped in polythene sheet and transported to the laboratory for examination. In large colonies (plate 2-3m diameter) this procedure was not possible, the endoecie being too heavy. In these nests fungus combs and food stores were removed by hand and the base-plate broken into manageable pieces. In large nests, this procedure alone takes several days since the termites continually rebuild the nest. In general, the epigeal part of the nest was devoid of termites, but pockets of termites occurred in the habitacle walls and these were removed with a short-handled mattock and brush. Foragers returning to the nest were collected from the habitacle walls for several days following removal of the endoecie, until the number dwindled to insignificance. The methods were necessarily crude but the fact that the termites were never observed to leave the nest but always tried to rebuild it inside the habitacle was an advantage. It is considered that by constantly returning to the nest site to make further collections, a very high proportion of individuals were obtained.

Fungus combs often contained large numbers of termites, particularly larvae. These were either extracted by hand after air-drying the combs overnight, (fresh combs are moist and fragile), or by leaving the combs overnight in a specially constructed heat/light extraction apparatus similar to a Tüllgren funnel. This consisted of a supported wooden frame covered in chicken wire with two large funnels (30 x 30 cm) beneath. A box lid containing eight 40 watt bulbs provided heat and light which drove the termites out of the combs and into collecting trays beneath the funnels. Combs were quickly checked by hand following this treatment.

Termites were collected from the base-plate and nest debris using a Salt and Hollick (1944) soil washing apparatus with a series of sieves. The finer details of this method varied from nest to nest, depending largely on how cleanly the combs were removed by hand. Larger comb pieces were trapped in the sieves but smaller pieces passed through and floated off with the termites. After soaking the comb-termite mixture for a few hours in water the comb became saturated and remained in the settling can, but after a time the termites lost their hydrophobic properties too. As a last resort a benzene/water mixture was sometimes used to separate them in measuring cylinders. The coarser pieces of comb caught in the sieves invariably had to be hand-sorted for major soldiers. The termites were stored in 70% alcohol, allowed to settle for some time, the excess alcohol poured off and the volume of termites measured. For two small nests all the termites were counted and for one nest five 21.75 cc samples (7.5 x 2.5 cm specimen tube) were counted. The method finally chosen and used for the remainder of the nests was to count 10-20 samples of 4.8 - 5.0 cc (small specimen tube). Each caste was recorded separately and the total population estimated from the mean number of individuals per sample corrected for the total volume of termites.

Fungus combs were dried for 48 hours at 80-100$^{o}$C and weighed. These results are given in Section 3.4 (production of faeces). Food stores generally contained a few termites and were sorted prior to drying for at least 48 hours at 80-100$^{o}$C. The food stores were difficult to remove intact and in three nests were not weighed due to excessive losses in handling.

The biomass of the various castes was estimated from six colonies of the spiral plate type. It was not possible to use these nests for population counts since, for biomass studies, it was important that the animals should be undamaged. Sorting castes was very time-consuming and sample size was determined by the time available before the animals began to dry out. The sample size was therefore variable but, in calculation of the means, it has been assumed that the variance of each caste biomass was the same for all colonies, i.e. the values have been treated as equally good estimates. On some occasions it was not possible to estimate the weight of all castes before desiccation set in. Larvae were particularly sensitive and only four estimates could be made. Dry weights of all the castes were obtained after 24 hours of drying at 60-80$^{o}$C. There are no dry weights for one colony (F) and these have been estimated from the mean percentage dry values from the other colonies.

The calorific values for all sterile castes and alates were obtained from five ball-milled samples of each. Samples were burnt in a Newham Electronics micro-bomb calorimeter attached to a Venture Servoscribe Potentiometric Recorder.

## 3.2.3 RESULTS AND DISCUSSIONS

### 3.2.3.1 The Abundance and Distribution of M. bellicosus Colonies.

The numbers, heights and widths of epigeal colonies recorded in the three censuses are given in Tables 3.2.1, 3.2.2 and 3.2.3. Their exact localities are given in Figures 3.2.1, 3.2.2 and 3.2.3. There were 40 epigeal colonies present in 1974 (6.67 $ha^{-1}$), 43 in 1975 (7.17 $ha^{-1}$) and 33 in 1976 (5.5 $ha^{-1}$) with a mean for all years of 38.67 or 6.45 $ha^{-1}$. It will be seen later that an estimate of 45 has been calculated for the number of young, entirely hypogeal colonies, (7.5 $ha^{-1}$).

Table 3.2.4 gives other records for the abundance of large mounds of the Macrotermitinae in Africa, and also data on Nasutitermes spp. from Australia, which have large mounds and populations and parallel the mound-building Macrotermitinae of Africa, (Wood and Lee 1971). Abundance of the species listed is less than 10 $ha^{-1}$ and in general closely resembles the abundance of M. bellicosus in Mokwa. Mound-building species with smaller colonies may reach much higher densities - Trinervitermes geminatus (a polycalic species) up to 500 $ha^{-1}$ (Sands 1965a), Cubitermes fungifaber 875 $ha^{-1}$ (Maldague 1964). Lee and Wood (1971) give a further review.

Measurements of the distances between organisms and their "nearest neighbours" have been used by plant ecologists (Clark and Evans 1954, Cottam and Curtis 1956) for assessing population density when random dispersal is assumed, and the pattern of dispersal when density is known. Blackith (1958) has used the method for estimation of grasshopper populations.

The relationship between the density of the population (m) and the mean of the nearest neighbour distances ($\bar{r}$), in the same units of measurement, is given by:

$$m = \frac{a}{\bar{r}^2}$$

where a is a constant known as the dispersion coefficient, (Wood and Lee 1971). If the organisms are randomly dispersed a = 0.25, if clumped in a single mass a = 0, and if dispersed at the corners of a regular network of hexagons then a = 1.158. Values between 0.25 and 1.158 indicate a degree of overdispersion.

Nearest neighbour distances in the three censuses are given in Tables 3.2.1, 3.2.2 and 3.2.3. Calculations of the coefficients of dispersion are as follows:-

$$1974 \quad a = m.\bar{r}^{2} = \frac{40}{60{,}000} \cdot 23.51^2 = \underline{0.37}$$

$$1975 \quad a = m.\bar{r}^{2} = \frac{43}{60{,}000} \cdot 19.91^2 = \underline{0.28}$$

$$1976 \quad a = m.\bar{r}^{2} = \frac{33}{60{,}000} \cdot 20.12^2 = \underline{0.22}$$

In addition, a dispersion coefficient has been calculated for all the 1974 colonies plus new colonies found in 1975 and 1976. Some of these may have been present as hypogeal colonies in 1974. The result was a = 0.26.

Although a slight degree of overdispersion is indicated in 1974, the general conclusion is that there is no evidence to suggest that intra-specific competition is an important factor in the distribution of *M. bellicosus* colonies at Mokwa.

Overdispersion has been found to be a common phenomenon in ants, (Waloff and Blackith 1962, Pontin 1961, 1963, Brian 1965), and in some termites, (Wood and Lee 1971). However, Sands (1965a) found that *Trinervitermes geminatus* nests were aggregated and attributed this to the species' habit of building mounds in open situations. Wood and Lee (1971) found that 11 out of 13 mound-building termites studied showed some degree of overdispersion. However, both *Nasutitermes exitiosus* and *N. triodiae*, which have large, populous mounds of densities less than 10 $ha^{-1}$, had low dispersion coefficients in the region of 0.2 - 0.4. Pomeroy (1976) considered *M. bellicosus* colonies in old farmland near Kampala to be randomly dispersed or clumped. Glover et al. (1964), however, found *Odontotermes* sp. mounds to be very regularly distributed in the Loita Plains, Kenya.

It is possible that evidence for overdispersion of *M. bellicosus* on the study area has been obscured:

1) By dead mounds. In 1975 there were 205 abandoned mounds on the study area, in all stages of decay. Such mounds may render their immediate area uninhabitable to new colonies, perhaps as a result of compaction of the soil surface.

2) By interspecific competition for nest sites. Wood and Lee (1971) recorded a dispersion coefficient of 0.63 for a mixed community of *Nasutitermes exitiosus* and *Coptotermes lacteus*, compared with 0.22, 0.31 and 0.45 for three communities of *N. exitiosus* alone. At Mokwa the most likely competitors were other wood-feeding Macrotermitinae. These all had subterranean nests and could not be included in a nearest neighbour study.

I have no data to suggest whether either of these suggestions applies to *M. bellicosus* at Mokwa.

TABLE 3.2.1 The distribution of *M. bellicosus* colonies in March 1974

| COLONY NUMBER | MAP SQUARE | EXACT LOCATION OF COLONY METRES FROM CORNER POSTS | | NEAREST NEIGHBOUR m (r) | MOUND HEIGHT m |
|---|---|---|---|---|---|
| 1 | Aa | 2.1 NE | 23.2 NW | 19.2 | 1.8 |
| 2 | Aa | 11.3 NW | 22.2 NE | 14.5 | 0.4 |
| 3 | Ab | 6.3 E of SW | | 22.2 | 1.0 |
| 4 | Af | 6.9 SE | 19.4 SW | 49.0 | 1.7 |
| 5 | Ba | 17.8 NW | 11.9 NE | 14.5 | 0.9 |
| 6 | Bb | 9.8 NW | 16.9 NE | 23.0 | 1.0 |
| 7 | Bc | 18.5 NW | 17.2 NE | 25.8 | 2.6 |
| 8 | Bd | 14.5 SW | 14.3 NW | 25.8 | 1.9 |
| 9 | Cc | 8.6 NW | 17.3 NE | 14.7 | 0.3 |
| 10 | Cc | 3.8 E of SW | | 22.2 | 0.2 |
| 11 | Cg | 10.2 NW | 17.0 SW | 54.0 | 0.5 |
| 12 | Db | 22.0 NW | 4.5 NE | 22.3 | 0.8 |
| 13 | Dc | 6.3 NE | 18.5 NW | 14.7 | 0.2 |
| 14 | Dd | 15.5 SE | 9.5 SW | 31.3 | 0.6 |
| 15 | Eh | 13.7 NW | 16.5 SW | 21.0 | 0.7 |
| 16 | Fd | 15.4 NE | 13.0 NW | 16.2 | 0.9 |
| 17 | Fe | 19.8 NE | 6.0 NW | 16.0 | 1.6 |
| 18 | Fe | 10.3 SW | 15.6 SE | 19.3 | 1.5 |
| 19 | Fh | 13.0 NE | 13.8 NW | 21.2 | 0.5 |
| 20 | Gc | 18.3 NE | 16.5 SE | 2.8 | 0.5 |
| 21 | Gc | 17.0 SE | 14.6 SW | 2.8 | 1.7 |
| 22 | Gc | 20.5 SE | 4.7 NE | 15.0 | 0.9 |
| 23 | Gd | 21.0 NW | 5.2 NE | 15.6 | 0.5 |
| 24 | Ge | 12.5 NE | 18.1 SE | 16.0 | 0.3 |
| 25 | Ha | 17.3 SW | 10.2 NW | 30.5 | 0.3 |
| 26 | Hd | 5.9 NW | 19.2 SW | 29.3 | 0.3 |
| 27 | Hf | 25.0 NW | 13.8 SW | 34.2 | 0.7 |
| 28 | Hh | 15.8 NW | 15.2 SW | 35.0 | 1.7 |
| 29 | Ia | 7.9 S of NW | | 30.5 | 4.4 |
| 30 | Ie | 12.0 NE | 18.7 NW | 29.2 | 1.2 |
| 31 | Ig | 8.0 SW | 21.1 SE | 14.2 | 0.4 |
| 32 | Ig | 7.2 NW | 20.0 NE | 14.2 | 0.3 |
| 33 | Jb | 5.2 SE | 20.3 SW | 8.0 | 0.2 |
| 34 | Jb | 12.2 SW | 13.0 SE | 8.0 | 0.5 |
| 35 | Je | 13.5 SE | 17.8 SW | 4.0 | 0.5 |
| 36 | Je | 14.0 SW | 14.4 SE | 4.0 | 1.8 |
| 37 | Ka | 12.3 NE | 12.9 NW | 38.0 | 0.7 |
| 38 | Kf | 10.9 NE | 15.2 SE | 23.5 | 0.4 |
| 39 | Ld | 8.8 NE | 20.2 NW | 59.5 | 0.3 |
| 40 | Lf | 6.9 SW | 19.3 NW | 44.0 | 0.5 |

$\sum r = 940.3$

TABLE 3.2.2 The distribution of *M. bellicosus* colonies in February 1975, with indication of their presence in 1974.

| COLONY NUMBER | MAP SQUARE | EXACT LOCATION OF COLONY METRES FROM CORNER POSTS | | NEAREST NEIGHBOUR m ($r$) | HEIGHT m | WIDTH m | PRESENT IN 1974 |
|---|---|---|---|---|---|---|---|
| 1 | Ab | 6.2 E of SW | | 22.5 | 0.9 | 1.3 | x |
| 2 | Af | 9.0 NW | 20 NE | 15.0 | 0.55 | 0.8 | |
| 3 | Af | 6.7 SE | 20.4 NE | 18.5 | 1.25 | 1.0 | x |
| 4 | Ag | 2.9 NW | 22.3 NE | 8.0 | 0.65 | 0.7 | |
| 5 | Bc | 18.0 SW | 18.6 NW | 22.5 | 2.2 | 1.6 | x |
| 6 | Bd | 14.6 SW | 14.6 NW | 25.0 | 1.65 | 1.4 | x |
| 7 | Bf | 19.8 NE | 5.5 SE | 8.0 | 0.65 | 0.75 | |
| 8 | Cg | 2.7 N of SW | | 7.5 | 0.5 | 0.5 | |
| 9 | Cg | 14.5 SE | 16.0 NE | 18.0 | 0.4 | 0.6 | |
| 10 | Ch | 5.0 S of NW | | 7.5 | 0.05 | 0.1 | |
| 11 | Ch | 8.0 NE | 18.5 SE | 19.0 | 0.2 | 0.3 | |
| 12 | Df | 5.9 SW | 19.9 SE | 17.0 | 0.5 | 0.4 | |
| 13 | Df | 6.8 SE | 18.3 NE | 18.0 | 0.4 | 0.55 | |
| 14 | Dg | 9.9 SW | 15.2 NW | 18.0 | 0.5 | 0.9 | |
| 15 | Ec | 8.1 NW | 17.6 SW | 39.5 | 0.2 | 0.6 | |
| 16 | Ed | 7.5 SE | 17.7 NE | 27.5 | 0.3 | 0.6 | |
| 17 | Ef | 13.6 SE | 16.4 SW | 17.0 | 0.2 | 0.55 | |
| 18 | Eh | 13.5 NW | 16.7 SW | 27.0 | 0.8 | 0.8 | x |
| 19 | Fd | 15.2 SE | 11.6 SW | 10.0 | 0.25 | 0.4 | |
| 20 | Fe | 6.5 NE | 18.7 SE | 17.0 | 0.85 | 1.0 | |
| 21 | Fe | 6.0 NW | 22.7 SW | 10.0 | 2.05 | 1.35 | x |
| 22 | Fe | 1.8 SW | 23.3 SE | 9.0 | 0.35 | 0.7 | |
| 23 | Fe | 15.5 SE | 10.6 SW | 9.0 | 2.05 | 1.6 | x |
| 24 | Fg | 9.0 NE | 16.7 SE | 24.5 | 0.2 | 0.5 | |
| 25 | Ge | 12.4 NE | 18.0 SE | 15.5 | 0.5 | 0.85 | x |
| 26 | Hd | 7.5 SE | 19.0 NE | 25.0 | 0.25 | 0.4 | |
| 27 | Hf | 25.0 NW | 15.0 SW | 24.5 | 0.9 | 0.7 | x |
| 28 | Ia | 16.7 SW | 30.0 SE | 18.0 | 4.6 | 3.1 | x |
| 29 | Ia | 12.8 SW | 13.3 SE | 18.0 | 0.35 | 0.65 | |
| 30 | If | 11.3 SE | 14.5 SW | 13.0 | 0.4 | 0.85 | |
| 31 | Ig | 6.8 NW | 20.2 SW | 13.0 | 0.55 | 1.05 | x |
| 32 | Ig | 7.2 SW | 21.1 SE | 14.0 | 1.2 | 0.6 | x |
| 33 | Ib | 12.8 SE | 12.4 SW | 8.0 | 1.0 | 1.05 | x |
| 34 | Ib | 5.4 SE | 20.5 SW | 8.0 | 0.15 | 0.45 | x |
| 35 | Jf | 15.8 SW | 9.2 SE | 16.0 | 0.3 | 0.2 | |
| 36 | Ka | 12.5 NE | 12.6 NW | 38.0 | 1.3 | 1.1 | x |
| 37 | Kc | 24.0 SW | 3.9 SE | 27.0 | 0.4 | 0.75 | |
| 38 | Kf | 11.1 NE | 23.7 NW | 23.5 | 0.35 | 0.6 | x |
| 39 | Kh | 26.6 NW | 21.0 SW | 29.0 | 0.4 | 0.35 | |
| 40 | La | 4.4 SW | 21.0 SE | 38.0 | 0.35 | 1.0 | |
| 41 | Ld | 16.5 SW | 13.6 NW | 43.0 | 0.4 | 1.1 | |
| 42 | Lf | 6.7 SW | 22.1 SE | 40.5 | 0.85 | 1.22 | x |
| 43 | Lh | 19.0 NW | 10.2 NE | 29.0 | 0.45 | 0.5 | |

$\Sigma r = 856$

TABLE 3.2.3 The distribution of *M. bellicosus* colonies in February 1976, with indication of their presence in 1974 and 1975.

| COLONY NUMBER | MAP SQUARE | EXACT LOCATION OF COLONY METRES FROM CORNER POSTS | | NEAREST NEIGHBOUR m (r) | HEIGHT m | WIDTH m | PRESENT IN | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | 1974 | 1975 |
| 1 | Ab | 6.4 SW | 18.6 SE | 22.0 | 1.95 | 1.3 | x | x |
| 2 | Af | 9.1 NW | 15.5 SW | 6.0 | 1.8 | 1.0 | | |
| 3 | Af | 16.5 SE | 16.3 SW | 13.5 | 0.42 | 0.5 | | |
| 4 | Bc | 17.2 NE | 17.1 SE | 22.0 | 3.8 | 1.85 | x | x |
| 5 | Bd | 14.15 SW | 14.1 NW | 25.0 | 3.5 | 1.55 | x | x |
| 6 | Bf | 5.6 SE | 19.9 NE | 9.5 | 0.66 | 0.83 | | x |
| 7 | Bf | 14.65 SE | 14.8 NE | 6.0 | 0.35 | 0.6 | | |
| 8 | Bf | 8.6 NE | 18.1 SE | 6.0 | 0.27 | 0.58 | | |
| 9 | Bg | 12.6 NW | 13.1 SW | 25.5 | 0.27 | 0.50 | | |
| 10 | Bh | 10.3 SW | 14.9 NW | 6.5 | 0.33 | 0.50 | | |
| 11 | Ca | 9.7 NW | 16.0 SW | 18.0 | 0.95 | 0.63 | | |
| 12 | Ch | 11.7 NW | 17.4 NE | 14.0 | 0.24 | 0.70 | | |
| 13 | Ch | 13.3 NE | 11.8 SE | 6.5 | 0.09 | 0.18 | | |
| 14 | Db | 2.7 NE | 23.2 SE | 18.0 | 0.15 | 0.55 | | |
| 15 | Dc | 13.9 NE | 16.6 NW | 33.0 | 0.65 | 1.0 | | |
| 16 | De | 2.2 W of NE | | 7.5 | 0.27 | 0.6 | | |
| 17 | De | 8.47 NE | 20.8 NW | 7.5 | 0.32 | 0.45 | | |
| 18 | Df | 15.7 NE | 18.5 SE | 5.0 | 0.27 | 0.60 | | |
| 19 | Df | 18.4 NE | 14.0 SE | 5.0 | 0.7 | 0.8 | | |
| 20 | Ec | 17.7 SW | 8.1 NW | 35.0 | 0.6 | 0.9 | | x |
| 21 | Ef | 8.9 SW | 16.8 NW | 10.5 | 0.11 | 0.15 | | |
| 22 | Ef | 21.6 NW | 16.1 SW | 10.5 | 0.5 | 0.7 | | x |
| 23 | Eh | 13.7 NW | 19.7 NE | 21.5 | 1.05 | 0.8 | x | x |
| 24 | Fh | 10.5 W of NE | | 21.5 | 0.45 | 0.7 | | |
| 25 | Gb | 5.4 E of SW | | 48.5 | 0.24 | 0.6 | | |
| 26 | Ia | 7.55 S of NW | | 38.0 | 4.5 | 3.0 | x | x |
| 27 | Ie | 9.7 NE | 17.0 NW | 2.5 | 0.7 | 0.9 | | |
| 28 | Ie | 7.0 NE | 18.8 NW | 2.5 | 0.5 | 0.55 | | |
| 29 | Ib | 20.45 SW | 5.9 SE | 39.0 | 0.3 | 0.6 | x | x |
| 30 | Ka | 12.4 NE | 13.0 NW | 38.0 | 1.65 | 1.15 | x | x |
| 31 | La | 4.05 SW | 21.0 SE | 39.0 | 1.1 | 1.0 | | x |
| 32 | Ld | 13.2 NW | 16.3 SW | 50.5 | 0.75 | 1.1 | | x |
| 33 | Lf | 19.4 NW | 15.0 NE | 50.5 | 0.35 | 0.65 | | |

$\Sigma r = 664.0$

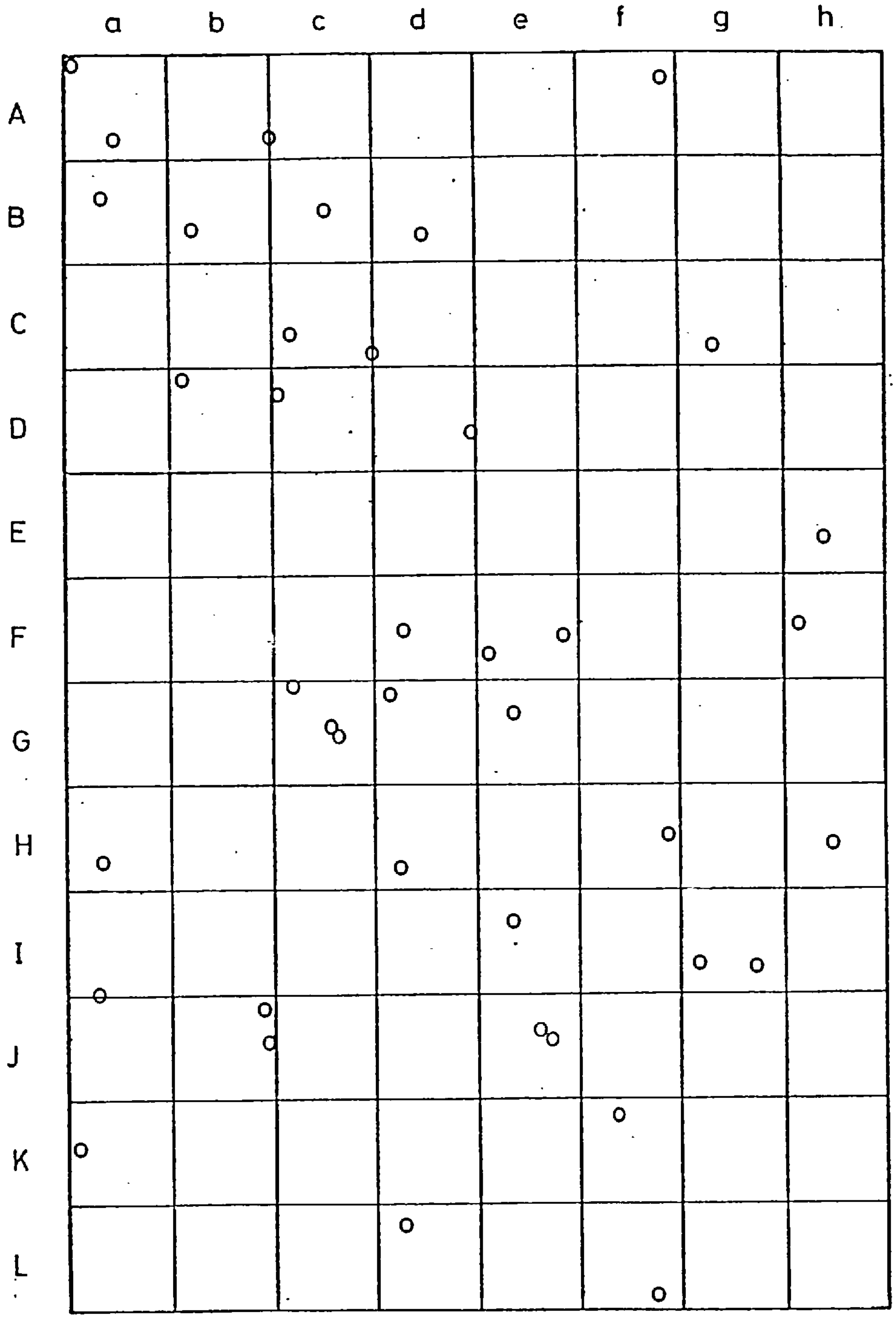


FIGURE 3.2.1 The distribution of epigeal *Macrotermes bellicosus* colonies on the 6 ha study area in March 1974 (40 colonies).

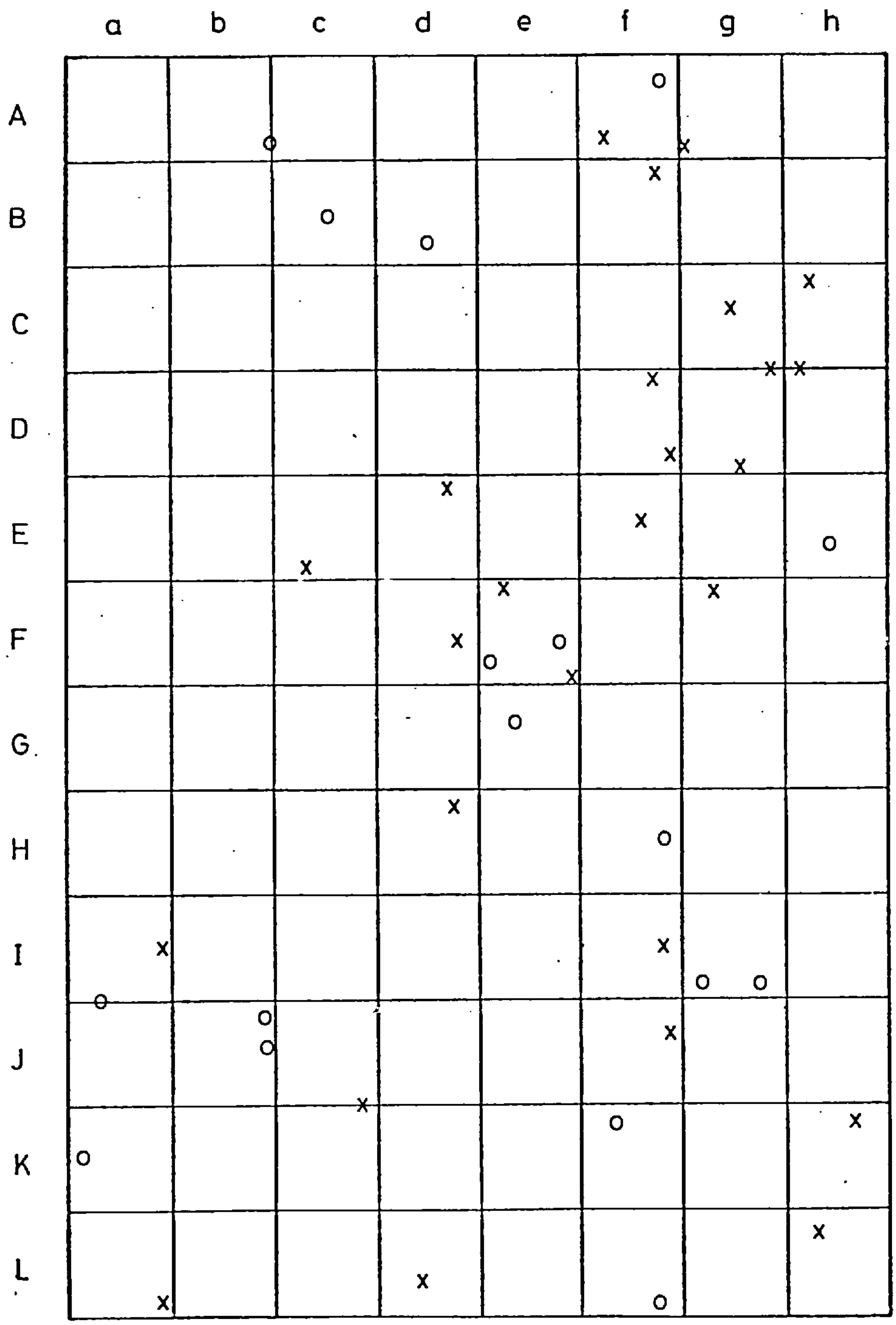


FIGURE 3.2.2 The distribution of epigeal Macrotermes bellicosus colonies on the 6 ha study area in February 1975. Key: 0 = mounds also present in March 1974 (17), x = new colonies (26). Total 43 colonies.

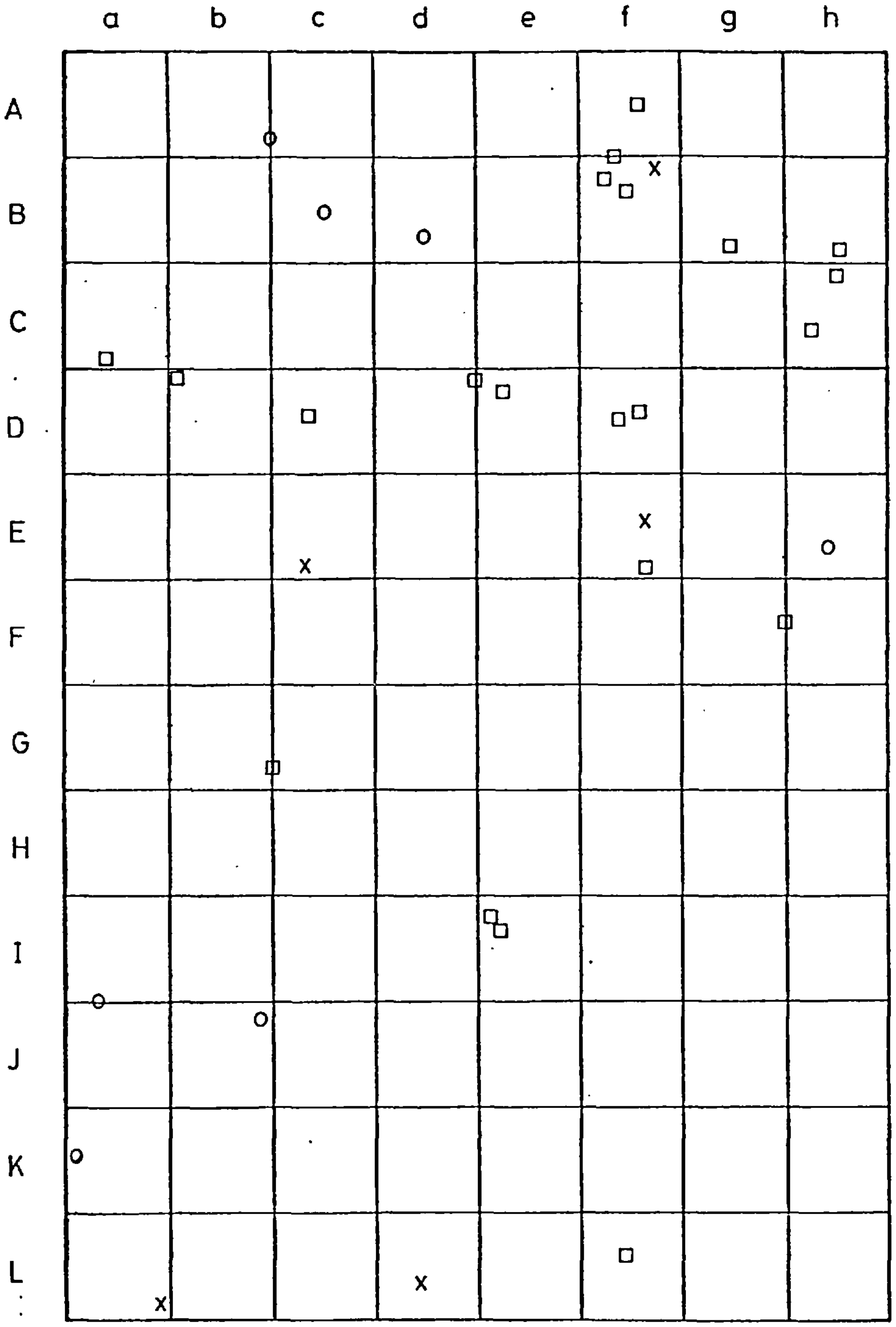


FIGURE 3.2.3 The distribution of epigeal <u>Macrotermes bellicosus</u> colonies on the 6 ha study area in February 1976. Key: 0 = mounds also present in March 1974 and February 1975 (7), x = mounds also present in February 1975 (5) □ = new colonies (21). Total 33 colonies.

TABLE 3.2.4 Abundance of various epigeal termite nests. (Adapted from Lee and Wood 1971, Table 5)

| SPECIES | NUMBER MOUNDS $ha^{-1}$ | HABITAT AND LOCALITY | AUTHOR AND REFERENCE |
|---|---|---|---|
| Macrotermitinae | | | |
| <u>Odontotermes</u> sp. | 6.5 | Savanna, Kenya | Glover et al. 1964 |
| <u>Macrotermes</u> <u>bellicosus</u> | 2-3 | Savanna, Zaire | Bouillon & Kidieri 1964 |
| <u>Macrotermes</u> spp. | 3-4 | Savanna, E.Africa | Hesse 1955 |
| <u>Macrotermes</u> <u>bellicosus</u> | 1.4-4.2 | Old farmland, Uganda | Pomeroy 1976 |
| <u>Macrotermes</u> <u>bellicosus</u> | 5.5-7.2 | S.Guinea Savanna, Nigeria | Present work |
| Nasutitermitinae | | | |
| <u>Nasutitermes</u> <u>exitiosus</u> | 4-9 | Sclerophyll forest S. Australia | Wood & Lee 1971 |
| <u>Nasutitermes</u> <u>triodiae</u> | 3-7 | Tree savanna, N. Australia | Wood & Lee 1971 |

### 3.2.3.2 Mound Size and Colony Age Distributions for *Macrotermes bellicosus*

The determination of age is a prerequisite to the description of age distribution and the construction of a survivorship curve (Southwood 1966). The life-span of *M. bellicosus* colonies has been estimated at 80 years, Grassé (1949), 5-10 years (Nye 1955) and 4-10 years (Pomeroy 1976). Pomeroy (*loc. cit.*) studied the growth of seven mounds over a period of five years and calculated a mean growth rate by linear regression, noting, however, that growth was slower in large colonies than in small ones. Since my study period was only two years, this approach was not feasible. Instead, a composite picture of mound growth has been constructed from yearly growth increments of a number of different-sized mounds. Pomeroy (*loc. cit.*) used mound volume as a growth parameter while I have found height to be more useful for the "cathedral" type mounds. Volume, however, is a function of height and width and these two parameters have been shown to be closely correlated (Table 3.1.2).

Table 3.2.5 gives height data for 17 mounds present in 1974 and 1975 and 12 mounds present in 1975 and 1976. Some nests are represented twice, being present in all three census years. With consideration of the observation that, in general, mound growth rate decreases with age, a quadratic curve of the form:

$$y = ax + bx^2 + c$$

has been generated to fit the data by a multiple regression of $H_{t+1}$, Ht and $Ht^2$ (Figure 3.2.4), where $H_t$ = height in first year and $H_{t+1}$ = height in second year. This gave the best fit:

$$H_{t+1} = 1.2456 \cdot H_t - 0.0654 \cdot H_t^2 + 0.2258$$

Correlation coefficient = 0.9084, $n = 29$, $p < 0.001$

F value = 59.0039 (h.s.)

The correlation coefficient for a linear regression of $H_{t+1}$ against $H_t$ was 0.9043 so although the contribution of the $H_t^2$ factor is small, it has improved the correlation. It should be noted however, that any biological basis for the use of a quadratic function of mound height is obscure. In reality the situation would undoubtedly be far more complex, involving functions of colony size, respiratory rate, fungus comb biomass and local conditions of soil, microclimate etc. Such detailed data are not available and the quadratic function has been accepted as a useful form which approximates to field observations. Additionally, the simple curve in Figure 3.2.4 is taken as a single representative of a family of curves. Mound growth rates and maximum heights vary enormously between colonies, as suggested by the scatter of data obtained.

In order to use this relationship to generate a growth curve, a starting point must be designated. Tables 3.2.2 and 3.2.3 show that in 1975 and 1976 a total of 47 colonies produced epigeal mounds that were not present in the previous year's census. The mean height of these mounds was 0.4145m ± 0.0802 (95% confidence limits). Pomeroy (1976) considered that M. bellicosus colonies remained hypogeal for 1-2 years. I agree with this contention and, using a starting point of 0.4145m at two years I have generated a growth curve by iteration of the above relationship between $H_{t+1}$ and $H_t$, the resulting data being given in Table 3.2.6 and Figure 3.2.5. The asymptote of the curve is reached when $H_{t+1} = H_t$, at approximately 4.5m height. This describes the situation on the study area very well, the largest mound recorded being 4.6m high. However, the curve is generated from data on mound growth and comments on Figure 3.2.4 (above) also apply in this case. The growth curve is representative of an "average" colony. Some mounds exceed 6m in height, while others never reach 4.5m. Nevertheless, despite the over-simplification which Figure 3.2.5 clearly represents, the growth curve can be used to examine the approximate age distribution of colonies on the study area.

Table 3.2.7 gives the number of colonies on the study area in 1974, 1975 and 1976, divided into height ranks at 0.5m intervals. The number of colonies present at each height rank is well described by linear regression analysis on a double log scale, giving a power law relationship of the form:

$$\log(N + 1) = 0.7190 - 1.0515 \log \bar{H}_r$$

or $$N+1 = 5.236\, \bar{H}_r^{-1.0515} \qquad \text{(Table 3.2.7)}$$

where $N$ = number of living colonies, $\bar{H}_r$ = mean of mound height rank.

In Table 3.2.8, this relationship has been used to calculate the expected number of colonies at each 0.5m height rank (with intermediate values bracketed) and the age of the colonies has been estimated from the growth curve (Fig. 3.2.5). In Figure 3.2.6 the number of colonies has been plotted in their height/estimated age ranks in the form of a survivorship curve. The actual data from the study area (mean of three censuses), are superimposed in histogram form.

In Table 3.2.9 the survivorship data have been described in the form of a life-table (after Deevey 1947 and Southwood 1966) corrected so as to commence with 1000 colonies at year one. This life-table represents the mortality of colonies with time, i.e. it begins with the number of colonies that are successfully started, not the number of alates released or tandems formed. It assumes that mortality for a given age group, and the formation of colonies are relatively constant.

The survivorship curve (Figure 3.2.6) is similar to Slobodkin's (1962) Type IV curve where mortality rate acts more heavily on the younger colonies, declining as the colony ages. The type IV curve is probably the most common in nature, (Slobodkin _loc_. _cit_.) but although Kofoid (1934) has demonstrated high mortality in the early stages of _Kalotermes minor_ colonies, there are no other published comparisons of life-tables from the Isoptera.

TABLE 3.2.5 Yearly increments of mound height increase for 29 colonies of *Macrotermes bellicosus*.

| LOCATION OF MOUND | HEIGHT m 1974 ( Ht ) | HEIGHT m 1975 ($H_{t+1}$) |
|---|---|---|
| Ab | 1.0 | 0.9 |
| Bc | 2.6 | 2.2 |
| Bd | 1.9 | 1.65 |
| Eh | 0.7 | 0.8 |
| Ia | 4.4 | 4.6 |
| Jb | 0.2 | 0.15 |
| Ka | 0.7 | 1.30 |
| Af | 1.7 | 1.25 |
| Fe | 1.6 | 2.05 |
| Fe | 1.5 | 2.01 |
| Ge | 0.3 | 0.5 |
| Hf | 0.7 | 0.9 |
| Ig | 0.3 | 0.55 |
| Ig | 0.4 | 1.2 |
| Jb | 0.5 | 1.0 |
| Kf | 0.4 | 0.35 |
| Lf | 0.5 | 0.85 |
|  | Ht (1975) | $H_{t+1}$ (1976) |
| Ab | 0.9 | 1.95 |
| Bc | 2.2 | 3.8 |
| Bd | 1.65 | 3.5 |
| Eh | 0.8 | 1.05 |
| Ia | 4.6 | 4.5 |
| Jb | 0.15 | 0.3 |
| Ka | 1.3 | 1.65 |
| Bf | 0.65 | 0.66 |
| Ec | 0.2 | 0.6 |
| Ef | 0.2 | 0.5 |
| La | 0.35 | 1.1 |
| Ld | 0.4 | 0.75 |

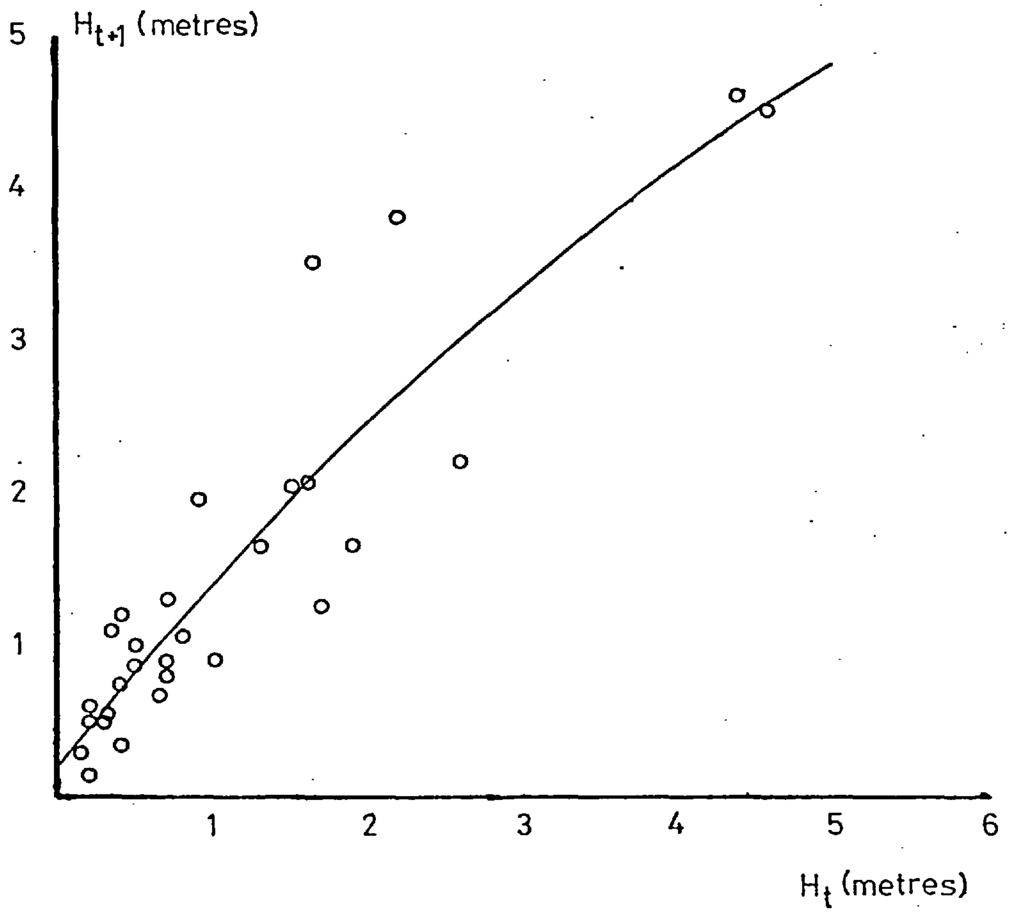


FIGURE 3.2.4 Data from Table 3.2.5 plotted as mound height in one year ($H_{t+1}$) against mound height in the previous year ($H_t$). The quadratic equation for the best fit has been computed by a multiple linear regression of $H_t$, $H_t^2$ and $H_{t+1}$

$$H_{t+1} = 1.2456 \cdot H_t - 0.0654 \cdot H_t^2 + 0.2258$$

TABLE 3.2.6 Iteration of the formula

$$H_{t+1} = 1.245782\ H_t - 0.06537475\ H_t^2 + 0.225848884$$

with $H_t$ at year two = 0.4145 m.

| YEAR | HEIGHT m | YEAR | HEIGHT m |
|---|---|---|---|
| 1 | | 21 | 4.5089 |
| 2 | 0.4145 | 22 | 4.5129 |
| 3 | 0.7309 | 23 | 4.5156 |
| 4 | 1.1013 | 24 | 4.5173 |
| 5 | 1.5183 | 25 | 4.5184 |
| 6 | 1.9664 | 26 | 4.5192 |
| 7 | 2.4223 | 27 | 4.5197 |
| 8 | 2.8594 | 28 | 4.5201 |
| 9 | 3.2530 | 29 | 4.5203 |
| 10 | 3.5859 | 30 | 4.5204 |
| 11 | 3.8517 | 31 | 4.5205 |
| 12 | 4.0536 | 32 | 4.5206 |
| 13 | 4.2007 | 33 | 4.5206 |
| 14 | 4.3046 | 34 | 4.5206 |
| 15 | 4.3762 | 35 | 4.5206 |
| 16 | 4.4247 | | |
| 17 | 4.4573 | | |
| 18 | 4.4789 | | |
| 19 | 4.4932 | | |
| 20 | 4.5027 | | |

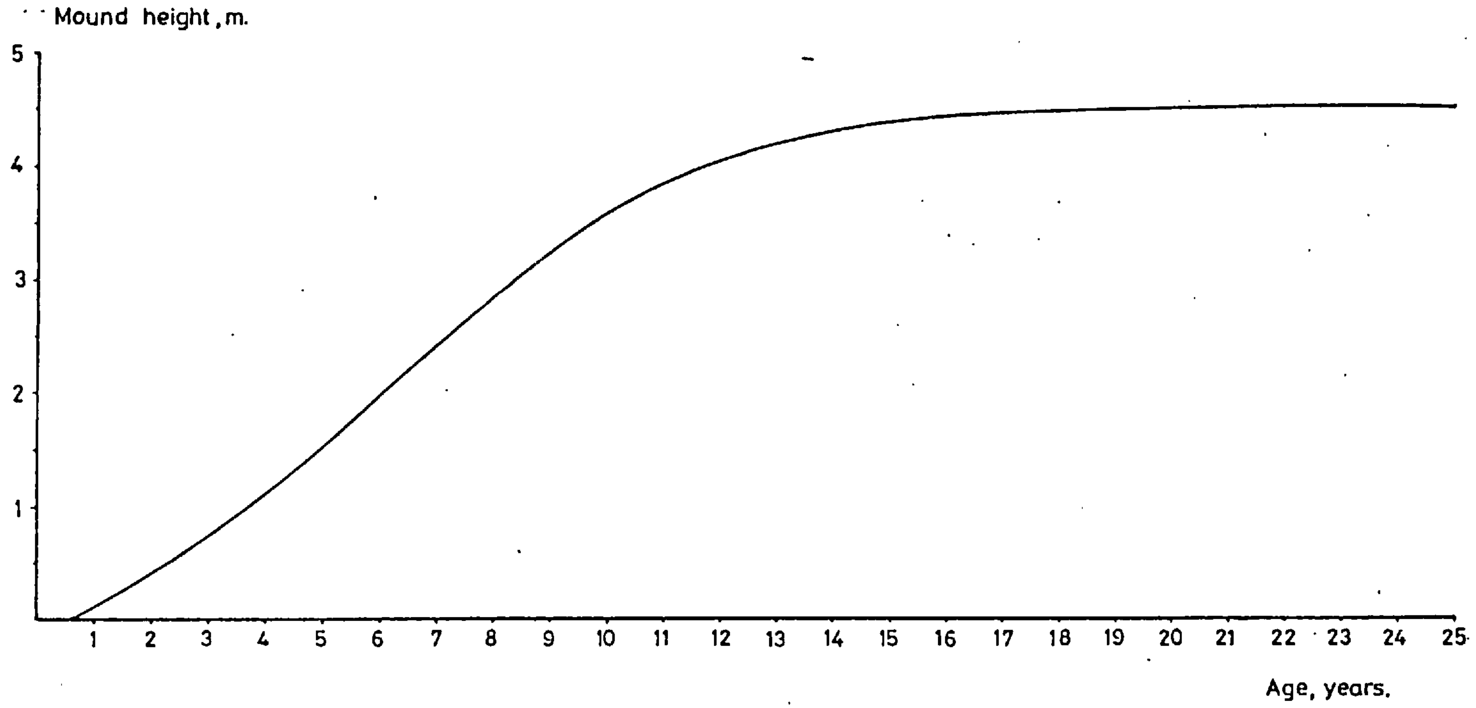


FIGURE 3.2.5 A model for growth of *M. bellicosus* mounds developed by iteration of the relationship between $H_t$ and $H_{t+1}$ (Fig. 3.2.4) with a starting point of 0.4145 m at two years of age.

TABLE 3.2.7 The number of living *M. bellicosus* colonies on the study area during the three censuses, divided into mound height ranks, with a regression analysis of log number of living colonies plus one against log mean of mound height rank.

| MOUND HEIGHT RANK m | LOG MEAN OF MOUND HEIGHT RANK ($\bar{H}_r$) | NUMBER OF LIVING COLONIES | | | |
|---|---|---|---|---|---|
| | | 1974 | 1975 | 1976 | MEAN ($\bar{N}$) |
| 0 - 0.5 | $\bar{1}.3979$ | 19 | 25 | 18 | 20.66 |
| 0.51 - 1.0 | $\bar{1}.8751$ | 10 | 10 | 7 | 9 |
| 1.01 - 1.5 | 0.0969 | 2 | 3 | 2 | 2.33 |
| 1.51 - 2.0 | 0.2430 | 7 | 1 | 3 | 3.66 |
| 2.01 - 2.5 | 0.3522 | 0 | 3 | 0 | 1 |
| 2.51 - 3.0 | 0.4392 | 1 | 0 | 0 | 0.33 |
| 3.01 - 3.5 | 0.5119 | 0 | 0 | 1 | 0.33 |
| 3.51 - 4.0 | 0.5740 | 0 | 0 | 1 | 0.33 |
| 4.01 - 4.5 | 0.6284 | 1 | 0 | 1 | 0.66 |
| 4.51 - 5.0 | 0.6767 | 0 | 1 | 0 | 0.33 |
| | TOTAL | 40 | 43 | 33 | 38.66 |

$\log(N + 1) = 0{\cdot}7190 - 1{\cdot}0515 \log \bar{H}_r$

Correlation coefficient (r) = −·896 (h.s.)

F value = 114·6 (h.s.)

Standard error = ·2032

T value for slope = −10·7 (h.s.)

T value for intercept = 15·6 (h.s.)

TABLE 3.2.8 Number of living colonies expected on the study area for each height/estimated age rank (unbracketed values), as predicted from the regression given in Table 3.2.7. Bracketed figures are values for intermediate heights/ ages and have no meaning as area-specific estimates.

| MEAN VALUES OF MOUND HEIGHT RANKS, m | NO. OF LIVING COLONIES EXPECTED $6ha^{-1}$ | ESTIMATE OF COLONY AGE (YEARS) |
|---|---|---|
| 0.25 | 21.4940 | 1.44 |
| (0.50) | ( 9.8526) | (2.28) |
| 0.75 | 6.0855 | 3.00 |
| (1.00) | (4.2360) | (3.72) |
| 1.25 | 3.1409 | 4.34 |
| (1.50) | (2.4185) | (4.95) |
| 1.75 | 1.9070 | 5.52 |
| (2.00) | (1.5262) | (6.09) |
| 2.25 | 1.2319 | 6.65 |
| (2.50) | (0.9979) | (7.20) |
| 2.75 | 0.8073 | 7.80 |
| (3.00) | (0.6493) | (8.40) |
| 3.25 | 0.5162 | 9.08 |
| (3.50) | (0.4025) | (9.75) |
| 3.75 | 0.3044 | 10.76 |
| (4.00) | (0.2188) | (11.77) |
| 4.25 | 0.1435 | 15.89 |
| (4.50) | (0.0768) | (20.00) |
| 4.75 | 0.0173 | |
| (5.00) | ( 0 ) | |

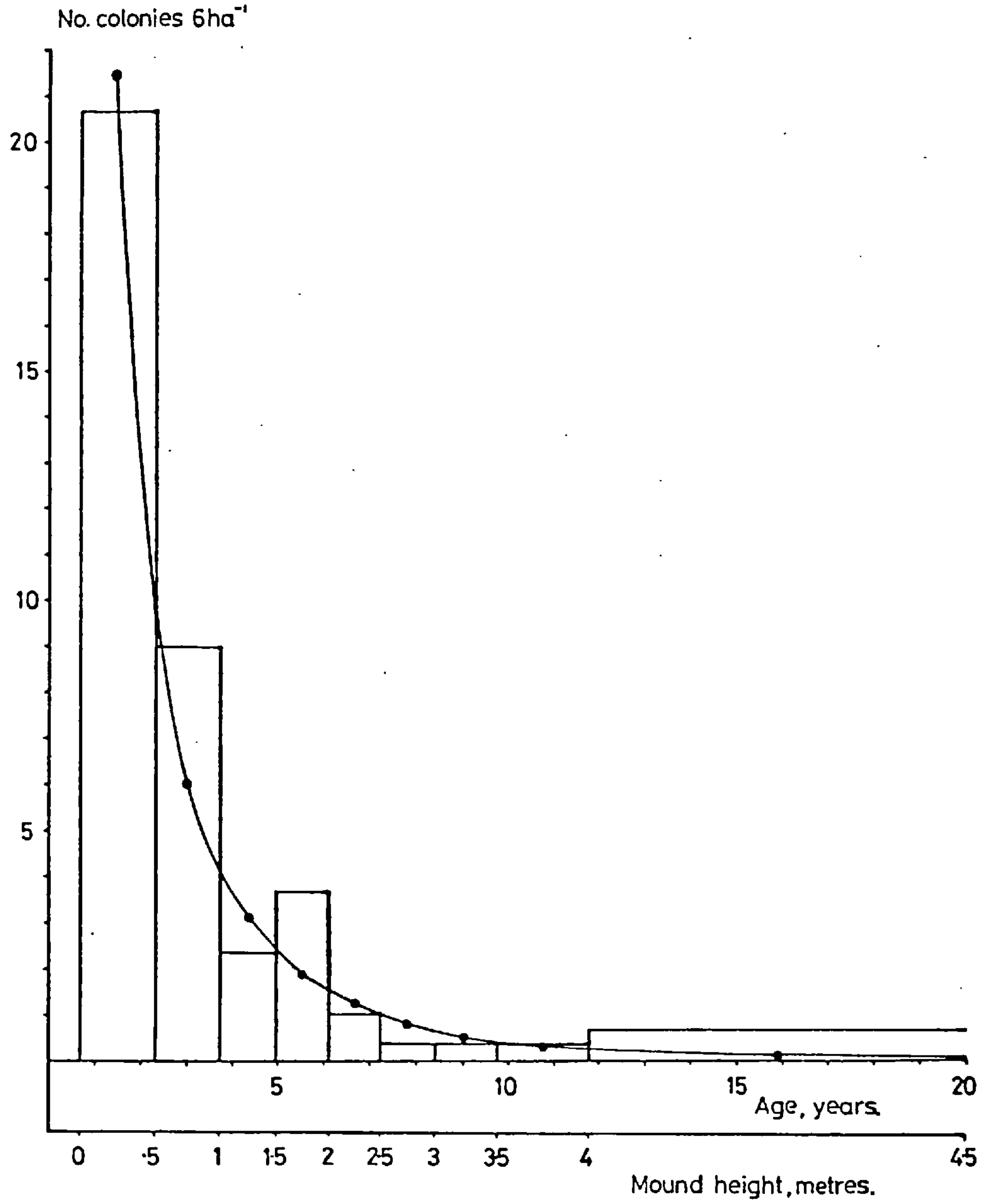


FIGURE 3.2.6 The height/age distribution of Macrotermes bellicosus colonies on the study area, represented as the mean of three censuses (histograms). The curve is the best fit through the census data, transformed to an age basis from a linear regression of mound numbers at each height rank on a log-log scale (see Tables 3.2.7, 3.2.8).

TABLE 3.2.9 A time-specific life-table for *Macrotermes bellicosus* colonies. Values of lx have been read from Figure 3.2.6 and extrapolated to begin with 1000. Original values at x = 0 and 1 were difficult to assess and the table is approximate.

| x | lx | dx | Lx | Tx | ex | 1000qx | O.V. |
|---|---|---|---|---|---|---|---|
| 1 | 1000 | 600 | 700 | 1106 | 1.11 | 600 | ~150 |
| 2 | 400 | 313 | 244 | 406 | 1.02 | 783 | ~ 60 |
| 3 | 87 | 47 | 64 | 162 | 1.86 | 540 | 13.1 |
| 4 | 40 | 16 | 32 | 98 | 2.45 | 400 | 6.0 |
| 5 | 24 | 8 | 20 | 66 | 2.75 | 333 | 3.6 |
| 6 | 16 | 5 | 14 | 46 | 2.88 | 313 | 2.4 |
| 7 | 11 | 3.7 | 9.2 | 32 | 2.91 | 336 | 1.5 |
| 8 | 7.3 | 2.3 | 6.2 | 23 | 3.15 | 315 | 1.1 |
| 9 | 5.0 | 1.7 | 4.2 | 17 | 3.40 | 340 | .75 |
| 10 | 3.3 | 0.8 | 2.9 | 13 | 3.94 | 242 | .50 |
| 11 | 2.5 | 0.5 | 2.3 | 10 | 4.00 | 200 | .37 |
| 12 | 2.0 | 0.5 | 1.8 | 7.7 | 3.85 | 250 | .30 |
| 13 | 1.5 | 0.2 | 1.4 | 5.9 | 3.93 | 133 | .22 |
| 14 | 1.3 | 0.3 | 1.2 | 4.5 | 3.46 | 231 | .20 |
| 15 | 1.0 | .27 | .87 | 3.3 | 3.30 | 270 | .14 |
| 16 | .73 | .06 | .70 | 2.4 | 3.29 | 82 | .11 |
| 17 | .67 | .07 | .64 | 1.7 | 2.54 | 104 | .10 |
| 18 | .60 | .07 | .57 | 1.1 | 1.83 | 117 | .09 |
| 19 | .53 | .13 | .47 | 0.5 | 0.94 | 245 | .08 |
| 20 | .40 | - | .03 | .03 | 0.08 | - | .06 |

Key:

x = the pivotal age for the age class, in years.

lx = the number of colonies surviving at the beginning of age class x, extrapolated to begin with 1000.

dx = the number of colonies dying during the age interval x.

Lx = the number of colonies alive between ages x and x + 1.

Tx = the total number of colonies x years beyond the age x.

ex = the expectation of life remaining for individuals of age x.

1000qx = the mortality rate per year expressed as the rate per 1000 alive at the start of that interval.

O.V. = the original values read or estimated from Figure 3.2.6.

(Constructed after Southwood 1966)

### 3.2.3.3 Populations of *Macrotermes bellicosus* Colonies.

Table 3.2.10 gives mound size, population size and estimated ages of 19 *M. bellicosus* colonies. Details of these population counts are given in Appendix 3.2. In Figure 3.2.7 the population size has been plotted against age. Colony 19 has been omitted since its age could not be determined.

The data appeared to be divided into three regions:

1) Colonies apparently on a steeply ascending growth curve (colonies 1-12, colonies are numbered with increasing age).

2) Colonies apparently on a curve declining from a high point on the growth curve (colonies 16, 18) or in the region from which such a decline curve appears to have originated (colony 11).

3) Colonies apparently on a curve declining from a median point on the growth curve (colonies 13, 14, 15, 17) or in the region of the high point from which such a decline appears to have originated (colony 12).

In addition, there is a faint suggestion of a decline curve originating at 400,000 - 425,000 individuals (colonies 9, 10) but since the data are few, this curve will not be considered further.

The three curves have been fitted as follows:

1) The growth curve. An exponential (geometric) curve of the form $y = a.e^{bx}$ describes the data well. This is the form of Lotka's (1922) equation for geometric increase of a population $Nt = No.e^{r_m t}$. Linear regression analysis of growth curve: (colonies 1-12)

Best fit: $\ln Nt = 9.43005 + 0.7767 . t$

or $Nt = 12457.2075.e^{0.7767.t}$

where $Nt$ = number of individuals at time t

$No$ = number of individuals at $t = 0$ (12457.20754)

$e$ = 2.71828

$r_m$ = innate capacity for increase (0.7767)

$t$ = time in years

| | | |
|---|---|---|
| Correlation coefficient (r) | = | 0.948 |
| F value | = | 89.242 |
| Standard error | = | 0.4366 |
| T-value for slope ($r_m$) | = | 9.447 |
| T-value for intercept ($N_o$) | = | 32.256 |
| Number of data pairs | = | 12 |

2) The high point decline curve. This has been fitted to colonies 16, 18 and 11 as follows:

a) A curve was drawn through the points by eye and estimates of N at years 6-16 read off (Table 3.2.11).

b) A plot of ln ln $\frac{Nt}{Nt+1}$ against age was found to be well fitted by a straight line of the form:

$$\ln \ln \frac{Nt}{Nt+1} = 0.2174t - 5.3393$$

or $$\frac{Nt}{Nt+1} = \exp\left[\exp(0.2174t - 5.3393)\right]$$

with correlation coefficient (r) = 0.9952.

c) The best fit for ln ln $\frac{Nt}{Nt+1}$ for years 0-22 has been calculated and transformed to the form $\frac{Nt}{Nt+1}$ (Table 3.2.11)

d) Nt has been solved for all $\left(\frac{Nt}{Nt+1}\right)$ values by iteration of the formula $Nt = Nt+1\left(\frac{Nt}{Nt+1}\right)$ for years 7-0 (not drawn in Figure 3.2.7) and by iteration of the formula $Nt+1 = Nt - \left(\frac{Nt}{Nt+1}\right)$ for years 9-22. N8 = 757,000 was chosen as a starting point which was fairly well supported by the data points.

3) The low point decline curve. This was fitted to colonies 13, 14, 15 and 17 in a similar fashion to that described above. Table 3.2.12 gives the data for N as fitted by age. They were well fitted by the formula

$$\ln \ln \frac{Nt}{Nt+1} = 0.5566t - 6.4524. \quad , r = 0.9993$$

or $$\frac{Nt}{Nt+1} = \exp\left[\exp(0.5566t-6.4524)\right]$$

In Table 3.2.12 the formula has been used to solve Nt for the values of $\left(\frac{Nt}{Nt+1}\right)$, using a starting point of $N_8$ = 495,000, which is well supported by the data.

A full statistical analysis of the two decline curves has not been given since the curves were calculated from imaginary points on a curve drawn by eye through the few available data points.

Noirot (1969) and Bodot (1966) note that in the ageing of a termite colony it is possible to distinguish three distinct phases: a juvenile period when the population increases rapidly and only neuter castes are developed; an adult period when the society regularly produces winged imagoes, and a senile period when this production declines, stops, and the colony dies out. This framework can be applied to my data but will be deferred until later, (Section 3.2.4) since, for a full understanding, the data on biomass and caste composition are required.

However, since the growth curve given in Figure 3.2.7 will be used as a predictive model, a few comments on its validity must be inserted here. Firstly, there are clearly not sufficient data points on the curves, particularly the decline curves, to be absolutely confident of their accuracy. The data I could gather became fewer as the mound size increased, for obvious reasons. The calculation of approximate mound ages has, however, allowed a biologically meaningful model to be fitted - a distinct advantage over the population/mound parameter models that are often used for prediction in this type of work. The decline curves are curious in that the data points lie on two distinct lines. There is no obvious reason for this; mounds were all taken from the same area and most of them were collected in the rainy season. It might be expected that the points would be more chaotic, representing a continuous spectrum of declining colonies. A genetic reason, with a pair of alleles found in the heterozygous and homozygous condition, is a possibility, albeit unlikely. In the absence of more detailed data on growth of individual colonies, it seems that the scatter is purely fortuitous. This is clearly a most unsatisfactory conclusion and further work is required, but for the purposes of prediction, a mean decline curve (dashed line in Figure 3.2.7) will be used in later sections.

Since the ages of colonies have been estimated from mound height data, it follows that in older colonies, mounds of similar sizes may have very different populations. Most of the volume of the endoecie is taken up by the fungus combs, whose biomass will be seen to be closely correlated with mound height (Section 3.4). Hence it is likely that the volume of combs dictates mound size, (the termites themselves occupy only a fraction of the space). Annual faeces (comb) production by a given population is the product of the biomass of combs and their turnover rate. Since the comb biomass appears to be constant at a given age (or height) of mound, and the population may vary, I can only conclude that the overall turnover time must vary also. As will be seen later, "dead" combs accumulate as the colony ages and it may be that these combs accumulate faster in rapidly decaying colonies, causing continued mound growth at a rate equivalent to that of more populous colonies, whose combs, as a whole, are being turned over more quickly. Again, this conclusion is not satisfactory, but the dynamics of the termites and the fungus combs are too poorly understood to discuss the matter further.

TABLE 3.2.10 Mound size, population size and estimated age of 19 *Macrotermes bellicosus* colonies.

| COLONY NO. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MOUND HEIGHT (m) | 0 | .15 | .36 | .49 | .60 | .70 | .90 | .95 | 1.30 | 1.45 | 1.50 | 1.85 | 2.58 | 2.67 | 3.00 | 3.50 | 3.55 | 4.40 | 5.79 |
| MOUND CIRCUMFERENCE m | 0 | .65 | 1.20 | 1.52 | 1.72 | 2.80 | 1.20 | 2.90 | 2.70 | 5.00 | 3.20 | 4.15 | 5.20 | 5.00 | 5.27 | 5.25 | 6.80 | 9.55 | 8.50 |
| MOUND WIDTH (m) | 0 | .20 | .38 | .52 | .60 | .80 | .76 | .90 | 1.00 | 1.15 | 1.20 | 1.26 | 1.68 | 1.56 | 1.66 | 1.80 | 2.34 | 3.00 | 2.86 |
| MEAN MOUND ARC (m) | 0 | — | .76 | 1.14 | 1.435 | 1.76 | 1.875 | 2.175 | 2.575 | 2.025 | 3.225 | 3.70 | 5.30 | 5.575 | 6.325 | 7.25 | 7.175 | — | — |
| HABITACLE HEIGHT (m) | .22 | .37 | .45 | .38 | .45 | .55 | .50 | — | .80 | — | .70 | .80 | .95 | .80 | .75 | 1.00 | 1.00 | 1.70 | 1.35 |
| HABITACLE WIDTH (m) | .19 | .26 | .34 | .28 | .48 | .37 | .70 | — | .90 | — | .85 | 1.08 | 1.25 | 1.10 | 1.30 | .80 | 1.70 | 2.85 | 2.50 |
| MOUND VOLUME (x1000cc) | 0 | 1.555 | 13.475 | 34.348 | 55.99 | 116.128 | 134.75 | 201.48 | 336.98 | 502.10 | 559.90 | 761.33 | 1,888 | 1,684 | 2,143 | 2,970 | 5,039 | 10369 | 12276 |
| ESTIMATED AGE, (YEARS) | 0.6 | 1.15 | 1.90 | 2.25 | 2.60 | 2.90 | 3.45 | 3.60 | 4.50 | 4.85 | 4.95 | 5.75 | 7.40 | 7.57 | 8.39 | 9.75 | 9.90 | 15.50 | ? |
| STERILE CASTES POPULATION, (TOTAL) | 9476 | 38070 | 63272 | 55530 | 112242 | 143255 | 371234 | 235497 | 418440 | 409776 | 798318 | 554801 | 520261 | 512580 | 471189 | 717315 | 360765 | 481120 | 526327 |
| ln STERILE CASTES POPULATION | 9.1565 | 10.5472 | 11.0552 | 10.9247 | 11.6284 | 11.8724 | 12.8246 | 12.3695 | 12.9443 | 12.9234 | 13.5903 | 13.2264 | | | | | | | |

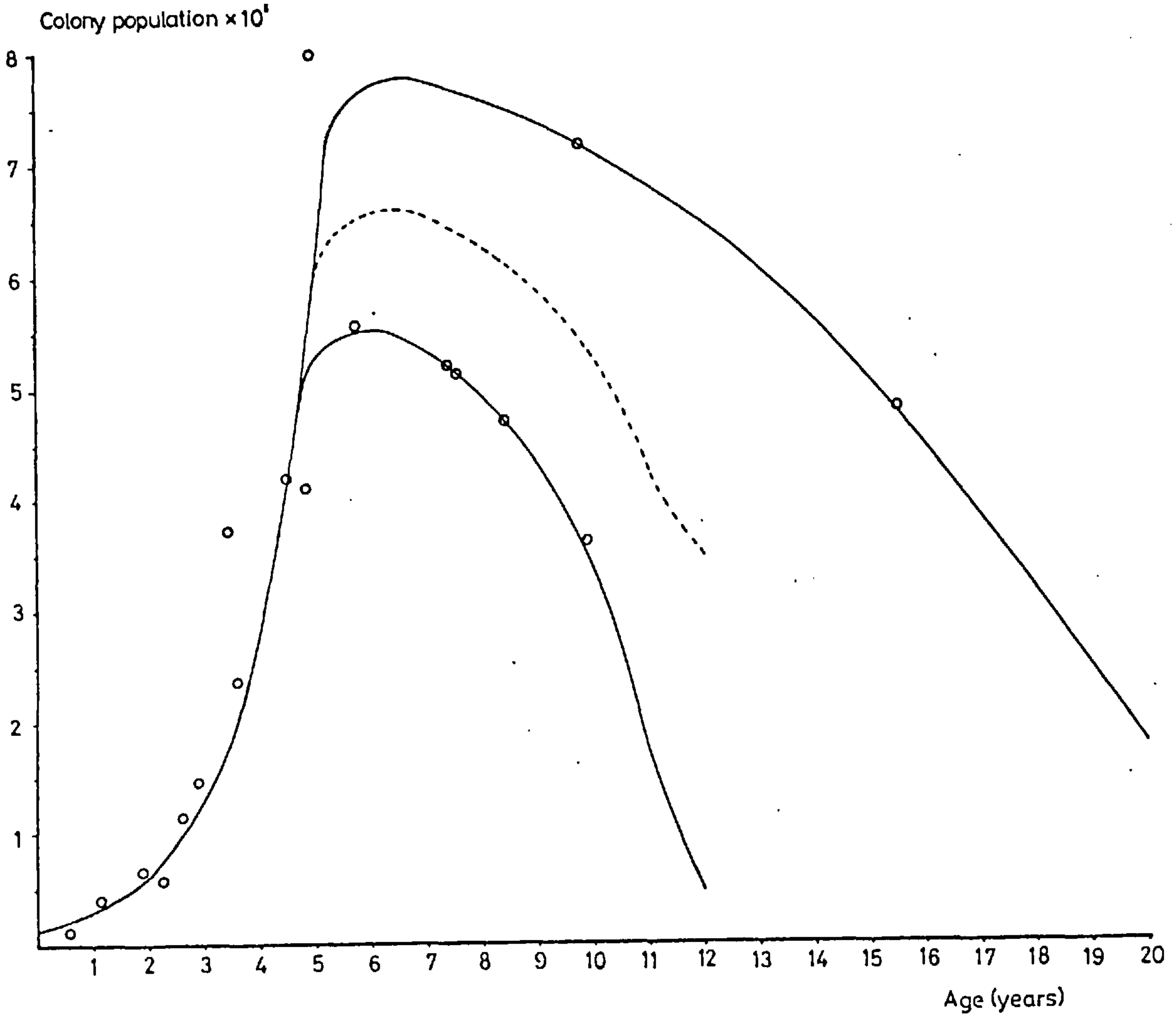


FIGURE 3.2.7 A model for Macrotermes bellicosus colony growth, developed from assessments of the population of 18 colonies. The dashed line represents a "mean decline curve", used for the purposes of extrapolation.

TABLE 3.2.11 The fitting of a curve to the high point decline data

| ESTIMATED POPULATION | AGE YEARS, t | $\frac{Nt}{Nt+1}$ | $\ln \ln \frac{Nt}{Nt+1}$ |
|---|---|---|---|
| 788,000 | 6 | 1.0168 | -4.0962 |
| 775,000 | 7 | 1.0238 | -3.7508 |
| 757,000 | 8 | 1.0299 | -3.5236 |
| 735,000 | 9 | 1.0352 | -3.3637 |
| 710,000 | 10 | 1.0440 | -3.2130 |
| 682,000 | 11 | 1.0541 | -2.9435 |
| 647,000 | 12 | 1.0607 | -2.8321 |
| 610,000 | 13 | 1.0796 | -2.5687 |
| 565,000 | 14 | 1.1078 | -2.2787 |
| 510,000 | 15 | 1.1461 | -1.9926 |
| 445,000 | 16 | | |

Estimated population data from fitting a curve through the high point decline data by eye.

Linear regression: $\ln \ln \frac{Nt}{Nt+1} = 0.2174\ t - 5.3393$ , $r = 0.9952$

| Year (t) | Best fit $\ln \ln \frac{Nt}{Nt+1}$ | $\frac{Nt}{Nt+1}$ | Best fit Nt |
|---|---|---|---|
| 0 | -5.3393 | 1.0048 | 830475 |
| 1 | -5.1219 | 1.0060 | 826507 |
| 2 | -4.9044 | 1.0074 | 821578 |
| 3 | -4.6870 | 1.0093 | 815543 |
| 4 | -4.4696 | 1.0115 | 808028 |
| 5 | -4.2522 | 1.0143 | 798842 |
| 6 | -4.0347 | 1.0178 | 787579 |
| 7 | -3.8173 | 1.0222 | 773805 |
| 8 | -3.5999 | 1.0277 | 757000 |
| 9 | -3.3824 | 1.0345 | 736596 |
| 10 | -3.1650 | 1.0431 | 712031 |
| 11 | -2.9476 | 1.0539 | 682611 |
| 12 | -2.7301 | 1.0674 | 647700 |
| 13 | -2.5127 | 1.0844 | 606801 |
| 14 | -2.2953 | 1.1060 | 559573 |
| 15 | -2.0779 | 1.1334 | 505943 |
| 16 | -1.8604 | 1.1684 | 446394 |
| 17 | -1.6430 | 1.2134 | 382056 |
| 18 | -1.4256 | 1.2717 | 314864 |
| 19 | -1.2081 | 1.3482 | 247593 |
| 20 | -0.9907 | 1.4496 | 183647 |

$\frac{Nt}{Nt+1}$ solved for various ages and Nt iterated from starting point at age eight years.

TABLE 3.2.12 The fitting of a curve to the low point decline data.

| Estimated Population (N) | Year (t) | $\frac{Nt}{Nt+1}$ | ln ln $\frac{Nt}{Nt+1}$ |
|---|---|---|---|
| 560,000 | 6 | 1.0467 | - 3.0863 |
| 535,000 | 7 | 1.0808 | - 2.5548 |
| 495,000 | 8 | 1.1379 | - 2.0463 |
| 435,000 | 9 | 1.2609 | - 1.4619 |
| 345,000 | 10 | 1.5333 | - 0.8499 |
| 225,000 | 11 | | |

Estimated population data from fitting a curve through the low point decline data by eye.

Linear regression ln ln $\frac{Nt}{Nt+1}$ = 0.5566t - 6.4524, r = 0.9993

| Year (t) | Best fit ln ln $\frac{Nt}{Nt+1}$ | $\frac{Nt}{Nt+1}$ | Best fit Nt |
|---|---|---|---|
| 0 | -6.4524 | 1.0016 | 592,456 |
| 1 | -5.8958 | 1.0028 | 591,509 |
| 2 | -5.3393 | 1.0048 | 589,858 |
| 3 | -4.7827 | 1.0084 | 587,040 |
| 4 | -4.2261 | 1.0147 | 582,150 |
| 5 | -3.6696 | 1.0258 | 573,716 |
| 6 | -3.1130 | 1.0455 | 559,287 |
| 7 | -2.5564 | 1.0807 | 534,947 |
| 8 | -1.9998 | 1.1449 | 495,000 |
| 9 | -1.4433 | 1.2664 | 432,352 |
| 10 | -0.8867 | 1.5099 | 341,403 |
| 11 | -0.3301 | 2.0520 | 166,376 |
| 12 | -0.2264 | 3.5048 | 47,470 |

$\frac{Nt}{Nt+1}$ solved for various ages and Nt iterated from a starting point at age eight years.

### 3.2.3.4 Total Population Density of *Macrotermes bellicosus*

The relationship between the age of a colony and its number of inhabitants (Figure 3.2.7) can be used to estimate the abundance of individuals on the study area when the number of colonies in age/height ranks is known. These numbers have been given in Table 3.2.7 and the best fit for the means of the three censuses given in Table 3.2.8 and Figure 3.2.6. The relationship between height and age has been given in Figure 3.2.5.

In Table 3.2.13 these data have been brought together. For each age range a mean population has been estimated from Figure 3.2.7. For ranks on the growth curve the mean is taken as the mean of the populations at each end of the rank concerned. These calculations and the confidence limits for the predicted populations, are given in Table 3.2.14. For age ranks on the decline curves mean figures for both high and low curves are given along with a "mean curve" value. The mean curve, shown in Figure 3.2.7, follows the means of the Nt data from high and low curves. Colonies over 4m high are considered to be on the high decline curve. Colonies over 4.5m high could not be allocated to an age and their populations are taken to be the same as 4.0-4.5m mounds. 95% confidence limits have not been given for the decline curves for reasons stated earlier. From the product of the number of colonies at each rank and the mean population of these colonies, total populations on the study area have been estimated. Since there are four estimates of numbers of colonies (three censuses and the survivorship curve) and three estimates of population at each rank (high, mean and low decline curves), there are a total of 12 possible population estimates. However, the censuses give a more accurate estimate of populations on the study area and values from the survivorship curve are not given.

There was considerable variation between years, the mean curve population ha$^{-1}$ declining from 1,449,409 (1974) to 1,161,425 (1975) and 1,012,440 (1976). For the purposes of future calculations the mean of these values is used i.e. 1,207,758 inds. ha$^{-1}$. However, there were always a number of hypogeal colonies which were not a part of these censuses. Figure 3.2.5 suggests that colonies begin to grow epigeal mounds when 0.6 years old. The survivorship curve (Figure 3.2.6) suggests that there were at least 45 0.5 year colonies on the study area. This number is assumed to be present in all future calculations. The population curve (Figure 3.2.7) suggests that these colonies had populations of about 10,000 individuals, (the actual intercept is at 12,457, but this is clearly erroneous since at age 0 only the royal pair are present). Hence, the total population of termites in hypogeal nests is taken to be 450,000 6ha$^{-1}$. Thus the total population of neuter castes of Macrotermes bellicosus is equal to 1,282,758 inds. ha$^{-1}$.

Figure 3.2.8 shows histograms of the number of individuals in each rank, estimated from the mean curve population data of the three censuses and from the survivorship curve. In the histograms of the censuses there is considerable variation but in general they are similar to the survivorship curve which represents a general pattern that might emerge over a longer period of time or over a larger area. The comparatively large blocks in the 12-20 year period of the census figures represent a single colony and hence are probably unrepresentative.

The bulk of the population is noticeably concentrated in 1-1.5m, (4-7 year old), colonies. It is these colonies that are in their mature period and are believed to be producing many alates.

TABLE 3.2.13 Calculation of population estimates for the study area, excluding hypogeal colonies.

| HEIGHT RANGE (m) | AGE RANGE (YEARS) | MEAN POPULATION ESTIMATES USING: | | | NUMBER OF COLONIES ON THE STUDY AREA | | | TOTAL POPULATION ESTIMATE FROM 1974 CENSUS | | | TOTAL POPULATION ESTIMATE FROM 1975 CENSUS | | | TOTAL POPULATION ESTIMATE FROM 1976 CENSUS | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LOW CURVE | MEAN CURVE | HIGH CURVE | 1974 | 1975 | 1976 | LOW CURVE | MEAN CURVE | HIGH CURVE | LOW CURVE | MEAN CURVE | HIGH CURVE | LOW CURVE | MEAN CURVE | HIGH CURVE |
| 0 - 0.5 | 0.6 - 2.28 | 46,525 | 46,525 | 46,525 | 19 | 25 | 18 | 883975 | 883975 | 883975 | 1163125 | 1163125 | 1163125 | 837450 | 837450 | 837450 |
| 0.51 - 1.0 | 2.28 - 3.72 | 157,152 | 157,152 | 157,152 | 10 | 10 | 7 | 1571520 | 1571520 | 1571520 | 1571520 | 1571520 | 1571520 | 1100064 | 1100164 | 1100164 |
| 1.01 - 1.5 | 3.72 - 4.95 | 403,098 | 403,098 | 403,098 | 2 | 3 | 2 | 806196 | 806196 | 806196 | 1209294 | 1209294 | 1209294 | 806196 | 806196 | 806196 |
| 1.51 - 2.0 | 4.95 - 6.09 | 565,000 | 626,609 | 684,109 | 7 | 1 | 3 | 3955000 | 4386263 | 4788763 | 565000 | 626609 | 684109 | 1695000 | 1879827 | 2052327 |
| 2.01 - 2.5 | 6.09 - 7.2 | 541,000 | 659,500 | 779,000 | 0 | 3 | 0 | 0 | 0 | 0 | 1623000 | 1978500 | 2337000 | 0 | 0 | 0 |
| 2.51 - 3.0 | 7.2 - 8.4 | 499,000 | 629,000 | 761,500 | 1 | 0 | 0 | 499000 | 629000 | 761500 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3.01 - 3.5 | 8.4 - 9.75 | 419,500 | 577,500 | 734,500 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 419500 | 577500 | 734500 |
| 3.51 - 4.0 | 9.75 - 11.77 | 221,000 | 454,000 | 687,000 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 221000 | 454000 | 687000 |
| 4.01 - 4.5 | 11.77 - 20 | ← | ← | 419,500 | 1 | 0 | 1 | 419500 | 419500 | 419500 | 0 | 0 | 0 | 419500 | 419500 | 419500 |
| 4.51 - 5.0 | - | ← | ← | 419,500 | 0 | 1 | 0 | 0 | 0 | 0 | 419500 | 419500 | 419500 | 0 | 0 | 0 |
| 5.01 - 5.5 | - | ← | ← | 419,500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TOTALS (6 HECTARE) | | | | | 40 | 43 | 33 | 8135190 | 8696454 | 9231454 | 6551439 | 6968548 | 7384548 | 5498710 | 6074637 | 6637137 |
| TOTALS PER HECTARE | | | | | | | | 1355865 | 1449409 | 1538576 | 1091907 | 1161425 | 1230758 | 916452 | 1012440 | 1106190 |

TABLE 3.2.14 Mean populations, with confidence limits, for height ranks in the growth curve.

| HEIGHT RANK (m) | AGE FROM FIGURE 5 (YEARS) | ln N FROM TABLE | N | MEAN N | ln MEAN N (y) | AGE AT ln MEAN N (x) | 95% CONF. LIMITS OF ln N AT AGE x |
|---|---|---|---|---|---|---|---|
| 0 — | 0.6 | 9.8961 | 19,853 | | | | |
| | | | | 46525 | 10.7477 | 1.6966 | ± 1.04972 |
| 0.5 — | 2.28 | 11.2009 | 73,196 | | | | |
| | | | | 157,152 | 11.9650 | 3.2638 | ± 1.01259 |
| 1.0 — | 3.72 | 12.3193 | 223,977 | | | | |
| | | | | 403,098 | 12.9069 | 4.4766 | ± 1.03885 |
| 1.5 — | 4.95 | 13.2746 | 582,218 | | | | |
| | | | | 996,744 | 13.8122 | 5.6422 | ± 1.10635 |
| 2.0 | 6.09 | 14.1600 | 1,411,269 | | | | |

95% confidence limits of y (predicted) = $y_p \pm t\, S_R \sqrt{(1 + \frac{1}{n} + \frac{(xp - \bar{x})^2}{\Sigma x^2 - (\Sigma x)^2/n}}$ (Parker 1973)

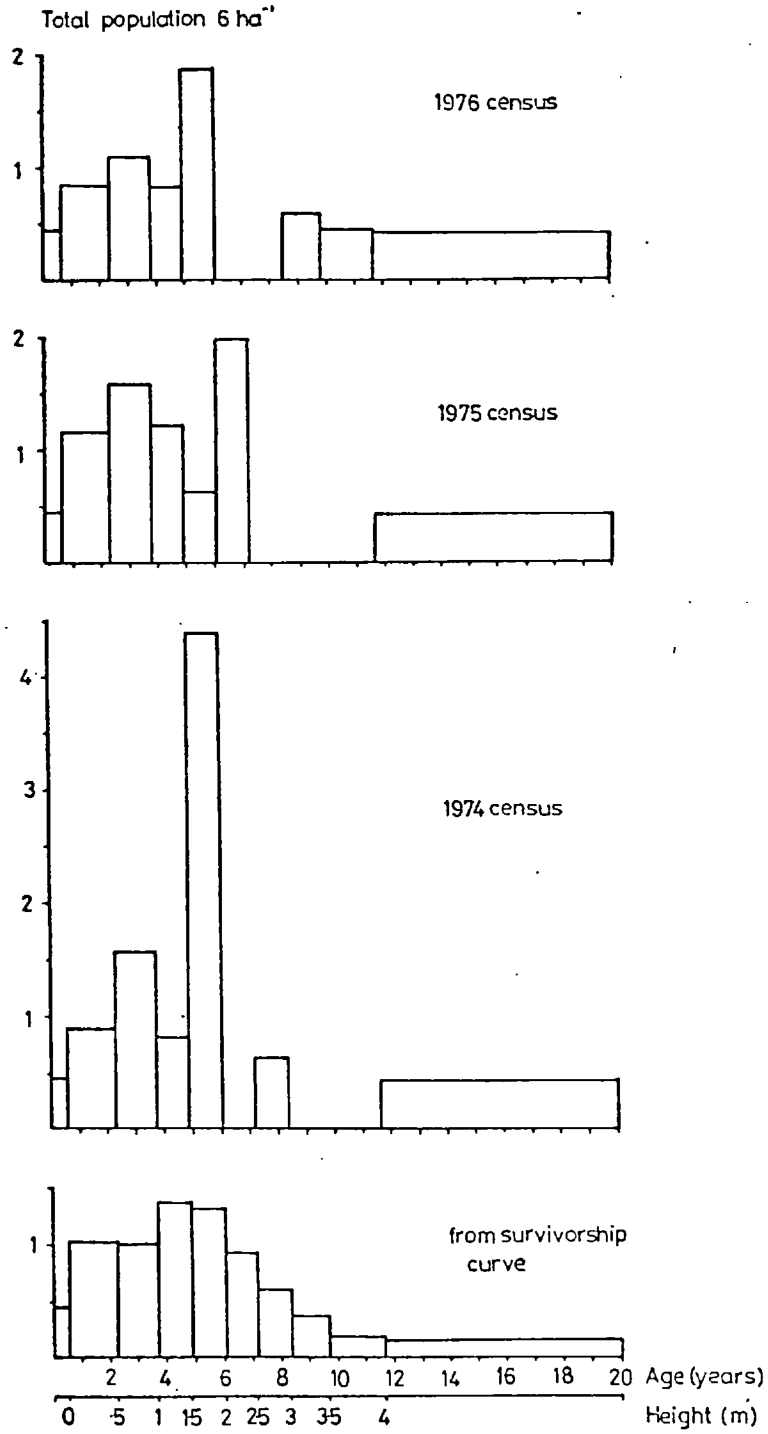


FIGURE 3.2.8 Populations of Macrotermes bellicosus at each height/age rank, as estimated from census data and the survivorship curve (Fig. 3.2.6).

### 3.2.3.5 Caste Composition in Macrotermes bellicosus Colonies

Numerical estimates of castes in 19 M. bellicosus colonies are given in Table 3.2.15 and as a percentage of total population in Table 3.2.16. The mean percentages given in Table 3.2.16 are correct for the sample but the sample has a biassed age range and does not conform with the age structure of colonies on the study area. Although it is theoretically possible, the means cannot be corrected by allowing for changes in caste proportion with age because of lack of replication and variable data.

However, Table 3.2.17 gives the mean percentage of workers + soldiers and larvae at three age ranges. In general these ranges apply to the juvenile, mature and senile growth periods, although the 15-20 year section has only two colonies, both of which were fairly active. Despite the fact that the data are few and variable, there appears to be a reduction in the proportion of larvae in the older colonies. Bodot (1966) reported similar findings in a study of Cubitermes severus. She was able to take a far larger sample of this species since it attains a colony size of only 50,000 individuals. The suggestion is that a reduction in larval proportion in old colonies may be a widespread phenomenon in the Termitidae.

Bodot (loc.cit) considered that the colonies with the largest numbers of individuals were the senescent ones in Cubitermes severus. This is clearly not the case with Macrotermes bellicosus. Figure 3.2.9 shows the number of workers + soldiers and larvae for the various colonies. As with the total population curve (Figure 3.2.7), larvae appear to approach a maximum number at around 5 years, and then decline. If colony 19 is assumed to be 20 years old then it adds weight to this suggestion. Workers + soldiers, however, appear to increase more gradually, the scatter is considerable but the old colonies (18 and 19) still have large populations, indeed colony 19 contained the highest worker + soldier population recorded. The tentative conclusion is that the worker + soldier population increases rapidly to around age five years then remains fairly constant or may increase slowly. The larval population also increases rapidly to age five years but then quickly declines.

TABLE 3.2.15 Population data from 19 colonies of *Macrotermes bellicosus*, divided into castes.

| COLONY NO. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HEIGHT (METRES) | 0 | 0.15 | 0.36 | 0.49 | 0.60 | 0.70 | 0.90 | 0.95 | 1.30 | 1.45 | 1.50 | 1.85 | 2.58 | 2.67 | 3.00 | 3.50 | 3.55 | 4.40 | 5.79 |
| ESTIMATED AGE (YEARS) | 0.6 | 1.15 | 1.90 | 2.25 | 2.60 | 2.90 | 3.45 | 3.60 | 4.50 | 4.85 | 4.95 | 5.75 | 7.40 | 7.57 | 8.39 | 9.75 | 9.90 | 15.50 | ? |
| POPULATION OF STERILE CASTES | 9476 | 38070 | 63272 | 55530 | 112242 | 143255 | 371234 | 235497 | 418440 | 409776 | 798318 | 554801 | 520261 | 512580 | 471189 | 717315 | 360765 | 481120 | 526327 |
| NUMBER OF MAJOR SOLDIERS | 109 | 63 | 177 | 377 | 357 | 925 | 343 | 2555 | 3124 | 2310 | 848 | 2037 | 1557 | 4200 | 4417 | 3045 | 1131 | 9600 | 6872 |
| NUMBER OF MINOR SOLDIERS | 142 | 389 | 646 | 508 | 908 | 1075 | 3965 | 3755 | 5571 | 6243 | 4239 | 3640 | 1521 | 2340 | 3699 | 2706 | 877 | 7840 | 9052 |
| NUMBER OF MAJOR WORKERS | 645 | 1672 | 9855 | 4576 | 10319 | 8321 | 34719 | 32263 | 44963 | 29645 | 84179 | 48707 | 24763 | 35820 | 59234 | 52826 | 12027 | 78400 | 157832 |
| NUMBER OF MINOR WORKERS | 1789 | 8574 | 15167 | 19450 | 26650 | 25542 | 109936 | 136108 | 141713 | 107360 | 246608 | 183171 | 61340 | 152760 | 175771 | 215856 | 27605 | 209200 | 252376 |
| NUMBER OF LARVAE | 6791 | 27372 | 37427 | 30619 | 74008 | 107393 | 222271 | 62432 | 223069 | 264220 | 462444 | 317246 | 431080 | 317460 | 227768 | 442882 | 318500 | 176080 | 100195 |

TABLE 3.2.16 Caste proportions in 19 *Macrotermes bellicosus* colonies, expressed as % of total population.

| COLONY NUMBER | ESTIM. AGE (YEARS) | % MAJOR SOLDIERS | % MINOR SOLDIERS | % MAJOR WORKERS | % MINOR WORKERS | % LARVAE | % SOLDIERS +WORKERS |
|---|---|---|---|---|---|---|---|
| 1 | 0.6 | 1.15 | 1.50 | 6.81 | 18.88 | 71.67 | 28.33 |
| 2 | 1.15 | 0.17 | 1.02 | 4.39 | 22.52 | 71.90 | 28.10 |
| 3 | 1.90 | 0.28 | 1.02 | 15.58 | 23.97 | 59.15 | 40.85 |
| 4 | 2.25 | 0.68 | 0.92 | 8.24 | 35.03 | 55.14 | 44.86 |
| 5 | 2.60 | 0.32 | 0.81 | 9.20 | 23.74 | 65.94 | 34.06 |
| 6 | 2.90 | 0.65 | 0.75 | 5.81 | 17.83 | 74.97 | 25.03 |
| 7 | 3.45 | 0.09 | 1.07 | 9.35 | 29.61 | 59.87 | 40.13 |
| 8 | 3.60 | 1.08 | 1.58 | 13.61 | 57.40 | 26.33 | 73.67 |
| 9 | 4.50 | 0.75 | 1.33 | 10.75 | 33.87 | 53.31 | 46.69 |
| 10 | 4.85 | 0.56 | 1.52 | 7.23 | 26.20 | 64.48 | 35.52 |
| 11 | 4.95 | 0.11 | 0.53 | 10.55 | 30.89 | 57.93 | 42.07 |
| 12 | 5.75 | 0.37 | 0.66 | 8.76 | 33.02 | 57.18 | 42.82 |
| 13 | 7.40 | 0.30 | 0.29 | 4.76 | 11.79 | 82.86 | 17.14 |
| 14 | 7.57 | 0.82 | 0.46 | 6.99 | 29.80 | 61.93 | 38.07 |
| 15 | 8.39 | 1.00 | 0.79 | 12.57 | 37.30 | 48.34 | 51.66 |
| 16 | 9.75 | 0.42 | 0.37 | 7.36 | 30.09 | 61.74 | 38.26 |
| 17 | 9.90 | 0.30 | 0.24 | 3.33 | 7.65 | 88.30 | 11.70 |
| 18 | 15.50 | 2.00 | 1.63 | 16.30 | 43.48 | 36.60 | 63.40 |
| 19 | ? | 1.31 | 1.72 | 29.99 | 47.95 | 19.04 | 80.96 |
| MEAN | | 0.65 | 0.96 | 10.08 | 29.53 | 58.77 | 41.23 |
| 95% CONF. LTS. | | ± 0.24 | ± 0.23 | ± 2.90 | ± 5.80 | ± 8.38 | ± 8.38 |

TABLE 3.2.17 The proportions of workers/soldiers and larvae at three age ranges.

| AGE RANGE (YEARS) | NUMBER OF COLONIES EXAMINED | MEAN % WORKERS & SOLDIERS | MEAN % LARVAE | AVERAGE POPULATION |
|---|---|---|---|---|
| 0 - 4 | 8 (1-8) | 39.38 | 60.62 | 128,572 |
| 4.5 - 10 | 9 (9-17) | 35.99 | 64.01 | 529,272 |
| 15 - 20 | 2 (18-19) | 72.18 | 27.82 | 503,724 |

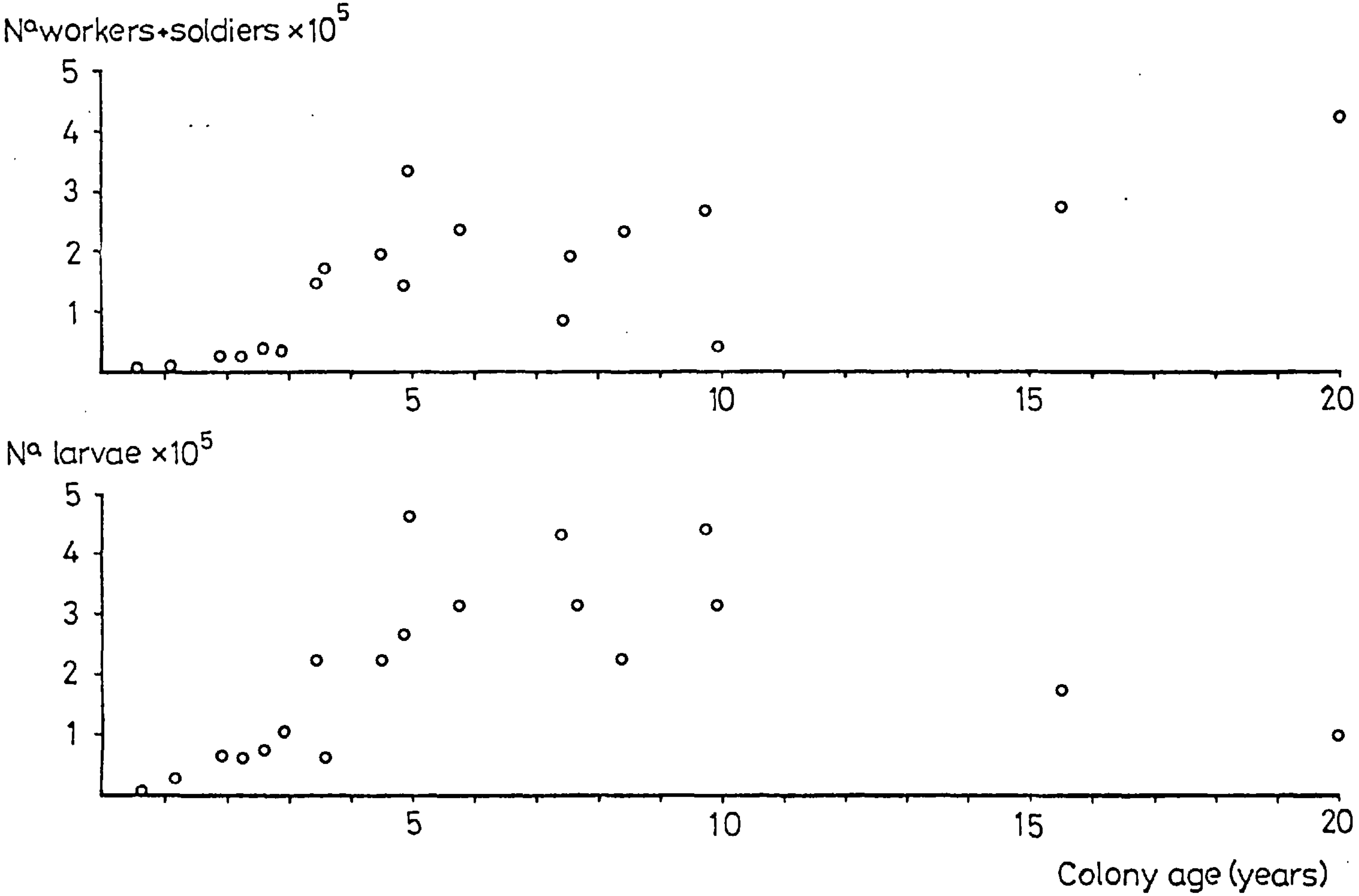


FIGURE 3.2.9 The number of workers + soldiers and larvae in 19 *Macrotermes bellicosus* colonies of various ages.

### 3.2.3.6 Biomass of *M. bellicosus* Castes, Total Biomass Estimates for the Colonies Sampled and Estimates of Area-specific Biomass.

Table 3.2.18 gives estimates of individual wet and dry weight for neuter castes from six spiral plate type *M. bellicosus* colonies. Sample size varied for each colony but all nests have been given equal weighting in calculation of means. Colony F dry weights were estimated from the mean percentage dry weights of the other colonies. These data have been used to calculate the wet weight biomass of each caste, and the total biomass, of the 19 colonies sampled (Table 3.2.19). Numbers of each caste were given in Table 3.2.15. Log biomass correlates significantly with log population in a linear regression analysis: (log wet weight biomass = $1.02656 \cdot$ log population $- 2.6064$,) correlation coefficient (r) = 0.9899, see Table 3.2.19 for further analysis. This relationship has been used to predict the biomass of colonies at each height/age rank using mean curve population data from Table 3.2.13.

Predicted values of biomass for each height rank (with confidence limits), the number of colonies present at each census and the total estimated biomass for each height range for each year of the census, are given in Table 3.2.20. Note that the estimated 45 hypogeal colonies have been included. The mean value for the three censuses is used in further calculations, i.e.:

Total wet weight biomass of *M. bellicosus* neuter castes = 4442.54 g ha$^{-1}$.

By predicting the biomass in this way, it has been possible to avoid the use of values of the mean caste composition given in Table 3.2.16. This is desirable since the 19 colonies sacrificed had a different age structure from that within the study area. The method still has the drawback that no distinction can be made between the biomass of the juvenile and the senescent colonies, which numerically may be identical, but have very different caste compositions and therefore dissimilar biomass, (e.g. colonies 13 and 19, Table 3.2.19). The error involved here is unavoidable without more data on caste composition.

The alternative method for estimating biomass is to calculate the biomass of 100 individuals of mean caste composition as in Table 3.2.16 and biomass as in Table 3.2.18 (shown in Table 3.2.24 column 4). This is equal to 349.185 mg. The population on the study area was estimated as 1,282,758 $ha^{-1}$, so the total biomass is 1,282,758 ÷ 100 x 349.185 mg i.e. 4479.198 g $ha^{-1}$. This estimate is clearly similar to the previous one.

My data on alate production are few, only two of the colonies sampled containing alates. Colony 9 contained 16,216 alate nymphs (3.875% of neuter caste population) and colony 18, 15,440 alates and alate nymphs (3.209%), with a mean value of 3.542%. As discussed later, I consider that only colonies older than about four years produce alates. Assuming that all colonies in height ranks greater than 1m are able to produce alates at 3.542% of the neuter population in each year, the expected alate production can be calculated from Table 3.2.13. The population of neuters in colonies of that size (mean curve values) on the study area in 1974-1976 were 6,240,959, 4,233,903 and 4,137,023 respectively, with a mean of 4,870,628 or 811,711.4 $ha^{-1}$. Alate production is estimated at 3.542% of this, i.e. 28752.9 alates $ha^{-1}a^{-1}$.

The biomass of individual alates has been estimated from 20 adult specimens at 77.20 mg. Lepage (1974, p.202), estimated the dry wt : wet wt biomass for alates at 0.4678 (*Macrotermes subhyalinus*), and this value will be used here. Hence the annual production of alates on the study area can be estimated as 2219.73 g $ha^{-1}$ wet weight and 1038.31 g $ha^{-1}$ dry weight.

In calculating an annual mean biomass for all *M. bellicosus* castes, the observations that individual alates are only present in the nest for about three months of the year, and grow from a biomass of 0 to 77.2 mg during that period, must be considered. The mean biomass of alates over a whole year is thus 2219.73 x 0.25 x 0.5, i.e. 277.47 g ha$^{-1}$ wet weight, 129.79 g ha$^{-1}$ dry weight. Hence, the total mean biomass of all *M. bellicosus* castes can be calculated from neuter caste biomass plus mean (over the year) alate biomass, i.e.:

Annual mean biomass of *M. bellicosus* neuters + alates = 4720.01 g ha$^{-1}$ wet weight.

This figure will be used later (Section 3.3) in calculations of annual mean weight-specific consumption rates.

TABLE 3.2.18 Biomass of *Macrotermes bellicosus* castes.

| | MAJOR SOLDIERS | | | | MINOR SOLDIERS | | | | MAJOR WORKERS | | | | MINOR WORKERS | | | | LARVAE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ind. wet wt | Ind. dry wt | % Dry | Sample size | Ind. wet wt. | Ind. dry wt | % Dry | Sample size | Ind. wet wt. | Ind. dry wt | % Dry | Sample size | Ind. wet wt. | Ind. dry wt | % Dry | Sample size | Ind. wet wt | Ind. dry wt | % Dry | Sample size |
| A | 30.640 | 11.520 | 37.60 | 25 | 5.330 | 1.147 | 21.50 | 75 | 9.038 | 3.368 | 37.26 | 500 | 3.564 | 0.920 | 25.81 | 500 | 1.766 | 0.353 | 19.98 | 516 |
| B | 27.685 | 6.50 | 23.50 | 200 | 5.560 | 1.15 | 20.68 | 100 | 8.805 | 2.88 | 32.71 | 200 | 3.045 | 0.875 | 28.74 | 200 | 2.513 | 0.325 | 12.933 | 600 |
| C | 34.930 | 8.77 | 25.107 | 100 | 6.950 | 1.76 | 25.324 | 100 | 8.440 | 2.376 | 28.152 | 250 | 4.132 | 1.072 | 25.944 | 250 | 1.308 | 0.193 | 14.755 | 1443 |
| D | 27.350 | 7.135 | 26.088 | 200 | 6.350 | 1.68 | 26.457 | 100 | 6.643 | 2.015 | 30.333 | 1,000 | 3.015 | 0.833 | 27.612 | 400 | - | - | - | - |
| E | 35.065 | 7.82 | 22.30 | 200 | 6.660 | 1.20 | 18.02 | 50 | - | - | - | - | 4.100 | 0.800 | 19.50 | 100 | - | - | - | - |
| F | 40.323 | 10.855 | 26.919 | 72 | 9.144 | 2.048 | 22.396 | 68 | 7.494 | 2.407 | 32.114 | 144 | 6.070 | 1.549 | 25.521 | 240 | 2.738 | 0.435 | 15.889 | 360 |
| MEANS | 32.666 | 8.767 | 26.837 | | 6.666 | 1.498 | 22.465 | | 8.084 | 2.609 | 32.274 | | 3.988 | 1.008 | 25.280 | | 2.081 | 0.327 | 15.690 | |

TABLE 3.2.19 Calculation of biomass estimates for the 19 colonies sacrificed for population studies, with results for a linear regression analysis of log biomass against log population.

| COLONY NUMBER | POPULATION | LOG POPULATION (x) | WET WT. BIOMASS (GRAMMES) | | | | | TOTAL BIOMASS g | LOG TOTAL BIOMASS |
|---|---|---|---|---|---|---|---|---|---|
| | | | MAJOR SOLDIERS | MINOR SOLDIERS | MAJOR WORKERS | MINOR WORKERS | LARVAE | | |
| 1 | 9476 | 3.9766 | 3.561 | 0.947 | 5.214 | 7.135 | 14.132 | 30.989 | 1.4912 |
| 2 | 38070 | 4.5806 | 2.058 | 2.593 | 13.516 | 34.193 | 56.961 | 109.321 | 2.0387 |
| 3 | 63272 | 4.8012 | 5.782 | 4.306 | 79.668 | 60.484 | 77.886 | 228.128 | 2.3582 |
| 4 | 55530 | 4.7445 | 12.315 | 3.386 | 36.992 | 77.567 | 63.718 | 193.978 | 2.2878 |
| 5 | 112242 | 5.0500 | 11.662 | 6.053 | 83.419 | 106.280 | 154.011 | 361.425 | 2.5580 |
| 6 | 143255 | 5.1562 | 30.216 | 7.166 | 67.267 | 101.861 | 223.485 | 429.995 | 2.6335 |
| 7 | 371234 | 5.5696 | 11.204 | 26.431 | 280.668 | 438.425 | 462.546 | 1,219.274 | 3.0861 |
| 8 | 235497 | 5.3720 | 83.462 | 25.031 | 260.814 | 542.799 | 129.921 | 1,042.027 | 3.0179 |
| 9 | 418440 | 5.6216 | 102.049 | 37.136 | 363.481 | 565.151 | 464.207 | 1,532.024 | 3.1853 |
| 10 | 409776 | 5.6126 | 75.458 | 41.616 | 239.650 | 428.152 | 549.842 | 1,334.718 | 3.1254 |
| 11 | 798318 | 5.9022 | 27.701 | 28.257 | 680.503 | 983.473 | 962.346 | 2,682.280 | 3.4285 |
| 12 | 554801 | 5.7441 | 66.541 | 24.264 | 393.747 | 730.486 | 660.189 | 1,875.227 | 3.2731 |
| 13 | 520261 | 5.7162 | 50.861 | 10.139 | 200.184 | 244.624 | 897.077 | 1,402.885 | 3.1470 |
| 14 | 512580 | 5.7098 | 137.197 | 15.598 | 289.569 | 609.207 | 660.634 | 1,712.205 | 3.2336 |
| 15 | 471189 | 5.6732 | 144.286 | 24.658 | 478.848 | 700.975 | 473.985 | 1,822.752 | 3.2607 |
| 16 | 717315 | 5.8557 | 99.468 | 18.038 | 427.045 | 860.834 | 921.637 | 2,327.022 | 3.3668 |
| 17 | 360765 | 5.5573 | 36.945 | 5.846 | 97.226 | 110.089 | 662.799 | 912.905 | 2.9604 |
| 18 | 481120 | 5.6822 | 313.594 | 52.261 | 633.786 | 834.290 | 366.422 | 2,200.353 | 3.3425 |
| 19 | 526327 | 5.7212 | 224.481 | 60.341 | 1,275.914 | 1,006.475 | 208.506 | 2,775.717 | 3.4434 |

Regression of log biomass (y) against log population (x):

$$y = 1.0266 \cdot x - 2.6064$$

Correlation coefficient (r) = 0.9899

F value = 832.28

Standard error = .07822

T value for slope = 28.849

T value for intercept = -13.5778

TABLE 3.2.20 Biomass calculations for all colonies on the study area in the three censuses.

| HEIGHT RANGE (m) | POPULATION ESTIMATED FROM MEAN GROWTH CURVE (FIG. 3.2.7. ) | LOG ESTIMATED POPULATION | ESTIMATED LOG BIOMASS (TABLE 3.2.19.) | ± 95% CONFIDENCE LIMITS OF BIOMASS ESTIMATE | ESTIMATED BIOMASS g (WET WEIGHT) | NUMBER OF COLONIES ON THE STUDY AREA | | | TOTAL ESTIMATED BIOMASS FOR COLONIES ON THE STUDY AREA (g f.w.) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1974 | 1975 | 1976 | 1974 | 1975 | 1976 |
| HYPOGEAL | 10,000 | 4.000 | 1.4999 | ±.19816 | 31.6183 | 45 | 45 | 45 | 1422.825 | 1422.825 | 1422.825 |
| 0-0.5 | 46,525 | 4.6677 | 2.1854 | ±.17737 | 153.2413 | 19 | 25 | 18 | 2911.585 | 3831.032 | 2758.343 |
| 0.51-1.0 | 157,152 | 5.1963 | 2.7281 | ±.16984 | 534.642 | 10 | 10 | 7 | 5346.422 | 5346.422 | 3742.496 |
| 1.01-1.5 | 403,098 | 5.6054 | 3.1480 | ±.17024 | 1406.144 | 2 | 3 | 2 | 2812.288 | 4218.432 | 2812.288 |
| 1.51-2.0 | 626,609 | 5.7970 | 3.3447 | ±.17233 | 2211.613 | 7 | 1 | 3 | 15481.293 | 2211.613 | 6634.850 |
| 2.01-2.5 | 659,500 | 5.8192 | 3.3675 | ±.17264 | 2330.870 | 0 | 3 | 0 | 0 | 6992.610 | 0 |
| 2.51-3.0 | 629,000 | 5.7987 | 3.3464 | ±.17235 | 2220.277 | 1 | 0 | 0 | 2220.277 | 0 | 0 |
| 3.01-3.5 | 577,500 | 5.7616 | 3.3083 | ±.17185 | 2033.8656 | 0 | 0 | 1 | 0 | 0 | 2033.8656 |
| 3.51-4.0 | 454,000 | 5.6571 | 3.2010 | ±.17069 | 1588.723 | 0 | 0 | 1 | 0 | 0 | 1588.723 |
| 4.01-4.5 | 419,500 | 5.6227 | 3.1658 | ±.17038 | 1464.912 | 1 | 0 | 1 | 1464.912 | 0 | 1464.912 |
| 4.51-5.0 | 419,500 | 5.6227 | 3.1658 | ±.17038 | 1464.912 | 0 | 1 | 0 | 0 | 1464.912 | 0 |
| TOTALS 6 $ha^{-1}$ | | | | | | | | | 31659.602 | 25487.846 | 22458.293 |
| TOTALS $ha^{-1}$ | | | | | | | | | 5276.600 | 4247.974 | 3743.049 |

95% confidence limits of biomass estimates from

$$y \pm t\, s_R \sqrt{\left(1+\frac{1}{n} + \frac{(xp-\bar{x})^2}{\Sigma x^2-(\Sigma x)^2/}\right.}$$

(Parker 1973)

where $S_R = 0.078219469$

$t = 2.110$

$\Sigma x^2 - (\Sigma x)^2/n = 4.8318$

$\bar{x} = 5.370884210$

### 3.2.3.7 Food Stores

As described in Section 3.1, the food stores consist of finely comminuted plant material stored in masses on top of the endoecie, above the fungus combs. Table 3.2.21 shows the weights of food stores found in 16 M. bellicosus nests and gives statistical data for the relationship between log food stores (y) and mound height (x). The two variables have been found to be best described by the linear relationship:

$$y = 0.3241 \cdot x - 0.6993$$

with $r = 0.8091$ , $p < 0.001$.

In Table 3.2.22, this relationship has been used to predict mean food store weights for nests of each height range. Confidence limits have been given and it is clear that despite the good correlation, the scatter of points is considerable. This is probably caused by seasonal variation in feeding, which cannot be accurately quantified from the available data. Table 3.2.22 shows the mean standing crop of food stores for the three years to be 4.6150 kg $ha^{-1}$. The estimated 45 hypogeal colonies have been included in this table and their individual food store weights estimated as 150 g per nest.

There is little published information concerning food stores in this species and their precise function is unknown. It is assumed that foragers returning from a food source deposit their food on the stores for distribution to other individuals at a later date. During the interval, the stores may undergo some biological degradation, or absorb moisture, which makes them more palatable. There are no data available for the rate of turnover of food stores.

During the course of a study on the turnover rate of fungus combs in the rainy season of 1975 I provided a small M. bellicosus colony with a number of baits made of sawdust and gum. The diluted gum was mixed with a concentrated solution of neutral red dye prior to mixing with the sawdust. These baits were readily taken by the termites and the nest was removed for examination two weeks after the baits were removed. There were still pieces of red sawdust mixed in with the food stores. It can be concluded from this experiment that food may remain in the food stores for up to two weeks. The baiting procedure undoubtedly led to high foraging rates and a build-up of food stores, hence the figure may be a maximum. In addition, some food is eaten immediately by foragers and would never reach the food stores. From the few data available I therefore suggest that the mean turnover rate for food stores is 1-2 weeks, and probably one week to 10 days.

Given the mean standing crop of food stores (4.615 kg ha$^{-1}$), and their turnover rate, the total annual consumption can be calculated as follows:

| Turnover rate | Store standing crop | Estimated consumption |
|---|---|---|
| 7 days | 4.615 kg ha$^{-1}$ | 239.982 kg ha$^{-1}$ a$^{-1}$ |
| 10 days | 4.615 kg ha$^{-1}$ | 168.449 kg ha$^{-1}$ a$^{-1}$ |
| 14 days | 4.615 kg ha$^{-1}$ | 119.991 kg ha$^{-1}$ a$^{-1}$ |

The baiting method described in Section 2.4 suggested that consumption was 240.518 kg ha$^{-1}$ a$^{-1}$, which is similar to the consumption calculated for a food store turnover rate of one week.

The conclusions are two-fold, firstly the results in general support the consumption data from baiting and secondly, they suggest that all or almost all the food gathered, passes through the food stores. The period spent in the food stores probably increases the palatability of the food by microbial decay and/or humidification by metabolic water from the fungus combs.

TABLE 3.2.21 The weight of food stores in 16 nests of *Macrotermes bellicosus* and its correlation with mound size.

| COLONY NO. | HEIGHT, m (x) | ESTIMATED AGE, YEARS | WEIGHT OF FOOD STORES, kg | LOG WEIGHT OF FOOD STORES kg (y) |
|---|---|---|---|---|
| 1 | 0 | 0.6 | 0.067 | -1.1739 |
| 2 | 0.15 | 1.15 | 0.289 | -0.5391 |
| 3 | 0.36 | 1.90 | . | . |
| 4 | 0.49 | 2.25 | 0.120 | -0.9208 |
| 5 | 0.60 | 2.60 | 0.279 | -0.5544 |
| 6 | 0.70 | 2.90 | 0.445 | -0.3518 |
| 7 | 0.90 | 3.45 | 0.390 | -0.4089 |
| 8 | 0.95 | 3.60 | . | . |
| 9 | 1.30 | 4.50 | . | . |
| 10 | 1.45 | 4.85 | 1.638 | 0.2143 |
| 11 | 1.50 | 4.95 | 2.08 | 0.3181 |
| 12 | 1.85 | 5.75 | 4.226 | 0.6259 |
| 13 | 2.58 | 7.40 | 0.610 | -0.2147 |
| 14 | 2.67 | 7.57 | 0.861 | -0.0915 |
| 15 | 3.00 | 8.39 | 1.438 | 0.1577 |
| 16 | 3.50 | 9.75 | 0.500 | -0.3010 |
| 17 | 3.55 | 9.90 | 3.184 | 0.5030 |
| 18 | 4.40 | 15.50 | 13.170 | 1.1196 |
| 19 | 5.79 | ? | 14.703 | 1.1673 |

Linear regression analysis of log wt. of food stores (y) against mound height (x)

$\log y = 0.3241.x - 0.6993$

Correlation coefficient = 0.8091

F value = 26.5376

Standard error = 0.4059

T value for slope = 5.1515

T value for intercept = -4.2345

TABLE 3.2.22 Calculation of area-specific food store weights for three census years.

| HEIGHT RANGE m | MEAN OF HEIGHT RANGE m | ESTIMATED LOG WEIGHT OF FOOD STORES | ±95% CONFIDENCE LIMITS OF ESTIMATES | ESTIMATED WEIGHT OF FOOD STORES kg | NUMBER OF COLONIES ON THE STUDY AREA | | | TOTAL ESTIMATED WEIGHT OF FOOD STORES FOR COLONIES ON THE STUDY AREA | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 1974 | 1975 | 1976 | 1974 | 1975 | 1976 |
| HYPOGEAL | - | | | 0.150 | 45 | 45 | 45 | 6.7500 | 6.7500 | 6.7500 |
| 0-0.5 | 0.25 | -0.61829 | ±.93057 | 0.24083 | 19 | 25 | 18 | 4.5758 | 6.0207 | 4.3349 |
| 0.51-1.0 | 0.75 | -0.45622 | ±.91507 | 0.34977 | 10 | 10 | 7 | 3.4977 | 3.4977 | 2.4484 |
| 1.01-1.5 | 1.25 | -0.29414 | ±.90435 | 0.50799 | 2 | 3 | 2 | 1.0160 | 1.5240 | 1.0160 |
| 1.51-2.0 | 1.75 | -0.13207 | ±.89858 | 0.73779 | 7 | 1 | 3 | 5.1645 | 0.7378 | 2.2134 |
| 2.01-2.5 | 2.25 | 0.03001 | ±.89787 | 1.07154 | 0 | 3 | 0 | 0 | 3.2146 | 0 |
| 2.51-3.0 | 2.75 | 0.19208 | ±.90221 | 1.55626 | 1 | 0 | 0 | 1.5563 | 0 | 0 |
| 3.01-3.5 | 3.25 | 0.35415 | ±.91155 | 2.26024 | 0 | 0 | 1 | 0 | 0 | 2.2602 |
| 3.51-4.0 | 3.75 | 0.51623 | ±.92572 | 3.28268 | 0 | 0 | 1 | 0 | 0 | 3.2827 |
| 4.01-4.5 | 4.25 | 0.67830 | ±.94451 | 4.76764 | 1 | 0 | 1 | 4.7676 | 0 | 4.7676 |
| 4.51-5.0 | 4.75 | 0.84038 | ±.96766 | 6.92432 | 0 | 1 | 0 | 0 | 6.9243 | 0 |
| TOTALS 6 $ha^{-1}$ | | | | | | | | 27.3279 | 28.6691 | 27.0732 |
| TOTALS $ha^{-1}$ | | | | | | | | 4.5547 | 4.7782 | 4.5122 |

95% confidence limits for food estimates from:-

$$yp \pm t\, s_R \sqrt{\left(1+\frac{1}{n} + \frac{(xp - \overline{x})^2}{x^2 - (\ x)^2/n}\right)}$$

where $S_R = 0.405940757$

$t = 2.145$

$\Sigma x^2 - (\Sigma x)^2/n = 41.62$

$\overline{x} = 2.070625$

### 3.2.3.8 Calorific Values for Individuals of each Caste and Estimates of Calorific Equivalents of Populations.

Estimates of the calorific equivalent per gramme of each of the neuter and alate castes are given in Table 3.2.23.

In applying these data to the biomass of M. bellicosus per hectare it has been necessary to use the mean caste proportions estimated from the 19 colonies sacrificed. Table 3.2.24 shows how the biomass for each caste per 100 "random" neuter caste individuals has been calculated and the proportions assigned to the total biomass per hectare. These figures have been converted to dry weight (from Table 3.2.18) and the total calorific equivalent of the neuter caste biomass of 1043.56 g $ha^{-1}$, (dry weight) calculated as 4808.94 k cal $ha^{-1}$. The total annual production of alates of 28752.9 $ha^{-1}$ $a^{-1}$ (1038.31 g $ha^{-1}$ d.w., Section 3.2.3.6) is equivalent to 7985.54 k cal $ha^{-1}$ $a^{-1}$. The mean annual standing crop of alates in nests of 129.79 g $ha^{-1}$ (d.w.) is equivalent to 998.20 k cal $ha^{-1}$. Hence the annual mean standing crop biomass of neuter plus alate castes of M. bellicosus (1173.35 g $ha^{-1}$, d.w.) is equivalent to 5807.15 k cal $ha^{-1}$.

TABLE 3.2.23 Results of calorific equivalent estimations for neuter and alate castes of *Macrotermes bellicosus*

| CASTE | CALORIFIC EQUIVALENT ESTIMATIONS kcal $g^{-1}$ (DRY WT.) | | | | | MEAN kcal $g^{-1}$ d.w. | 95% CONFIDENCE LIMITS |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | | |
| MAJOR SOLDIER | 5.049 | 5.015 | 5.037 | 4.927 | 5.067 | 5.0190 | ±0.0680 |
| MINOR SOLDIER | 4.531 | 5.209 | 4.923 | 4.711 | 4.785 | 4.8318 | ±0.3152 |
| MAJOR WORKER | 4.894 | 4.637 | 5.049 | 4.883 | 4.496 | 4.7918 | ±0.2751 |
| MINOR WORKER | 4.226 | 4.721 | 4.568 | 4.084 | 4.217 | 4.3632 | ±0.3332 |
| LARVAE | 4.423 | 4.558 | 4.607 | 4.482 | 4.920 | 4.5980 | ±0.2400 |
| ALATES | 7.8222 | 7.8422 | 7.5645 | 7.7404 | 7.4852 | 7.6909 | ±0.1971 |

TABLE 3.2.24 Calculations of biomass ha$^{-1}$ of each caste and the calorific equivalents.

|  | CASTE PROPORTION % (CP) | INDIVIDUAL BIOMASS (IB) mg | CP x IB (BIOMASS/CASTE/100 INDIVIDUALS) | BIOMASS PROPORTION (BP) = $\frac{\text{CP x IB}}{\text{(CP x IB)}}$ | BP x TOTAL BIOMASS ha$^{-1}$(=BP ha$^{-1}$) | BP ha$^{-1}$ x % DRY FROM TABLE 3.2.18 | BP ha$^{-1}$ (dry) x cal. equiv. (TABLE 3.2.23) |
|---|---|---|---|---|---|---|---|
| MAJOR SOLDIER | 0.65 | 32.666 | 21.2329 | 0.0608 | 268.9215 | 72.1705 | 362.2236 |
| MINOR SOLDIER | 0.96 | 6.666 | 6.3994 | 0.0183 | 81.0505 | 18.2080 | 87.9774 |
| MAJOR WORKER | 10.08 | 8.084 | 81.4867 | 0.2334 | 1032.0552 | 333.0855 | 1596.0791 |
| MINOR WORKER | 29.53 | 3.988 | 117.7656 | 0.3373 | 1491.5391 | 377.0611 | 1645.1929 |
| LARVAE | 58.77 | 2.081 | 122.3004 | 0.3502 | 1548.9738 | 243.0340 | 1117.4703 |
| TOTALS | 100 |  | 349.1850 | 1.0000 | 4422.54<br>g ha$^{-1}$ (f.w.) | 1043.56<br>g ha$^{-1}$ (d.w.) | 4808.9433<br>kcal ha$^{-1}$ |

### 3.2.4 CONCLUSIONS

Noirot (1969) and Bodot (1966) note that in the ageing of a colony, three phases can be distinguished. The results given in Section 3.2.3 can be synthesised into a model relating internal changes in a colony to its age. In the account that follows, the foregoing data are used as a basis for such a model and various assumptions and data from later sections are included where they are necessary to formulate a logical and fairly complete description.

A. The juvenile period. Age 0-4.5/5.5 years. Mound height 0-1.25/1.75m.

i) The mound, (Fig 3.2.5). This is a period of rapid mound growth with the rate increasing throughout the period. The walls of the mound are relatively thin (Table 3.1.3). Fungus comb increases in weight and progressively more heat is given out in respiration (Section 3.5). The temperature (Section 3.1) and humidity (assumed) levels become increasingly stabilised as the ratio mound surface area to volume drops and fungal and termite metabolism increases. Mukerji (1970) notes that larval growth rates are dependent upon temperature and humidity, hence the efficiency of larval growth and adult neuter production probably increase during this period.

ii) Colony population. The population of neuter castes increases exponentially (Fig 3.2.7), towards a maximum of 4-8 x $10^5$ per colony. The growth curve in Fig. 3.2.7 represents a mean of a family of such curves. Kalshoven (1930) was able to distinguish three curves in the growth of Neotermes tectonae colonies using data from 300-400 colonies. Colony biomass increases exponentially as does the population.

iii) Caste composition. The proportion of larvae in these young nests is very high (around 60%). In incipient colonies Section 3.6) major soldiers are not reared, presumably because their cost, in energetic terms, is not economical for the colony. The caste composition in the juvenile period probably approaches an optimal level as the worker population grows and energy input from consumption increases.

iv) Survivorship. Figure 3.2.6 and Table 3.2.9 (life-table) show that mortality of colonies during the juvenile period is very high. Out of 1,000 colonies present in year one (and possibly twice this number of founding pairs), only 24 remain at year five. Clearly the young colony is vulnerable. During the rainy seasons, destruction of small, thin-walled mounds by rain was a common occurrence. This allowed access to predatory ants which may rapidly destroy an entire colony. The juvenile period may be seen as a high-risk period during which energy input is channelled into strengthening the defences of the colony by production of neuters and mound-building.

B. The adult period. Age 4.5/5.5 - 10/17 years. Height 1.25/1.75-3.5-4.5m.

i) The mound. Mound growth continues but at a gradually decreasing rate (Fig. 3.2.5). Mound walls are initially thin but begin to thicken in older mounds (Table 3.1.3). Temperature and humidity regimes are fairly stable (Section 3.1). Heat production from fungus combs is high (Section 3.5).

ii) Colony population. The population of neuter castes (workers, soldiers and larvae considered together) stabilises and begins to decline at a double exponential rate from whatever maximum the colony had reached, (Section 3.2.3.3).

iii) Caste composition. It is during this period that alates are produced. Alates were only found in colonies 9 (N = 418,440, age 4.48 years) and 18 (N = 481,120, age 15.5 years) but since most colonies were dug up during the rainy season after the alate flight in late April/early May it is assumed that other colonies in the age range also produced alates. The finding of alates in colony 9 supports my earlier suggestion that an early decline curve may begin in that region. Hence, although larval populations show a steady decline, this is probably balanced in terms of biomass, by the production of alates. The population of workers and soldiers appears to remain fairly steady during this period, (Fig. 3.2.9).

iv) Survivorship. (Fig. 3.2.6 and Table 3.2.9). Mortality gradually decreases and the survivorship curve flattens off. The expectation of life of the colonies increases up to a maximum of 4.0 years at age 11. Once a colony has reached the adult period it becomes relatively secure and life-expectancy is high. The mound is strong and tall with thicker walls. The population is maximal and the royal pair well defended from predators such as ants, aardvarks, etc.

C. The senile period. Age 10/17 - 12/20-25 years. Height 4.5m upwards.

i) The mound. There is no further increase in height. The maximum height is clearly more variable than may be suggested by Figure 3.2.5. The mound walls become very thick by addition to the inside and the central mound gallery becomes very narrow (Table 3.1.3). Temperature profiles are very stable but heat production may stabilise as dead fungus combs accumulate, (see later, Sections 3.4 and 3.5).

ii) Colony populations. The population of all neuter castes considered together declines precipitously as does the biomass.

iii) Caste composition. Alate production declines. Larval populations decline rapidly until recruitment cannot keep pace with mortality of workers and soldiers. The colony rapidly collapses.

iv) Survivorship. The expected life of senile colonies drops quickly. These colonies have survived the rigours of predation, starvation, etc. and the royal pair are senescent. Egg production presumably falls below the level where recruitment is equal to mortality.

One of the more interesting aspects of the generalised scheme developed above is the sudden onset of the adult period, characterised by cessation of exponential increase in neuter production and the beginning of alate production. The turning point appears to be very sharp (Figure 3.2.7). Kalshoven (1930) also found a very sharp turning point in young colonies of <u>Neotermes tectonae</u>. Bodenheimer (1937) fitted logistic curves to the data but did not portray them, and his calculations have been accepted by several authors despite their poor fit, (Figure 3.2.10). The points of inflexion are clearly much higher than half the asymptotic values and logistic curves are not strictly applicable. However, my data (Fig. 3.2.7) show only the population of neuter castes. If further data on alate production were available then a closer approximation to the logistic curve would be evident in the extension of the growth curve. The conclusion is that the true asymptotic level (in terms of population or biomass) is perceived by the colony shortly after the point of inflexion and results in a drop in larval rearing, (and thus the start of the double-log decline of the neuter population), maintenance of the worker/soldier population at a fairly constant level, (Figure 3.2.9), and a gradual energy switch into alate production, which constitutes the unseen peak of the logistic curve. In effect, there is a safety valve which ensures that the limits to growth are perceived early enough to prepare for the dispersal phase before the limiting resources become exhausted.

Bordereau (1975) has shown that removal of the royal pair from M. bellicosus colonies can result in differentiation of nymphs at unusual times of the year and he concludes that the royal pair produce a pheromone which suppresses differentiation of sexual individuals. Lüscher (1976) considers that the initial onset of alate production is thus the result of dilution of the pheromone. Since the onset of alate production may begin at a variety of colony sizes ($4 - 8 \times 10^5$) individuals in M. bellicosus at Mokwa then either the capacity of the royal pair to produce this pheromone must vary or an additional stimulus is involved. The former seems improbable since colonies with royal pairs that produce low quantities of the pheromone would be inherently unable to make full use of the resources of their micro-habitat before the onset of alate production. Conversely, if all royal pairs produced the pheromone at a certain high level but its effects could be over-ridden under conditions of poor resources, colony death prior to alate production would be prevented. Hence, it seems probable that stimuli from the micro-habitat of each colony also affect the onset of alate production in the adult period, giving the system greater flexibility.

Lüscher et al. (in Lüscher 1976) have presented preliminary data that suggest an hormonal control of differentiation. They have found that a low JH litre in queen haemolymph is followed by a low titre in eggs and, after 1-2 months, the production of sexual nymphs. They conclude that low JH eggs hatch into potential alates while high JH eggs become neuter larvae. Lüscher points out that this blastogenic determination is not irreversible and may be influenced during the first instar larva to comply with Bordereau's (1975) results.

The tentative conclusion is that in immature colonies the neuter castes increase exponentially under the influence of high royal pair pheromone titre and unlimiting resources of food, space, etc. The adult phase may begin as the result of a combination of factors:

1) Dilution of the royal pair pheromone, thus preventing low JH eggs (potential alates) from reverting to neuter differentiation at the first larval instar.
2) Perception of environmental hardship prior to dilution of the royal pair pheromone below the critical level. Whatever mechanism is involved here would probably involve the workers, who are in a position to react behaviourally to stresses such as low foraging efficiency (in terms of distance travelled and food collected). Workers might react either by increased oophagy or by indirect means such as altering the nutrition of brood or queen.

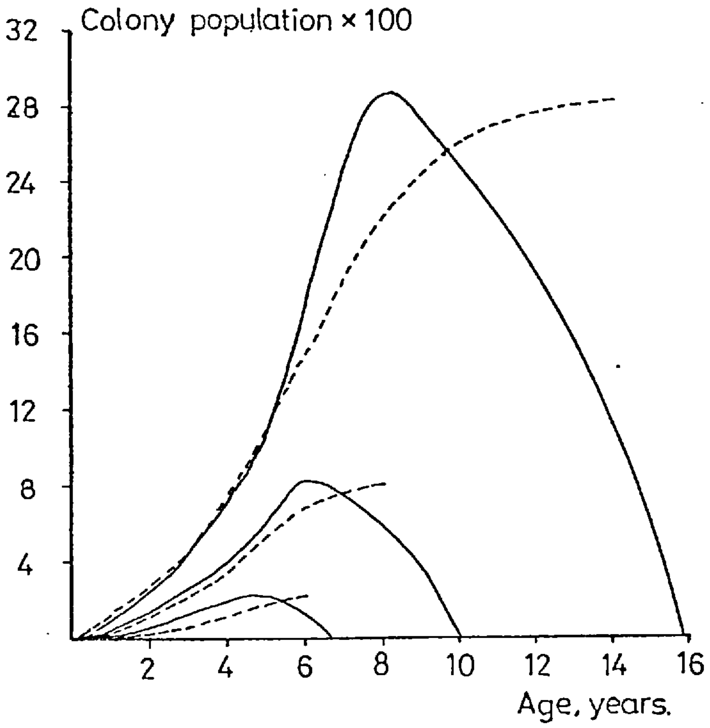


FIGURE 3.2.10 Kalshoven's (1930) data for growth of *Neotermes tectonae* colonies, with the logistic curves fitted by Bodenheimer (1937).

# SECTION 3.3

# CONSUMPTION STUDIES IN ISOLATION TANKS

## 3.3.1 INTRODUCTION

The consumption studies described in Section 2.3 and 2.4 were large scale field experiments with many uncontrollable variables affecting consumption (e.g. weather, species interactions). The consumption of *Macrotermes bellicosus* was therefore checked by another, more controlled, method on a smaller scale.

Many of the lower termites are amenable to laboratory culturing by virtue of: 1) relatively small diffuse nests in logs or branches which are easily transferred to the laboratory (e.g. Kalshoven 1936), 2) the ability of the neuters to survive for long periods in the absence of the royal pair (e.g. Grassé and Noirot 1960), 3) the ability to produce neotenic reproductives quite readily (exc. *Coptotermes*, Gay *et al*. 1955, Hrdý 1966). The higher termites (Termitidae) in general can be kept successfully in large groups (Becker 1969) but do not produce neotenic reproductives (exc. *Microcerotermes*, Becker *loc. cit.*) The Macrotermitinae are far more difficult to culture than species without fungus gardens but some success has been reported using *Odontotermes* spp. (Becker 1969, 1962), and *Macrotermes michaelseni*, (Lüscher 1976).

Preliminary attempts at keeping *M. bellicosus* neuter castes in plastic beakers at Mokwa were unsuccessful, all individuals died within 48 hours. Even larger artificial colonies with the royal pair, several hundred neuters and larvae and a few fungus combs, died within 2-3 weeks. Consumption studies on part colonies were therefore impractical. Incipient colonies were successfully cultured from dealate tandems collected after alate release in late April - early May (Section 3.6) but the limited availability of alates and length of time required for the colonies to reach a suitable size made this system impractical too. Hence, a method was developed to isolate entire colonies collected from the field, and measure their consumption rates over a range of wood densities.

### 3.3.2 METHODS

Some success in isolating entire colonies of Nasutitermes spp. in tanks was reported by T.G. Wood (pers. comm.) and the method was tried with M. bellicosus. Three sunken concrete tanks were built with inside dimensions 3.6 x 3.6 x 1.65 m depth (Plate 8). The inside faces and the bottoms of the tanks were rendered with concrete and completely sealed. Soil was replaced inside the tanks to a depth of 1.2m taking care to maintain the soil profile by replacing sub-soil then top-soil. Roots were removed as far as possible. The three tanks were covered by a thatched roof supported on poles 1m above the tank edge. The soil was kept moist by regularly spraying with water.

Small to medium-sized colonies were removed from the field by lifting the spiral base-plate from the pillar and transporting the nest, covered in polythene, to the tank. The nest was introduced into a previously prepared hole in the centre of the tank, dug to a suitable size and provided with a mock pillar. The mound itself was then reconstructed over the hole, using pieces of the original mound supported on a framework of aluminium tubing and plastered into place with mud, (Plate 10).

The colonies were left to settle in for about two weeks and were provided with natural wood litter spread around the tank. When foraging occurred over the whole area the colony was considered ready for consumption trials. One very small colony failed to re-establish. Examination of colonies after completion of the trials showed that the termites recreated the nest very successfully. They invariably plastered the walls of the "habitacle" with fine clay collected from deep galleries, reconstructed and extended the mound, and built a system of foraging galleries ramifying over the whole area available. They also built galleries up the tank sides which were brushed down daily.

The tanks were divided into 30 x 30 cm squares marked with wire pegs and in the consumption trials 2.5 x 2.5 x 1.25 cm pieces of softwood cut from planks were presented in a regular fashion. The central area (1.2 x 1.2 m), around the nest was left un-baited. The number of baits offered ranged from 25 to 1000, the trials were in randomised order, and each lasted four days exactly. Four colonies were studied in all, one tank being used twice. Baits were weighed dry before and after the trials and post-trial weighings were corrected for losses to factors other than termites, estimated from unattacked control baits.

After completion of the trials the nest was immediately removed and the termites counted by the methods described in Section 3.2. Samples were taken for biomass estimates. Colony one remained in the tank for about 6 months in all, while the method was being developed, but the other colonies were kept no longer than 3 months.

### 3.3.3 RESULTS

Estimations of population and biomass for the four colonies tested are given in Table 3.3.1. Colonies ranged from 40,000 to 410,000 individuals and 144 to 1171 g biomass (f.w.)

In Table 3.3.2 consumption data are expressed as mg consumed (d.w.) per g of termites (f.w.) per day, at each bait density. Mean consumptions (with 95% c.l.) are given for bait densities with three or four trials. Bait discovery per trial is recorded at each density and the weight of baits offered is approximated. The latter was calculated from the mean weight of a single bait (2.650 g) estimated from the total number (18,475), and total weight (48.917 kg), of all baits offered during the experiments. There was some variation in the actual weight given at any particular density due to slight differences in bait weights.

The maximum weight offered (2650 g at density 1000) is equivalent to 204 g $m^{-2}$ which approaches the mean standing crop of dead wood on the study area (282.1 g $m^{-2}$, including standing dead items).

Rogers (1972) developed the Random Predator Equation to describe the number of prey eaten by a predator searching at random. The value at any given prey density was dependent upon two constants, a: the search efficiency or attack coefficient, and b: the handling time, and was described by:-

$$\text{Neat} = N\left(1 - e^{-a\,(\text{Tt} - \text{Nat.b})}\right)$$

where Neat = the number of prey eaten, Nat = the number of prey attacked ( = Neat for a predator since prey found are eaten and not available for further attacks, cf. parasitism), Tt = total time available, N = prey density. In this form, the number of prey eaten increases at a decreasing rate as prey density increases. This response to prey density is known as the functional response (Holling 1959).

The isolation tank trials were similar in some respects to a predator/prey situation with the colony (predator) randomly searching for baits (prey), and the mean consumption results show a Type 2 functional response to bait density (Holling 1959). The data have therefore been interpreted according to the Random Predator Equation. Handling time for a whole bait was a relatively long period and many baits remained unfinished at the end of each trial. Therefore consumption is measured in mg, not number of baits found.

Hence: $C = N\left(1 - e^{-a\,(Tt\, -\, c.b.)}\right)$

where C = consumption (mg $g^{-1}$ $d^{-1}$), N = number of baits offered, Tt = 24 hours, b = handling time, a = search efficiency. The best values for a and b were computed by a least squares method and a model generated to fit the data:-

$$C = N\left(1 - e^{-0.0431\ (24 - c.\ 0.2138)}\right)$$

An analysis of variance gives a variance ratio (F) of 78.343 ($p < 0.001$ at 1 and 9 d.f.) and the model and data are plotted in Figure 3.3.1. At bait density 1000 the mean is low and the limits very wide due to an inexplicably low result from colony one. The model fits the data well and the handling time (b) of 0.2138 h $mg^{-1}$ $g^{-1}$ gives an expected maximum consumption of 112.254 mg $g^{-1}$ $d^{-1}$. The limits of consumption recorded (in mg $g^{-1}$ $d^{-1}$), were 112.988 (colony 1), 149.180 (colony 2), 94.322 (colony 3), 147.637 (colony 4) with a mean of 126.032.

TABLE 3.3.1 Estimates of population and fresh weight biomass of four *M. bellicosus* colonies transferred to isolation tanks for consumption studies

| Caste | Individual Biomass mg | Number of Individuals | Total Biomass per Caste g | Individual Biomass | Number of Individuals | Total Biomass per Caste g |
|---|---|---|---|---|---|---|
| Major soldier | 7.28 | 358 | 2.6066 | 30.64 | 2555 | 78.285 |
| Minor soldier | 6.247 | 347 | 2.1646 | 5.33 | 3755 | 20.014 |
| Major worker | 7.506 | 7169 | 53.8083 | 9.038 | 32263 | 291.593 |
| Minor worker | 2.749 | 19131 | 52.5902 | 3.564 | 136108 | 485.089 |
| Larvae | 2.385 | 12828 | 30.5953 | 1.766 | 62432 | 110.255 |
| Queen | 1,893 | 1 | 1.893 | 6,242 | 1 | 6.242 |
| King | 100 | 1 | 0.100 | 70 | 1 | 0.070 |
| Totals | | 39832 | 143.758 | | 237115 | 991.5482 |
| | ISOLATION TANK ONE | | | ISOLATION TANK TWO | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Major soldier | 27.685 | 1560 | 43.189 | 34.930 | 2310 | 80.688 |
| Minor soldier | 5.56 | 1238 | 6.883 | 6.950 | 6243 | 43.389 |
| Major worker | 8.805 | 11678 | 102.825 | 8.440 | 29645 | 250.204 |
| Minor worker | 3.045 | 29550 | 89.980 | 4.132 | 107360 | 443.612 |
| Larvae | 2.513 | 34733 | 87.284 | 1.308 | 264220 | 345.600 |
| Queen | - | 1 | ∼ 3.000 | 7,189 | 1 | 7.189 |
| King | - | 1 | ∼ .100 | 97 | 1 | 0.097 |
| Totals | | 78761 | 333.261 | | 409780 | 1170.779 |
| | ISOLATION TANK THREE | | | ISOLATION TANK FOUR | | |

TABLE 3.3.2 Bait discovery (per four days), and consumption (mg (d.w.) $g^{-1}$ (f.w.) $d^{-1}$) data for 4 isolated *M. bellicosus* colonies at various densities of food offered.

| APPROXIMATE WEIGHT OF BAITS OFFERED g | NUMBER OF BAITS OFFERED | ISOLATION COLONY ONE | | ISOLATION COLONY TWO | | ISOLATION COLONY THREE | | ISOLATION COLONY FOUR | | Mean Consumption mg $g^{-1}d^{-1}$ | ± 95% Confidence Limits |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Bait Discovery | Consumption mg $g^{-1}d^{-1}$ | Bait Discovery | Consumption mg $g^{-1}d^{-1}$ | Bait Discovery | Consumption mg $g^{-1}d^{-1}$ | Bait Discovery | Consumption mg $g^{-1}d^{-1}$ | | |
| 66 | 25 | 12 | 17.008 | 17 | 14.129 | 21 | 35.057 | - | - | 22.065 | 28.181 |
| 133 | 50 | 21 | 36.318 | 40 | 20.952 | 22 | 31.216 | - | - | 29.495 | 19.443 |
| 265 | 100 | 30 | 32.993 | 97 | 63.686 | 48 | 37.958 | 57 | 27.042 | 40.420 | 25.679 |
| 398 | 150 | - | - | 65 | 41.716 | 85 | 49.091 | - | - | - | - |
| 530 | 200 | 52 | 60.776 | 185 | 111.222 | 116 | 49.901 | 67 | 34.806 | 64.176 | 52.698 |
| 663 | 250 | - | - | 84 | 42.953 | 115 | 65.882 | - | - | - | - |
| 795 | 300 | 55 | 108.863 | 233 | 118.613 | 152 | 76.907 | 172 | 54.608 | 89.748 | 46.822 |
| 1060 | 400 | 55 | 131.408 | 88 | 39.185 | 112 | 79.883 | 106 | 58.189 | 77.166 | 63.323 |
| 1325 | 500 | 29 | 106.067 | 490 | 149.180 | 95 | 72.028 | 273 | 77.897 | 101.293 | 56.023 |
| 1590 | 600 | 92 | 112.988 | 198 | 100.822 | 128 | 92.867 | 179 | 81.553 | 97.058 | 21.065 |
| 1855 | 700 | - | - | - | - | - | - | 300 | 81.169 | - | - |
| 2120 | 800 | 209 | 94.158 | 641 | 125.531 | 96 | 85.113 | 323 | 121.218 | 106.505 | 31.668 |
| 2385 | 900 | - | - | - | - | - | - | 226 | 40.601 | - | - |
| 2650 | 1000 | 20 | 31.205 | 214 | 60.487 | 172 | 94.322 | 576 | 147.637 | 83.413 | 79.524 |

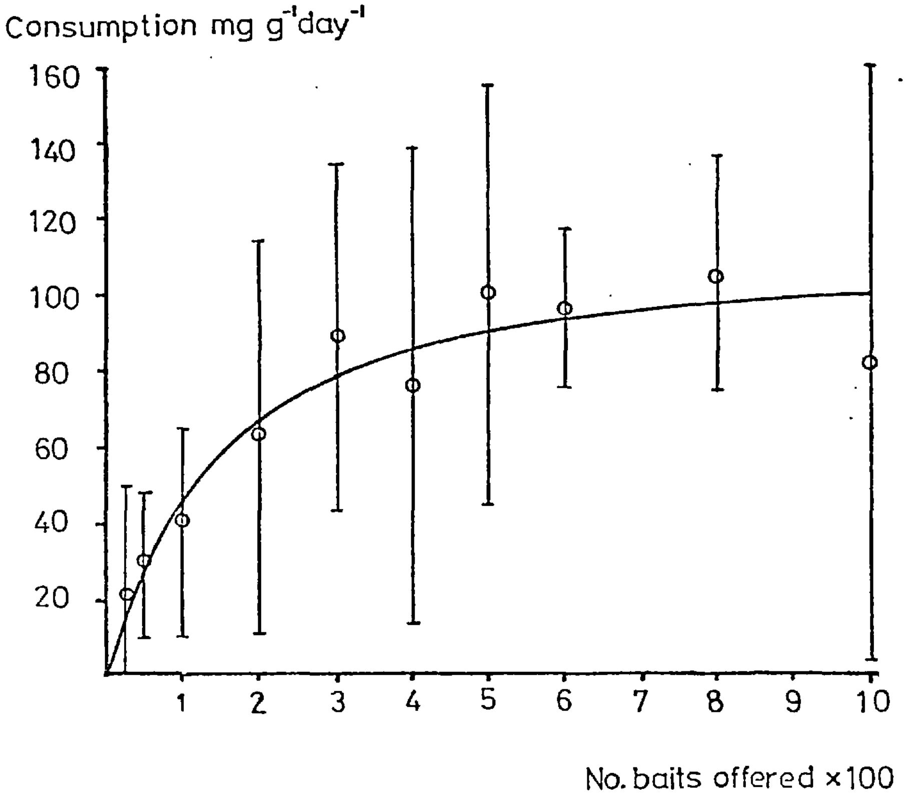


FIGURE 3.3.1 Mean consumption data from four isolated colonies of Macrotermes bellicosus fed at various densities of wood baits, with 95% confidence limits. The curve has been generated using the Random Predator Equation.

## 3.3.4 DISCUSSION

### 3.3.4.1 Isolation Tanks Consumption Results.

The general trend of consumption rate increasing with bait density to an asymptotic level of 100-150 mg $g^{-1}$ $d^{-1}$ is quite clear. Fitting of the Random Predator Equation has been fairly successful in describing the data and given values for search efficiency and handling time. These data are, however, of limited use in the absence of comparable results. The conditions of the tests were very specific and the constants would undoubtedly change with bait size, colony size, tank size and so on. However, further work along these lines could yield very interesting data on variation of the variables between taxonomic groups which would be of great value as extrapolation factors for population data. An essential basis of further work would be that whole colonies would be required since it is the colony as a whole that is considered as the "predator", not individual castes or foraging parties. The use of small groups of workers has undoubtedly led to much of the variation in estimates of consumption rates to be found in the literature.

It is unfortunate that my data are too variable to examine changes in search efficiency and handling time with colony size, factors which may well be of some importance in colony development, onset of alate production and so on. This could be a very fruitful line of research in a species with less populous colonies which are more easily maintained under laboratory conditions.

### 3.3.4.2 Synthesis of Consumption Data for Macrotermes bellicosus

Table 3.3.3 summarises all consumption data gathered during the course of this work. In general the results from the isolation tanks and food stores support the consumption data from the field. There is a suggestion that the latter may be slightly high, particularly in the light of the fact that experiments in the tanks were under fairly optimal conditions and in the absence of competitors.

Other laboratory and field consumption data for termites have been reviewed by Wood (in press) and discussed in Section 2.4.1. Laboratory data are largely from the lower groups of termites and range mainly between 10 and 50 mg $g^{-1}$ $d^{-1}$. Wood and Sands (in press) have used 30 mg $g^{-1}$ $d^{-1}$ as a working figure for all termites except the Macrotermitinae, for which they have used 60 mg $g^{-1}$ $d^{-1}$.

Field data for termites, particularly Macrotermitinae, are few. Josens (1972a) obtained a figure of 594 mg $g^{-1}$ $d^{-1}$ for four species, but this was undoubtedly over-estimated as a result of low population figures and short-term consumption measurements on baits. Lepage (1972) estimated consumption by Macrotermes sybhyalinus as 29.1 mg $g^{-1}$ $d^{-1}$ and Matsumoto's (1976) data can be used to estimate consumption by four species, (not all Macrotermitinae), as 149.61 mg $g^{-1}$ $d^{-1}$, (Section 2.4.1).

Clearly the study of consumption by Macrotermitinae is not well-advanced and it is difficult to generalise at this stage. However, it seems that in general the Macrotermitinae have higher weight-specific consumption rates than other groups and the deployment of this high input is examined in the following sections.

TABLE 3.3.3 Synthesis of data on consumption by *Macrotermes bellicosus*. Underlined data were measured directly.

| SOURCE OF DATA | MAXIMUM CONSUMPTION mg $g^{-1}$ $d^{-1}$ | FIELD CONSUMPTION kg $ha^{-1}$ $a^{-1}$ |
|---|---|---|
| TANK 1 | 112.988 | 194.656 |
| TANK 2 | 149.180 | 257.008 |
| TANK 3 | 94.322 | 162.498 |
| TANK 4 | 147.637 | 254.350 |
| MEAN OF TANKS | 126.032 | 217.128 |
| RANDOM PREDATOR EQUATION | 112.25 | 193.397 |
| FOOD STORES ($\theta$ = 7 d) | 139.297 | 239.982 |
| FOOD STORES ($\theta$ = 10 d) | 97.776 | 168.449 |
| DECOMPOSITION AND BAITING | 139.608 | 240.518 |

## SECTION 3.4

# FAECES PRODUCTION BY MACROTERMES BELLICOSUS: THE FUNGUS COMBS

### 3.4.1 INTRODUCTION

Present knowledge concerning the fungus combs of the Macrotermitinae can be summarised as follows.

1) Fungus combs in termite nests were first observed by König (1779) in the East Indies and by Smeathman (1781) in West Africa. There has been some controversy over the origin of the combs, Bathellier (1927), Grassé (1937) and Grassé and Noirot (1961) maintained that they are made of masticated, undigested plant material but Sands (1960) has observed that they are faecal in origin. Cmelik and Douglas (1970) agree with Grassé (*loc. cit.*) on the grounds that no uric acid was found in the combs of *Macrotermes falciger* or *Odontotermes badius* but Abo-Khatwa (1976) found a relatively high uric acid concentration in combs of *Macrotermes subhyalinus*. I agree with Sands on the basis of the available evidence, and as a result of my own observations on *Macrotermes bellicosus* and those of R.A. Johnson and T.G. Wood (pers. comm.) on *Microtermes usambaricus*. The combs are made up of spherical pellets identical to the faecal pellets in the termite hind-gut.

2) Fungi of the Basidiomycete genus *Termitomyces* grow on the combs, the mycelium infiltrating into all parts of them. There are two exceptions, no fungus grows on the combs of *Sphaerotermes sphaerothorax* (Grassé and Noirot 1948) or on *Microtermes* combs in Madagascar (Heim 1938, Harris and Sands 1965), although the latter observation requires further investigation. *Termitomyces* is not known to grow anywhere except on fungus combs (see Heim's bibliography in Sands 1969). Grassé (1959) noted that *Termitomyces* species are generally associated with

particular termite genera. Sands (1960) has shown that, at least in some cases, the fungal species are obligatory symbionts specific to a species of termite, but that the termites are less specific and survive well on a range of *Termitomyces* species. Fungus nodules, which grow on the middle-aged section of the comb, (see 3) below), (Grassé and Noirot 1958), are the conidiophores or conidia of the fungus and are also the primordia of the agaric phase (Bathellier 1927), which may grow out if not eaten by the termites (Grassé 1945), to produce fruiting bodies at the surface, (see diagrams in Sands 1969). Such fruiting bodies were not observed at Mokwa.

3) Combs are eaten by the termites from below and built up at the upper surface or replaced by new combs beneath (Kalshoven 1936, Grassé and Noirot 1957, Alibert 1964). The termites are stimulated to feed by the state of the comb, not its position (Alibert 1964). The action of the fungus changes the colour of the faeces, new deposits are dark, ageing to pale beige in *Macrotermes*, *Protermes*, *Odontotermes* and *Acanthotermes* or pale ageing to grey in *Ancistrotermes* and *Microtermes*, (Grassé and Noirot 1957).

4) The fungus combs appear to be essential to the long-term survival of the termites (Sands 1956, Ausat et al. 1960), but *Macrotermes* sp. has been kept alive in Paris for 18 months without combs (Grassé 1959).

5) Some cellulose is digested in the first passage of food through the gut of the termites (Sands 1969, Becker and Seifert 1962) and the fresh faeces and comb stain strongly for lignin (Grassé 1959). Chemical analysis of entire combs gives results of 43.3% for *Macrotermes falciger*, 23.8% for *Odontotermes badius* (Cmelik and Douglas 1970), 16.4% for *Macrotermes subhyalinus* (Abo-Khatwa 1976) and 15% for *Macrotermes natalensis* (Becker and Seifert 1962). The fungus appears to break lignin down into smaller molecules which the termites are subsequently

able to digest by virtue of their gut flora.

6) Fungus combs may be important to the termites as a source of nitrogen, vitamins and other substances. The combs have a higher nitrogen content than wood or leaves (Cmelik and Douglas 1970, Abo-Khatwa 1976) and the fungal nodules are particularly rich in this respect (Matsumoto 1976). D-mannitol has been recorded as 6.9% in combs of *Macrotermes sybhyalinus* (Abo-Khatwa 1976), 2% in combs of *Macrotermes falciger* and 0.7% in combs of *Odontotermes badius* (Cmelik and Douglas 1970). Abo-Khatwa (1976) suggests that this may be useful in suppressing growth of extraneous fungi or in retention of water. He also suggests that the low pH of fungus combs may be sub-optimal for fungi other than *Termitomyces*. pH values recorded are 4.3 for *Macrotermes falciger*, 4.4 for *M. bellicosus* (Hesse 1957), and 4.5 and 4.6 for *M. subhyalinus* (Hesse *loc. cit.*, Abo-Khatwa 1976).

### 3.4.2 METHODS

The methods for estimating biomass of fungus combs in *M. bellicosus* nests have been described in Section 3.2.2.

The annual production of faeces can be calculated from the standing crop biomass of combs and their turnover rate. Josens (1971, 1972a) offered sawdust baits with an admixture of soot to various species of Macrotermitinae, and was able to calculate turnover rate from the position of the soot on the combs after a given time. I attempted the same method but experienced some difficulty in locating the soot on the combs with precision, mainly because *M. bellicosus* did not find such baits very attractive and foraged at a low level. With *M. bellicosus* there was the added disadvantage that the length of time the soot-sawdust remained in the food stores was critical to the calculations. In order to avoid these problems the food stores themselves were marked with a concentrated emulsion of fluorescent Fire Orange Pigment. A shallow trench was dug to the side of two medium-sized colonies and the emulsion sprayed liberally on the food stores from a wash bottle. The small breach in the wall of the endoecie was subsequently plastered with mud. One colony died after treatment, possibly from ant attack. The pigment itself was non-toxic. After exactly 40 days the surviving mound was opened and the endoecie removed to the laboratory for examination. Although this method was successful, there was no time to repeat the experiment.

Carbon, nitrogen and mineral assays on food stores and fungus comb were done by Dr. Leuse of the International Institute of Tropical Agriculture, Ibadan, to whom I am grateful. Several replicates were assayed from food stores, and from the new (two nests), middle-aged and old (two nests), parts of the same fungus combs.

Calorific equivalents and ash content for ten replicates of old and new fungus comb were estimated using a Gallenkamp ballistic bomb calorimeter.

### 3.4.3 RESULTS

Table 3.4.1 shows the results of fungus comb biomass estimation for 19 _M. bellicosus_ colonies together with the mound height and estimated colony age (from Section 3.2.3.2). It was not possible to accurately assess the age of colony 19 due to its extreme height. Biomass of fungus comb per nest (Bfc) was found to be linearly correlated with colony age (t) on a double log basis.

$$\log \text{Bfc} = 1.8269.\ \log t + 2.4688 \qquad r = 0.8935,\ p < .001$$

Standard error : 0.33581

Variance ratio (F): 63.3790

't' for slope : 7.9611

This relationship has been used to predict the total standing crop of combs on the study area using the census and survivorship curve data (Table 3.4.2). The mean biomass ($\overline{B}fc$) of combs over the three years of the census is calculated as 26.060 kg $ha^{-1}$ (dry weight).

On removal of the nest treated with Fire Orange Pigment, no colouration was at first visible on the combs. However, inspection under an ultra-violet lamp revealed the pigment very clearly, by chance on, or very near to, the inner edge of the combs. The time taken for the pigment to be consumed with the food stores and undergo one turnover of the combs was thus exactly 40 days. Alibert (1964) stained leaf confetti food stores of Macrotermes lilljeborgi (Sjöstedt) with fluorescein. She found that although the stain appeared in worker guts 48 hours later, a period of 60 hours elapsed before the stain appeared on the combs. By extrapolation from this observation, the turnover of M. bellicosus combs is taken to be 40 minus 2.5, i.e. 37.5 days. This compares with Josens' (1972a p.192), results of 60 days for Microtermes toumodiensis and Ancistrotermes cavithorax and 48 days for Odontotermes sp. The shorter turnover time for M. bellicosus may be related to the fact that forage may remain in the food stores for up to two weeks, (Section 3.2.3.7), or to the fact that temperature regulation is more stable and at a higher level, thus accelerating fungal metabolism.

Before calculating the annual production of faeces, one further observation requires consideration. The action of Termitomyces in altering the colour of the faeces from dark brown to pale beige has already been mentioned. It became clear in the latter stages of the study that the central area of the nest invariably contained combs which were entirely beige, with no sign of fresh faeces. Combs in this state were later found to have a very low respiratory rate (Section 3.5).

Although the re-cycling of the faeces in this species is undoubtedly an efficient method of food conversion, it would clearly also serve to concentrate any toxins and noxious compounds either present in the foodstuff or produced as by-products of termite and fungal metabolism. Although it has not been possible to examine the central combs biochemically, their low respiration rate and lack of fresh faeces suggests that they are noxious remnants no longer of value to the termites and therefore left unutilised. Such combs have not been reported from other species of Macrotermitinae. The unused section of combs is assumed to be a constant proportion of the total biomass of combs in a nest of any given size, and therefore increases with the size and age of the colony. They were in fact unnoticeable in quite small colonies such as the one used for turnover studies, but quite obvious in larger ones, suggesting that this assumption may be an over-simplification.

Detailed quantification of the proportion of combs involved was not possible since their significance was only realised in the latter stages of this study. However, the fungus combs of colony 19 had a very low biomass (20.713 kg) for such a large mound, and the habitacle was noticeably empty. Most of these combs were of the pale unutilised type and were in a low mound near the centre of the plate. From the regression of comb biomass and age, an old colony (20-25 years) is predicted to contain 86.917 kg of comb (at 22.5 years). The combs present in this very old colony therefore represented only 24% of the expected amount. Some of the combs were still active and utilised by the large population of soldiers and workers present in the colony and I shall therefore assume that only about 63% of the combs present were inactive and conclude that approximately 15% of the expected biomass of combs were dead remnants and no longer turned over.

Colony 19 was undoubtedly a senile colony and the lack of combs and high proportion of workers and soldiers support this conclusion. In addition, the colony was dug out early in the rainy season and the combs may have been run down during the dry season. This process has been observed by R.A. Johnson (pers. comm.) in Microtermes spp. Noirot (1959) has also observed that Macrotermes gilvus in Cambodia survives flooding of rice fields by feeding largely on the combs.

This unexpected aspect of fungus comb utilisation - fungus comb "dumps", clearly requires further study. The percentage of inactive comb is vital to accurate calculation of the annual production of faeces. For the present purpose the data available will be used to permit construction of a complete energy budget and will be discussed at a later stage (Section 4.1), when assimilation can be separately assessed from production and respiration data.

Thus, assuming that 15% of combs in mounds of all ages are inactive, the annual production of faeces (F) can be calculated from standing crop biomass of combs ($\overline{B}fc$), the proportion being turned over (0.85) and the turnover rate ($\theta$).

$$F = \overline{B}fc.\ 0.85.\ \theta$$

equal to: $26.060.\ 0.85.\ \frac{365}{37.5}$ , i.e $\underline{215.603\ \text{kg ha}^{-1}\ \text{a}^{-1}\ \text{(d.w.)}}$

Results of the chemical analysis of fungus combs are given in Table 3.4.3. When compared with the food stores, all the new comb results are higher. The carbon to nitrogen ratio is therefore higher in food stores than in the fungus combs. Within the combs themselves, P and Mg appear to remain at a fairly constant level in all parts, while N, Ca and K are more concentrated in the middle comb section and at similar, but lower, levels in old and new comb. Carbon concentration is similar in middle and old comb but rather higher in new comb.

This latter observation is confirmed in the results of bomb calorimetry given in Table 3.4.4. The new comb has a calorific equivalent of 4.5295 kcal $g^{-1}$, whereas for old comb the value is 4.1535 kcal $g^{-1}$. Ash content is higher in old comb (12.72%) than in new (10.99%) as would be predicted from the values for minerals in Table 3.4.3.

The calorific equivalent of the annual production of faeces (using the figure for new comb), can therefore be calculated as equal to 976,574 kcal $ha^{-1}$ $a^{-1}$.

## 3.4.4 DISCUSSION

On the basis of annual faeces production of 215.603 kg $ha^{-1}$ $a^{-1}$ and annual consumption of 240.518 kg $ha^{-1}$ $a^{-1}$ (Section 3.3.4.2), the assimilation efficiency of M. bellicosus can be calculated as 10.36%. This figure involves errors due to variation in foodstuff and is more accurately assessed on a calorific basis. In these terms, annual consumption was 1,265,920 kcal $ha^{-1}$ $a^{-1}$ (Section 2.4), faeces production 976,574 kcal $ha^{-1}$ $a^{-1}$ and the calorific assimilation efficiency 22.86%, (but see Section 4.1.2 for a comparison with assimilation as calculated from annual respiration and production data).

These figures are low in comparison with laboratory colonies of lower termites and Nasutitermitinae reviewed by Wood and Sands (in press), which have assimilation efficiencies (by weight), ranging from 54 to 61%. It appears paradoxical that Macrotermes bellicosus should have a very high weight-specific consumption rate and yet be unable to utilise it more efficiently. This aspect is discussed more fully in Section 4.1.2 but it may be stated here that it appears to be by virtue of the association with the fungus Termitomyces sp. that Macrotermes bellicosus is able to process its food to provide a high-nutrient diet suitable for growth and reproduction. Losses of carbon are very high as a result, and assimilation efficiency therefore low.

As a corollary to the regression of comb biomass with colony age it is possible to calculate, from height and age distribution of mounds on the study area (from Section 3.2.3.2), an estimate of annual return of faeces to the environment by death of colonies. Calculations are given in Table 3.4.5. The number of colonies present on the study area (lx) was taken from the best fit of mound numbers and ages given earlier in Figure 3.2.6. The number of colonies dying at each age interval has been calculated and the annual return of combs estimated. The age intervals are uneven because of the use of mound height as a parameter for colony growth. It has been calculated that annual returns are of the order of 5.695 kg $ha^{-1}$ $a^{-1}$, with a calorific equivalent of 24,725 kcal $ha^{-1}$ $a^{-1}$, (using the mean calorific equivalent of old and new comb).

TABLE 3.4.1 The weight of fungus combs in 19 nests of *M. bellicosus*.

| COLONY NUMBER | MOUND HEIGHT m | ESTIMATED AGE |  | FUNGUS COMB BIOMASS (DRY) |  |
|---|---|---|---|---|---|
|  |  | YEARS | log YEARS | g | log g |
| 1 | 0 | 0.60 | -0.2218 | 201 | 2.3032 |
| 2 | 0.15 | 1.15 | 0.0607 | 669 | 2.8254 |
| 3 | 0.36 | 1.90 | 0.2788 | 853 | 2.9309 |
| 4 | 0.49 | 2.25 | 0.3522 | 378 | 2.5775 |
| 5 | 0.60 | 2.60 | 0.4150 | 2,097 | 3.3216 |
| 6 | 0.70 | 2.90 | 0.4624 | 1,104 | 3.0430 |
| 7 | 0.90 | 3.45 | 0.5378 | 5,238 | 3.7192 |
| 8 | 0.95 | 3.60 | 0.5563 | 717 | 2.8555 |
| 9 | 1.30 | 4.50 | 0.6532 | 11,899 | 4.0755 |
| 10 | 1.45 | 4.85 | 0.6857 | 1,833 | 3.2632 |
| 11 | 1.50 | 4.95 | 0.6946 | 7,180 | 3.8561 |
| 12 | 1.85 | 5.75 | 0.7597 | 13,750 | 4.1383 |
| 13 | 2.58 | 7.40 | 0.8692 | 16,500 | 4.2175 |
| 14 | 2.67 | 7.57 | 0.8791 | 12,331 | 4.0910 |
| 15 | 3.00 | 8.39 | 0.9238 | 19,000 | 4.2788 |
| 16 | 3.50 | 9.75 | 0.9890 | 6,386 | 3.8052 |
| 17 | 3.55 | 9.90 | 0.9956 | 38,381 | 4.5841 |
| 18 | 4.40 | 15.50 | 1.1903 | 62,630 | 4.7968 |
| 19 | 5.79 | ? | ? | 20,713 | 4.3162 |

log Bfc = 1.8269. log t + 2.4688, r = 0.8935.

where Bfc = biomass of fungus comb per nest, t = colony age.

TABLE 3.4.2 Calculation of biomass of fungus combs $ha^{-1}$ using census data and the correlation of colony age with fungus comb biomass given in TABLE 3.4.1.

| HEIGHT RANGE m | AGE RANGE (YEARS) | MEAN WEIGHT FUNGUS COMB PER NEST kg | NUMBER OF COLONIES | | | | ESTIMATED BIOMASS OF FUNGUS COMB (kg 6 $ha^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1974 | 1975 | 1976 | SURVIVORSHIP CURVE | 1974 | 1975 | 1976 | SURVIVORSHIP CURVE |
| HYPOGEAL | (0.5) | 0.083 | ∿ 45 | ∿ 45 | ∿ 45 | ∿ 45 | 3.735 | 3.735 | 3.735 | 3.735 |
| 0 - 0.5 | 0.6 - 2.28 | 0.722 | 19 | 25 | 18 | 21.49 | 13.718 | 18.050 | 12.996 | 15.516 |
| 0.51-1.0 | 2.28-3.72 | 2.286 | 10 | 10 | 7 | 6.09 | 22.860 | 22.860 | 16.002 | 13.922 |
| 1.01-1.5 | 3.72-4.95 | 4.356 | 2 | 3 | 2 | 3.14 | 8.712 | 13.068 | 8.712 | 13.678 |
| 1.51-2.0 | 4.95-6.09 | 6.725 | 7 | 1 | 3 | 1.91 | 47.075 | 6.725 | 20.175 | 12.845 |
| 2.01-2.5 | 6.09-7.2 | 9.411 | 0 | 3 | 0 | 1.23 | 0 | 28.233 | 0 | 11.576 |
| 2.51-3.0 | 7.2-8.4 | 12.602 | 1 | 0 | 0 | 0.81 | 12.602 | 0 | 0 | 10.208 |
| 3.01-3.5 | 8.4-9.75 | 16.613 | 0 | 0 | 1 | 0.52 | 0 | 0 | 16.613 | 8.639 |
| 3.51-4.0 | 9.75-11.77 | 22.731 | 0 | 0 | 1 | 0.30 | 0 | 0 | 22.731 | 6.819 |
| 4.01-4.5 | 11.77-20 | 48.337 | 1 | 0 | 1 | 0.14 | 48.337 | 0 | 48.337 | 6.767 |
| 4.51-5.0 | ∿ 20 | 70.072 | 0 | 1 | 0 | 0.02 | 0 | 70.072 | 0 | 1.401 |
| 5.01-5.5 | ∿22.5 | 86.917 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TOTALS (6 ha) | | | 85 | 88 | 78 | 80.65 | 157.039 | 162.743 | 149.301 | 105.106 |
| TOTALS (1 ha) | | | | | | 13.44 | 26.173 | 27.124 | 24.884 | 17.518 |

TABLE 3.4.3 Chemical analyses of food stores, and fungus combs at various stages of decay.

| | FOOD STORES | NEW COMB | MIDDLE COMB | OLD COMB |
|---|---|---|---|---|
| % N | 0.40 | 0.68<br>1.02 | 1.25 | 0.80<br>1.02 |
| % C | 20.00 | 31.00<br>29.00 | 29.00 | 29.00<br>29.00 |
| C/N | 50.00 | 35.29 | 23.20 | 31.87 |
| % P | 0.04 | 0.07<br>0.07 | 0.07 | 0.07<br>0.06 |
| % Ca | 0.75 | 0.07<br>1.25 | 1.60 | 0.85<br>1.45 |
| % Mg | 0.17 | 0.26<br>0.31 | 0.37 | 0.25<br>0.38 |
| % K | 0.10 | 0.10<br>0.10 | 0.15 | 0.10<br>0.15 |

TABLE 3.4.4 Calorific equivalents and ash content of new and old fungus comb.

| ASSAY NUMBER | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | MEAN | 95% CONF. LIMITS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CALORIFIC EQUIVALENT kcal $g^{-1}$ (Dry wt.) | NEW FUNGUS COMB | 4.5652 | 4.5571 | 4.4979 | 4.5714 | 4.4768 | 4.5154 | 4.4944 | 4.5248 | 4.4997 | 4.5925 | 4.5295 | ±0.0281 |
| | OLD FUNGUS COMB | 4.0909 | 4.1248 | 4.1274 | 4.1663 | 4.1104 | 4.2268 | 4.2320 | 4.1405 | 4.2828 | 4.0331 | 4.1535 | ±0.0535 |
| % ASH (Dry wt.) | NEW FUNGUS COMB | 11.06 | 11.43 | 10.81 | 10.36 | 11.11 | 11.08 | 11.24 | 10.28 | 11.25 | 11.32 | 10.99 | ±0.28 |
| | OLD FUNGUS COMB | 11.66 | 11.99 | 13.11 | 13.35 | 12.21 | 13.03 | 12.23 | 12.68 | 13.58 | 13.34 | 12.72 | ±0.47 |

TABLE 3.4.5 Calculation of return of fungus comb to the ecosystem per annum through colony mortality. The return of 5.695 kg ha$^{-1}$ a$^{-1}$ is equivalent to 24,725 kcal ha$^{-1}$a$^{-1}$. Note that the weight of fungus comb in a nest of each rank is not calculated by entering the mean age into the comb biomass/age regression, but is taken as the mean of the weights calculated for the ages delimiting the height/age rank, as given in Table 3.4.2. These figures differ because comb biomass is related to mound height on a double log scale.

| MOUND HEIGHT RANGE m | MEAN AGE FOR RANK, x (YEARS) | NUMBER OF COLONIES 6 ha$^{-1}$, lx | NO. COLONIES DYING IN AGE INTERVAL, $d_x$ $(=l_{x_{n+1}}-l_{x_n})$ | NO. COLONIES DYING IN ONE YEAR, da | WT. OF FUNGUS COMB IN NEST OF EACH RANK kg | COMB RETURN PER ANNUM kg a$^{-1}$ |
|---|---|---|---|---|---|---|
| HYPOGEAL | ~0.5 | ~ 45 | 23.51 | 25.01 | 0.083 | 2.076 |
| 0-0.5 | 1.44 | 21.49 | 15.40 | 9.87 | 0.722 | 7.126 |
| 0.51-1.0 | 3.00 | 6.09 | 2.95 | 2.20 | 2.286 | 5.029 |
| 1.01-1.5 | 4.34 | 3.14 | 1.23 | 1.04 | 4.356 | 4.530 |
| 1.51-2.0 | 5.52 | 1.91 | 0.68 | 0.60 | 6.725 | 4.035 |
| 2.01-2.5 | 6.65 | 1.23 | 0.42 | 0.37 | 9.411 | 3.482 |
| 2.51-3.0 | 7.80 | 0.81 | 0.29 | 0.23 | 12.602 | 2.898 |
| 3.01-3.5 | 9.08 | 0.52 | 0.22 | 0.13 | 16.613 | 2.160 |
| 3.51-4.0 | 10.76 | 0.30 | 0.16 | 0.03 | 22.731 | 0.682 |
| 4.01-4.5 | 15.89 | 0.14 | 0.12 | 0.03 | 48.337 | 1.450 |
| 4.51-5.0 | ~20.0 | 0.02 | 0.02 | 0.01 | 70.072 | 0.701 |
| 5.01-5.5 | ~22.5 | 0 | - | - | ~86.917 | - |
| TOTAL (6 ha) |  | 80.65 |  | 39.520 |  | 34.169 |
| TOTAL (1 ha) |  | 13.44 |  | 6.587 |  | 5.695 |

# SECTION 3.5

# RESPIROMETRY

## 3.5.1 INTRODUCTION

Measurement of the respiratory rate of termites presents one major problem peculiar to social insects: they normally respire in two quite distinct environments, the nest, where $CO_2$ concentration and temperature are high, (Ruelle 1964, this study Section 3.1), and the foraging galleries, where these factors are similar to the air or soil. Respiration is normally measured in $CO_2$-absorbing apparatus where the atmosphere is quite dissimilar to the nest, and the errors involved here have not yet been quantified. Wiegert (1970) measured respiration of individual castes of Nasutitermes costalis by manometric methods and respiration of whole colonies in situ with an infrared gas analyser. He found that the infrared method gave a higher estimate but attributed this to other fauna and flora decomposing the nest material, rather than to any atmospheric differences.

In addition, it has been shown by Abushama (1974) that the respiratory rate of M. bellicosus workers at 34°C is proportionally greater for single individuals than for groups of five or ten. However, Hébrant (1970), obtained similar respiratory results from whole colonies of Cubitermes exiguus and the sums of their individual castes.

## 3.5.2 METHODS

There were no facilities for respirometry at Mokwa and Dr. Ayanaba of the International Institute of Tropical Agriculture at Ibadan very kindly allowed me to use his Gilson respirometry apparatus. All the work was done on this apparatus, which is of the $CO_2$ absorption type, and hence the effects of a low $CO_2$ environment on the termites are no further elucidated.

Three nests were studied, colonies one and three were of the spiral plate type while colony two was of the plateless type. Each set of measurements took five days. On day one the endoecie of the chosen colony was dug out, put into a polythene-covered drum, and transported to Ibadan, (spiral plate type nests do not occur in the Ibadan region). On days 2-5 respiration rates of neuter castes and fungus combs were measured at 24°, 34°, 30° and 27°C respectively, by doing two four-hour runs on each day. This allowed a total of six replicates for each caste at each temperature and three replicates each for old and new comb (i.e. outer and inner edges of utilised fungus comb). In many cases there are missing replicates due either to leaking respirometers, shortage of material or death of individuals during the tests. Fungus combs degenerated very quickly after day four because of the damage to the nest necessitated by the measurements on days 2-4. As a result, comb measurements at 27°C were clearly abnormally low and although the data are recorded, they will not be used in the analysis.

Caste measurements were done using groups of individuals suited to the size and availability of the caste concerned. For major soldiers, three individuals were used; minor soldiers, four; major workers, six; minor workers, ten; and larvae, fifteen. Approximately 75-125 mg (f.w.) of combs were used. There was no opportunity to study changes in respiration with group size or to measure the respiratory quotient which will be assumed to be 1.0.

### 3.5.3 RESULTS AND DISCUSSION

The full respirometry results at each temperature are given in Appendices 3.5.1 to 3.5.4. The recorded log weights per individual are the means from each batch of termites used. Oxygen consumption of termites is given in $\mu l \ O_2 \ h^{-1} \ g^{-1}$ (f.w.), but for fungus combs in

$\mu l\ O_2\ h^{-1}\ g^{-1}$ (d.w.), since the proportion of water in the combs was more variable than in the termites. Comb samples were dried for 24 hours at 70°C to provide conversion factors.

Any differences between the colonies used in the experiments must be assessed and an analysis of variance has been done for castes and combs at four temperatures (castes) or three temperatures (combs). The variance ratios are recorded in Table 3.5.1 and show that for castes and combs there was no significant difference between colonies with the exception of major workers. This latter observation is difficult to interpret and may be erroneous. Conversely there were significant differences between temperatures for all castes but not for combs. Since the number of replicates in each case was variable, the mean values for each colony at each temperature were used in the calculation and some sensitivity was therefore lost. However, the general conclusion is that the spiral plate and plateless colonies did not differ significantly in the respiratory rates of their castes or combs and can be considered together in further calculations.

### 3.5.3.1 The effect of Temperature on Respiratory Rate

Respiration, especially in poikilotherms, is greatly influenced by temperature and termites are no exception. The data have been analysed by linear regression of respiratory rates of replicates from all colonies, against temperature. Transformation of the y-axis was not justified in most cases but would have reduced the error for larvae to some extent. Matsumoto (1976), however, found that Macrotermes carbonarius respiration increased exponentially with temperature and LaFage (1976) fitted an exponential quadratic function to data from Marginitermes hubbardi. This latter transformation seems particularly difficult to justify biologically. Results and $Q_{10}$ values for my data are given in Table 3.5.2 and the best lines drawn in Figure 3.5.1.

For fungus combs the correlation coefficients and variance ratios are low because of the continuous variation in respiration rate between new (outer) comb and old (inner) comb. It appears that in the aging of the combs, the utilisation of energy resources in the faeces becomes limited. Hence the level of respiration and the $Q_{10}$ values of old comb are lower than those of new comb. This is in keeping with the observation that fungal conidiophores are produced on the middle-aged comb, immediately after fungal respiration (and presumably growth) are at a peak and before resources are limiting.

Variation between respiratory level of the castes appears to be correlated with dry : wet weight ratios and thedegree of sclerotisation. Larvae, with the lowest dry : wet weight ratio (Section 3.2.3.6), respire at a low level, as do major soldiers with heavy chitinous armour. Conversely, minor workers with little chitin have a high respiratory level while major workers and minor soldiers are intermediate.

All castes except major soldiers have a $Q_{10}$ value between two and three, in accordance with van't Hoff's law, suggesting that there is no complication of the simple respiratory chemistry. Variation in major soldier respiration was greater than for other castes, possibly associated with their instinctive aggressive reaction to handling.

### 3.5.3.2 The Effect of Body Weight on Respiratory Rate

The relationship between body weight and respiratory rate has received considerable attention (e.g. Hemmingsen 1960, Zeuthen 1953). It has been reported from both inter- and intraspecific comparisons that small individuals have a higher weight specific rate of oxygen consumption than large ones.

Data are commonly expressed as a power function of body size in one of two ways; for weight specific metabolism the equation is:

$$O_2 \times \frac{1000}{W} = a\,W^{(b-1)}$$

$$\text{or, } \log \left(O_2 \times \frac{1000}{W}\right) = \log a + (b-1) \log W$$

while for total metabolism per individual the equation is:

$$O_2 = \frac{a\,W^b}{1000} \quad \text{or, } \log O_2 = \log a + b \log W - \log 1000$$

where $O_2$ = oxygen consumed per unit time (in µl)

$W$ = weight of animal (in mg)

$a$ = intercept

$b$ = slope in the log plot

The data for soldiers and workers at each temperature have been analysed on a weight specific basis by linear regression of a log - log transformation. Larvae were omitted because of their much lower dry : wet weight ratio (Section 3.2.3.6). The best lines are drawn in Figure 3.5.2 and statistical data given in Table 3.5.3.

The equations for Figure 3.5.2 can be transformed to the total metabolism basis by calculation of b from the slopes of the weight specific equations (b-1). Hence at e.g. 34°C the equation for weight specific metabolism reads:

$$O_2 \times \frac{1000}{W} = 1669.94\,W^{(-.39352)}$$

$$\text{or } \log \left(O_2 \times \frac{1000}{W}\right) = 3.2227 - .39352 \log W$$

and for total metabolism reads:

$$O_2 = \frac{1669.94\,W^{.60648}}{1000} \quad \text{or } \log O_2 = 3.227 + .60648 \log W - \log 1000$$

The data have been expressed in this way in order to be quickly comparable with other data which may be expressed in either form. Best lines for oxygen consumption on a basis of total metabolism per individual are given in Figure 3.5.3.

According to Zeuthen (1953), the value of b is approximately 0.76 for poikilotherms containing more than 1 mg N, and 0.95 for poikilotherms with less. These values should be viewed cautiously and are subject to variation caused by locomotory behaviour and other factors, (see Vernberg and Vernberg 1970 for review). However, the values for b in Table 3.5.3 vary between 0.606 and 0.744 and are clearly of the expected order. Wiegert (1970) obtained a value of 0.84 for Nasutitermes costalis while Wood and Sands (in press) calculated a mean for several sets of data of 1.0886. This latter slope implies that heavier individuals have a greater weight-specific respiratory rate than smaller ones, disagreeing with all previous work. Their calculations have included data from Matsumoto (1976) who found a higher weight-specific respiratory rate for major soldiers than for minor soldiers of Macrotermes carbonarius. In view of the evidence from other sources these findings are questionnable.

TABLE 3.5.1 Variance ratios from analyses of variance of respiratory rates between temperatures and between colonies. Significance has been tested at the 5% level.

| CASTE OR COMB | VARIANCE RATIO BETWEEN TEMPERATURES | SIGNIFICANCE AT 5% LEVEL | VARIANCE RATIO BETWEEN COLONIES | SIGNIFICANCE AT 5% LEVEL |
|---|---|---|---|---|
| Major soldier | 24.7896 | s<br>3 & 6d.f. | 0.6563 | n.s.<br>2 & 6d.f. |
| Minor soldier | 14.5671 | s<br>3 & 6d.f. | 0.1548 | n.s.<br>2 & 6d.f. |
| Major worker | 151.4901 | s<br>3 & 6d.f. | 12.6854 | s<br>2 & 6d.f. |
| Minor worker | 40.4999 | s<br>3 & 6d.f. | 0.8710 | n.s.<br>2 & 6d.f. |
| Larvae | 33.0774 | s<br>3 & 6d.f. | 1.9180 | n.s.<br>2 & 6d.f. |
| New fungus comb | 3.7137 | n.s.<br>2 & 4d.f. | 0.5483 | n.s.<br>2 & 4d.f. |
| Old fungus comb | 4.9289 | n.s.<br>2 & 4d.f. | 2.7937 | n.s.<br>2 & 4d.f. |

TABLE 3.5.2 The relationships between respiratory rates and temperature for five neuter castes of *Macrotermes bellicosus*, (R in µl $O_2$ $hr^{-1}$ $g^{-1}$ wet wt,) and fungus combs (R in µl $O_2$ $hr^{-1}$ $g^{-1}$ dry wt.), with relevant statistical data and $Q_{10}$ values.

| CASTE OR COMB | RELATIONSHIP BETWEEN RESPIRATORY RATE (R) AND TEMPERATURE (T) | STANDARD ERROR | CORRELATION COEFFICIENT (r) | VARIANCE RATIO OF REGRESSION (F) | t VALUE FOR SLOPE | n | p | $Q_{10}$ |
|---|---|---|---|---|---|---|---|---|
| Major soldier | R = 16.4565T-179.3460 | 63.17630 | 0.6887 | 56.8437 | 7.5395 | 65 | $<.001$ | 1.76 |
| Minor soldier | R = 35.3434T-563.5977 | 84.61711 | 0.8479 | 145.8497 | 12.0768 | 59 | $<.001$ | 2.24 |
| Major worker | R = 37.1856T-613.7694 | 50.48231 | 0.9355 | 413.7725 | 20.3414 | 61 | $<.001$ | 2.33 |
| Minor worker | R = 48.4251T-798.7279 | 86.54124 | 0.9021 | 292.9060 | 17.1145 | 69 | $<.001$ | 2.33 |
| Larvae | R = 24.8562T-443.3424 | 54.00723 | 0.8666 | 208.0905 | 14.4253 | 71 | $<.001$ | 2.62 |
| New fungus comb | R = 58.7181T-955.4122 | 214.84219 | 0.771 | 32.2567 | 5.6795 | 24 | $<.001$ | 2.29 |
| Old fungus comb | R = 10.2235T-70.5646 | 75.01923 | 0.5030 | 8.4687 | 2.9101 | 27 | $<.01$ | 1.58 |

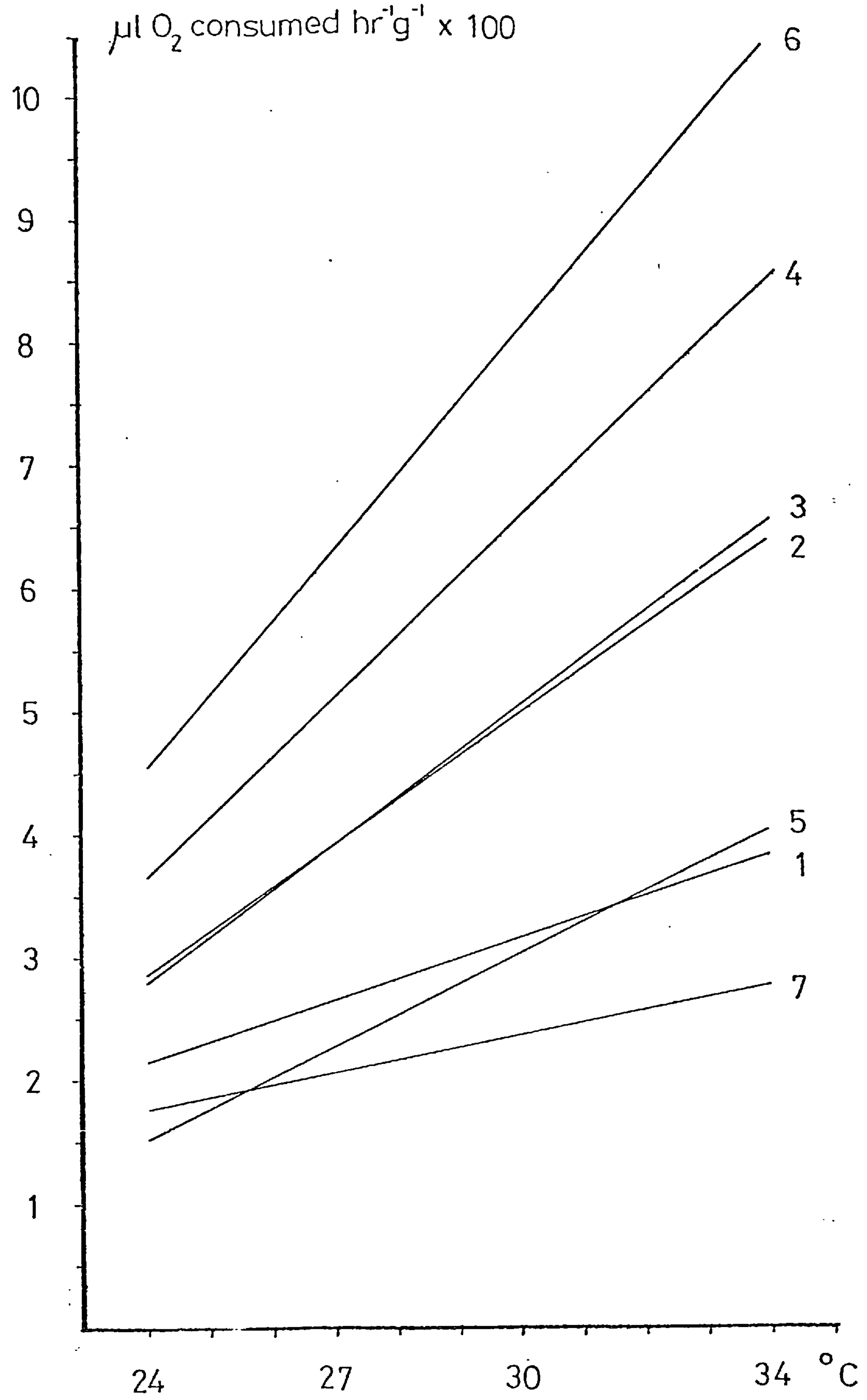


FIGURE 3.5.1 Linear regressions of oxygen consumption $g^{-1}$ (termites f.w., fungus combs d.w.), against temperature. Key:- 1) major soldiers, 2) minor soldiers, 3) major workers, 4) minor workers, 5) larvae, 6) new fungus comb, 7) old fungus comb. Equations are given in Table 3.5.6.

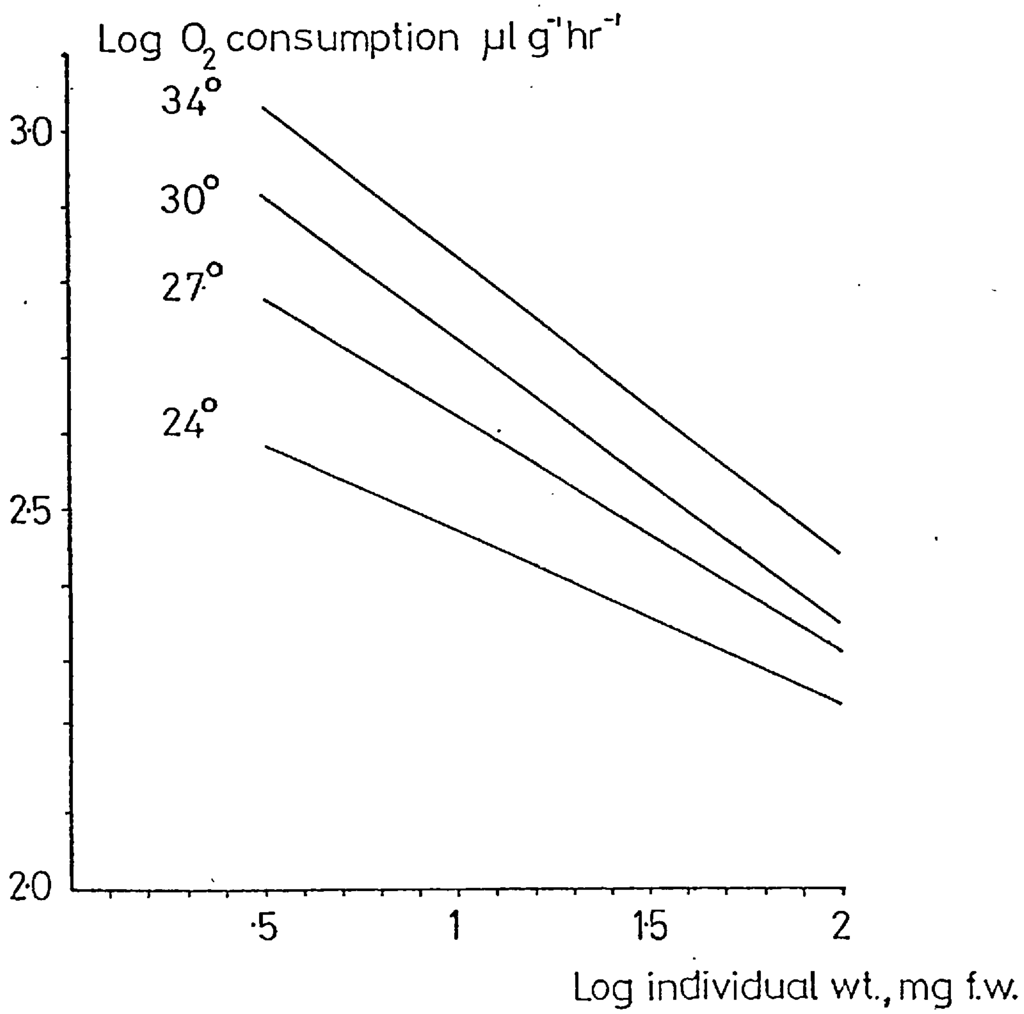


FIGURE 3.5.2 Linear regressions of log oxygen consumption $g^{-1}$ termites against log weight per individual, at four temperatures. (Equations and statistical data are in Table 3.5.3, see also Section 3.5.3.2). Larvae have been omitted from the correlations.

TABLE 3.5.3 Results of linear regression analyses of log $O_2$ consumption ($\mu l\ g^{-1}\ hr^{-1}$ f.w.) against log weight per individual (mg) for soldiers and workers of <u>Macrotermes</u> <u>bellicosus</u> at four temperatures. For explanation of 'b', see text.

| TEMPERATURE °C | INTERCEPT log a | SLOPE (b-1) | b | STANDARD ERROR | CORRELATION COEFFICIENT (r) | VARIANCE RATIO OF REGRESSION (F) | t VALUE FOR SLOPE | n | p |
|---|---|---|---|---|---|---|---|---|---|
| 24° | 2.73066 | -.25589 | 0.74411 | .09037 | -.6670 | 44.0796 | -6.6392 | 57 | $<.001$ |
| 27° | 2.93163 | -.31547 | 0.68453 | .08267 | -.7844 | 99.1795 | -9.9589 | 64 | $<.001$ |
| 30° | 3.10298 | -.38385 | 0.61615 | .08064 | -.8397 | 157.7848 | -12.5612 | 68 | $<.001$ |
| 34° | 3.2227 | -.39352 | 0.60648 | .06890 | -.87793 | 211.8318 | -14.5544 | 65 | $<.001$ |

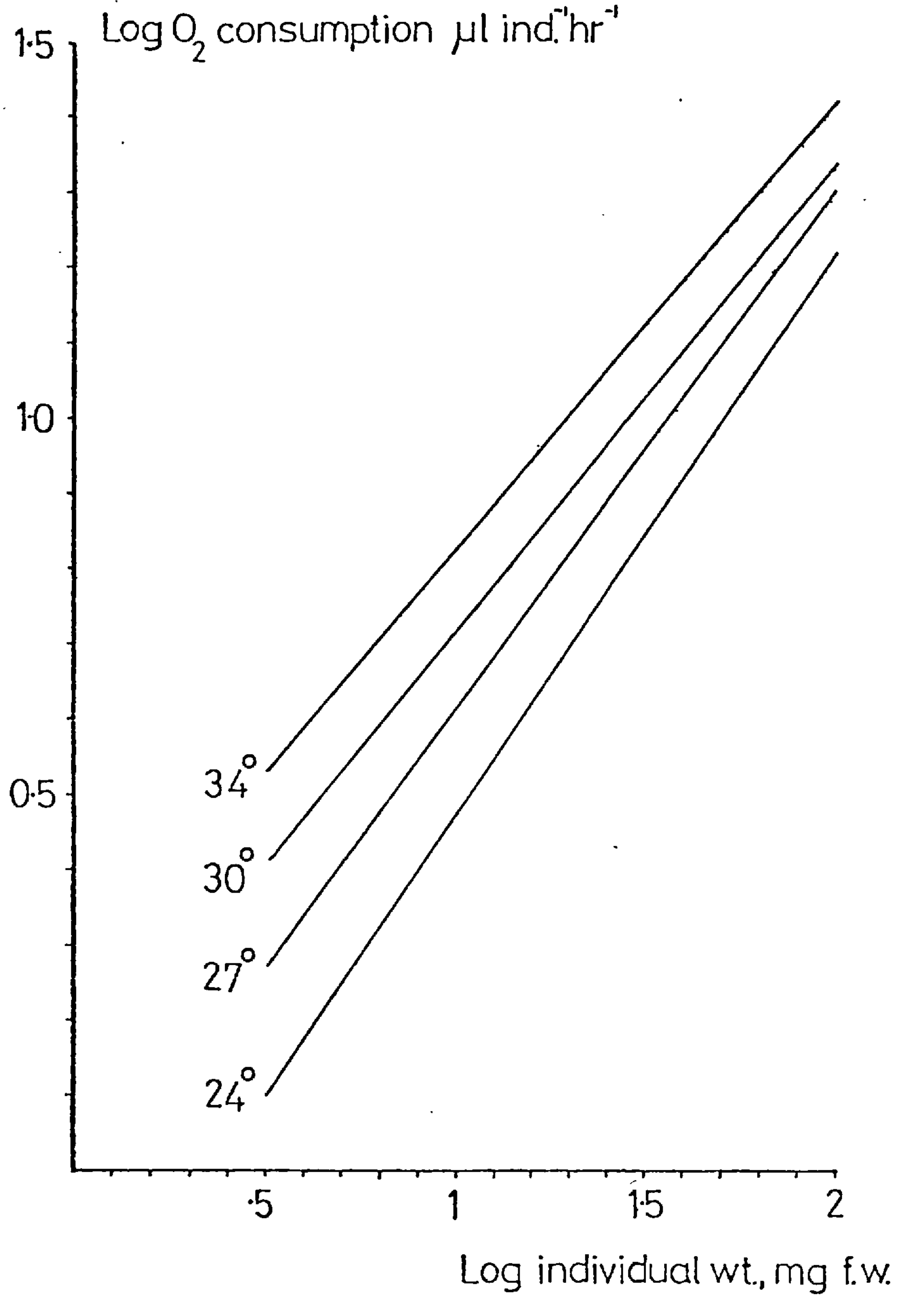


FIGURE 3.5.3 Linear regressions of log oxygen consumption per individual termite against log individual weight, at four temperatures. The lines have been calculated from data in Figure 3.5.2 and Table 3.5.3. (See text for further explanation, Section 3.5.3.2.) Larvae have been omitted from the correlations.

### 3.5.3.3 Population Respiration Calculations and the Relationship between Fungus Comb and Termite Respiration within Colonies

In Table 3.5.4 figures for population biomass of the various castes of M. bellicosus (from Section 3.2.3.6) are used to calculate annual respiration at 30°C simply by multiplying the weight specific respiratory rate by the biomass and converting it to the appropriate time scale. The temperature of 30°C has been chosen as an approximation to the nest temperature. In the case of alates a time scale of three months has again been used as an estimate of the length of time spent in the nest. Since the nymphs grow from 0 to 77.2 mg (f.w.) during this period, an assumed mean weight of 38.6 mg has been used to estimate respiratory rate from the weight specific 30°C regression given in Table 3.5.3.

i.e. $O_2 \times \frac{1000}{W} = a\,W^{(b-1)}$

$$\text{or,} \log \left(O_2 \times \frac{1000}{W}\right) = 3.10298 - 0.38385 \times 1.5866$$

$$\text{so, } O_2 \times \frac{1000}{W} = 311.8663\ \mu l\ h^{-1}\ g^{-1}$$

The mean weight of alates in the nests during the three months is 1109.88 g so the annual respiration is equivalent to:

$$311.8663 \times 1109.88 \times \frac{365}{4} \times 24 = 758.034 \text{ litres } ha^{-1}\ a^{-1}$$

In calculating the area-specific respiration of fungus combs the state of the combs as well as their biomass has been taken into account. In Section 3.4 it has been shown that the fungus comb biomass is equal to 26.060 kg ha$^{-1}$ (d.w.) and it has been estimated from observational evidence that 15% of these combs were unutilised. The respiratory rate of such combs is further assumed to be equal to the respiratory rate of the old part of utilised combs, i.e. 236.1404 $\mu l$ h$^{-1}$ g$^{-1}$ (d.w.) at 30°C. I tried to check this by measuring the respiratory rate of unutilised combs from colony three. Unfortunately the tests could only be run on day six and, as stated, combs began to degenerate after day four. Hence the results are not quantitatively reliable but do support the assumption qualitatively. While utilised comb gave results of 536.158 $\mu l\ g^{-1}$ (d.w.) $h^{-1}$, (new comb, i.e. outer edge) and 163.925 $\mu l\ g^{-1}\ h^{-1}$ (old comb), unutilised comb respired at 248.607 $\mu l\ g^{-1}\ h^{-1}$ (new comb) and 171.821 $\mu l\ g^{-1}\ h^{-1}$ (old comb). The mean respiratory rate for unutilised comb (210.214 $\mu l\ g^{-1}\ h^{-1}$), is only slightly higher than that of old utilised comb (163.925 $\mu l\ g^{-1}\ h^{-1}$).

In all cases the oxygen consumption has been converted to a calorific equivalent by assuming that glucose is the foodstuff being respired, (i.e. R.Q. is equal to 1.0).

$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 673$ kcal (Phillipson 1966)

Hence 1 litre of oxygen is equivalent to 673 ÷ (22.4 x 6), i.e. 5.00744 kcal.

The very high proportion of the respiratory budget attributable to the fungus combs is immediately striking and strongly suggests that the production of heat in nests of Macrotermes bellicosus is largely due to the combs.

To check this contention more thoroughly respiratory budgets have been calculated for termites, (excluding alates), and fungus combs in the 19 colonies sampled for population studies (see Table 3.2.19). Results are given in Table 3.5.5 in terms of calorific output per hour and as the ratio comb output : termite output. In all cases except colony 8 this ratio is greater than one. The estimated ages of the colonies have been included in Table 3.5.5 and although the data are not suitable for statistical analysis there is a suggestion that the ratio is high in very young and very old colonies but rather lower in the reproductive middle range when colonies are at their peak of production.

Further consideration of these respiration results is deferred until Section Four, when all the energetic data can be synthesised and ecological efficiencies calculated.

| CASTE | BIOMASS ($g\ ha^{-1}$, f.w.) | RESPIRATORY RATE AT 30°C ($\mu l\ O_2 hr^{-1}, g^{-1}$ f.w.) | 95% CONFIDENCE LIMITS | ANNUAL RESPIRATION PER BIOMASS CASTE ($litres\ ha^{-1}\ a^{-1}$) | CALORIFIC EQUIVALENT ($kcal\ ha^{-1} a^{-1}$) |
|---|---|---|---|---|---|
| Major soldiers | 268.92 | 314.349 | ± 124.869 | 740.524 | 3,708.130 |
| Minor soldiers | 81.05 | 496.7043 | ± 167.347 | 352.659 | 1,765.919 |
| Major workers | 1032.06 | 501.7986 | ± 99.828 | 4,536.684 | 22,717.173 |
| Minor workers | 1491.54 | 654.0251 | ± 170.952 | 8,545.420 | 42,790.678 |
| Larvae | 1548.97 | 302.3436 | ± 106.677 | 4,102.493 | 20,542.988 |
| Alates | 1109.88 (present for 3 months) | 311.8663 | | 758.034 | 3,795.810 |
| TOTALS | 4720.01 (Annual mean) | | | 19,035.814 | 95,320.696 |

| TYPE OF FUNGUS COMB | | STANDING CROP ($kg\ ha^{-1}$ d.w.) | RESPIRATORY RATE AT 30°C ($\mu l\ hr^{-1} g^{-1}$ d.w.) | 95% CONFIDENCE LIMITS | ANNUAL RESPIRATION PER COMB BIOMASS ($litres\ ha^{-1} a^{-1}$) | CALORIFIC EQUIVALENT ($kcal\ ha^{-1} a^{-1}$) |
|---|---|---|---|---|---|---|
| Utilised | New | 11.0755 | 806.1308 | ± 463.895 | 78,211.923 | 391,641.512 |
| | Old | 11.0755 | 236.1404 | ± 157.144 | 22,910.667 | 114,723.790 |
| Unutilised (Old) | | 3.909 | 236.1404 | ± 157.144 | 8,086.118 | 40,490.751 |
| TOTALS | | 26.060 | | | 109,208.708 | 546,856.053 |

TABLE 3.5.4 Annual respiration calculations, with calorific equivalents, for castes of <u>Macrotermes bellicosus</u> and fungus combs. 95% confidence limits are

$$y_p \pm t s_R \sqrt{\left(1 + \frac{1}{n} + \frac{(xp - \bar{x})^2}{x^2 - (\ x)^2/n}\right)}$$

(Parker 1973)

Calorific equivalents calculated from 6 moles $O_2$ ≡ 1 mole glucose, ≡ 673 kcals., i.e. 1 litre $O_2$ ≡ 5.00744 kcals.

TABLE 3.5.5 Calculations of hourly respiratory budgets (in kcals) for neuter castes and fungus combs of 19 colonies of Macrotermes bellicosus. Figures are calculated from biomass data given in Table 3.2.19 and weight specific respiration data given in Table 3.5.7.

| | NEUTER CASTE RESPIRATION cals h$^{-1}$ | | | | | NEUTER CASTE TOTAL kcal h$^{-1}$ | FUNGUS COMB kcals h$^{-1}$ | | FUNGUS COMB TOTAL kcal h$^{-1}$ | RATIO COMB: NEUTERS CAL. OUTPUT | ESTIMATED AGE OF COLONY (years) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAJOR SOLDIERS | MINOR SOLDIERS | MAJOR WORKERS | MINOR WORKERS | LARVAE | | UTILISED | UNUTILISED | | | |
| 1 | 5.61 | 2.36 | 13.10 | 23.37 | 21.40 | 0.066 | 0.446 | 0.036 | 0.481 | 7.29 | 0.6 |
| 2 | 3.24 | 6.45 | 33.96 | 111.98 | 86.24 | 0.242 | 1.484 | 0.119 | 1.603 | 6.62 | 1.15 |
| 3 | 9.10 | 10.71 | 200.18 | 198.09 | 117.92 | 0.536 | 1.892 | 0.151 | 2.043 | 3.81 | 1.90 |
| 4 | 19.39 | 8.42 | 92.95 | 254.03 | 96.47 | 0.471 | 0.838 | 0.067 | 0.905 | 1.92 | 2.25 |
| 5 | 18.33 | 15.06 | 209.61 | 348.07 | 233.17 | 0.824 | 4.652 | 0.372 | 5.023 | 6.10 | 2.60 |
| 6 | 47.56 | 17.82 | 169.02 | 333.59 | 338.35 | 0.906 | 2.449 | 0.196 | 2.645 | 2.92 | 2.90 |
| 7 | 17.64 | 65.74 | 705.24 | 1435.84 | 700.28 | 2.925 | 11.619 | 0.929 | 12.548 | 4.29 | 3.45 |
| 8 | 131.38 | 62.26 | 655.36 | 1777.66 | 196.70 | 2.823 | 1.590 | 0.127 | 1.718 | 0.61 | 3.60 |
| 9 | 160.63 | 92.37 | 913.33 | 1850.87 | 702.80 | 3.720 | 26.395 | 2.111 | 28.504 | 7.66 | 4.50 |
| 10 | 118.78 | 103.51 | 602.18 | 1402.19 | 832.44 | 3.059 | 4.066 | 0.325 | 4.391 | 1.44 | 4.85 |
| 11 | 43.60 | 70.28 | 1709.92 | 3220.87 | 1456.96 | 6.502 | 15.927 | 1.274 | 17.200 | 2.65 | 4.95 |
| 12 | 104.74 | 60.35 | 989.38 | 2392.34 | 999.51 | 4.546 | 30.501 | 2.439 | 32.938 | 7.25 | 5.75 |
| 13 | 80.06 | 25.22 | 503.01 | 801.14 | 1358.15 | 2.768 | 36.601 | 2.927 | 39.526 | 14.28 | 7.40 |
| 14 | 215.96 | 38.80 | 727.61 | 1995.15 | 1000.18 | 3.978 | 27.353 | 2.187 | 29.539 | 7.43 | 7.57 |
| 15 | 227.12 | 61.33 | 1203.22 | 2295.69 | 717.60 | 4.505 | 42.146 | 3.370 | 45.514 | 10.10 | 8.39 |
| 16 | 156.57 | 44.86 | 1073.05 | 2819.22 | 1395.33 | 5.489 | 14.166 | 1.133 | 15.298 | 2.79 | 9.75 |
| 17 | 58.16 | 14.54 | 244.30 | 360.54 | 1003.46 | 1.681 | 85.138 | 6.808 | 91.941 | 54.69 | 9.90 |
| 18 | 493.62 | 129.98 | 1592.53 | 2732.29 | 554.75 | 5.503 | 138.927 | 11.109 | 150.030 | 27.26 | 15.50 |
| 19 | 353.35 | 150.08 | 3206.03 | 3296.20 | 315.67 | 7.321 | 45.946 | 3.674 | 49.618 | 6.78 | 20-25 |

# SECTION 3.6

# PRODUCTION

## 3.6.1 INTRODUCTION

Population production (P) is the sum of reproduction (Pr) and body growth of individuals already present in the population (Pg). Hence: P = Pr + Pg (Petrusewicz and Macfadyen 1970)

To obtain a measure of production in a colony of Macrotermes bellicosus would require very precise information on natality, mortality, number, weight, growth rate and production of exuviae in all castes. Such a detailed study was beyond the scope of this project and it has only been possible to obtain an approximation of production by making certain assumptions and calculations which can be applied to the population as a whole.

Production due to reproduction (Pr) consists, in this species, of the production of eggs by the queen. Eggs were not counted in the estimates of colony populations and rate of egg-laying was not measured. Hence Pr cannot be calculated. However, by assuming that recruits grow from zero to adult weight during development, rather than from hatching weight to adult weight, at least the egg contents are accounted for. Egg-shells and exuviae are eaten by the termites.

Production due to growth (Pg) can be divided into growth of alates (Pga) and growth of neuters (Pgn):

i.e. P = Pr + (Pga + Pgn)

Alates are produced once a year by mature colonies and the production of alates has been calculated in Section 3.2.3.6 as approximately 28,753 alates $ha^{-1}$ $a^{-1}$, with a biomass of 2219.73 g $ha^{-1}$ (f.w.), or 1038.31 g $ha^{-1}$ (d.w.), and a calorific equivalent of 7986 kcal $ha^{-1}$.

Production of neuters has not been estimated directly but fairly detailed records of the proportion of larvae and adult neuters in colonies are available (Section 3.2.3.5). Assuming that the area-specific population of neuters and larvae was relatively constant, the larval population would have been recruited into the adult neuter population once during a period equal to the development time of the larvae. It is known that oophagy and cannibalism occur in these colonies and hence the entire larval population at any one instant will not enter the work force. However, this is to some extent accounted for in such an instantaneous assessment since individuals in the latter instars will have already been depleted during earlier instars, i.e. the number of 3rd instar larvae $<$ 2nd instar larvae $<$ 1st instar larvae $<$ eggs.

Further sources of error are the production due to growth of neuter castes in the adult stage, production of saliva used in mound-building and production of exuviae. It has not been possible to estimate any of these factors but they would be expected to be low in comparison to the growth of larvae.

Hence, annual production due to growth of neuter larvae (Pgn), with the reservations outlined above, can be estimated from the number of larvae ($N_l$), their development time or turnover rate ($\theta_l$), and the biomass per individual immediately following the final moult (Bn).

$$Pgn = \frac{365}{\theta} \cdot N_l \cdot Bn$$

### 3.6.2 METHODS

Dealate tandems were collected after the first flight of M. bellicosus in 1976, between 8 and 9 p.m. on April 17th. They were introduced into 20.5 x 25.5 cm glass culture plates. These plates consisted of two sheets of glass separated by thin glass strips on three sides and filled with sub-soil to a depth of 10 cm and with top-soil to a depth of a further 10 cm. For a few days after introduction of the tandems the plates were kept vertically, but once the copularium was well-formed, they were laid horizontally. Plates were kept moist, stored in a dark room and the progress of the incipient colonies examined three or four times a week.

### 3.6.3 RESULTS

A total of 11 observation plates were set up but only six survived the first week or so. Results for these colonies are given in Table 3.6.1. Colony 2 died before the larvae developed into adult neuters and colony 5 is considered unreliable since eggs and first larvae may have passed unobserved resulting in an apparent very fast development time. Colonies 1, 3, 4 and 6 showed larval development times, (first adult eclosion date minus first hatching date), of 38, 35, 32 and 32 days respectively, with a mean of 34.25 days. In all cases, major and minor workers appeared at the same time and minor soldiers with a short (< 2 days) delay. This would be expected from the mechanism of neuter development outlined for this species by Noirot (1955, as Bellicositermes natalensis). No major soldiers developed. On the basis of these observations it will be assumed that in field colonies, the entire larval population had a development time (turnover time) of 34.25 days.

In Section 3.2.3.4 the mean population of M. bellicosus was found to be 1,282,758 individuals $ha^{-1}$. In Table 3.2.16, it has been shown that the mean percentage of larvae in 19 colonies was 58.77%. Hence it can be calculated that the population of larvae was approximately 753,877 individuals $ha^{-1}$. From the development time of larvae it can be further calculated that the annual production of larvae was approximately:

$$\frac{365}{34.25} \times 753{,}877 = 8{,}034{,}018 \text{ individuals } ha^{-1}\ a^{-1}.$$

To convert this figure into biomass and hence production terms is not a simple matter since 1) several castes are involved, 2) the biomass of a newly developed adult is unknown (biomass measurements in 3.2.3.6 include gut contents), 3) some larvae will die and never become adults. However, to facilitate the calculation of an estimate of production, it will be assumed that all larvae developed into minor workers of fresh weight 3.988 mg and dry weight 1.008 mg (from 3.2.3.6). Use of data for this caste will underestimate production of other heavier castes, an error which will be offset by the exaggerated individual biomass (due to gut content), and exaggerated number of adults produced, (due to unquantified larval mortality).

Hence, production due to growth of neuters (Pgn) can be calculated as the product of the number of larvae developing annually (La) and their final biomass (Bn):

$$Pgn = La \cdot Bn$$

In terms of fresh weight:

$$Pgn = 8{,}034{,}018 \times 3.988 = 32{,}040 \text{ g (f.w.) } ha^{-1}\ a^{-1}.$$

and in terms of dry weight:

$$Pgn = 8{,}034{,}018 \times 1.008 = 8{,}098 \text{ g (d.w.) } ha^{-1}\ a^{-1}.$$

Since minor workers have a calorific equivalent of 4.3632 kcal $g^{-1}$ (d.w.) then:

$$Pgn = 8{,}034{,}018 \times \frac{1.008}{1000} \times 4.3632 = 35{,}334 \text{ kcal ha}^{-1} \text{ a}^{-1}.$$

Total production of alates and neuters together (but excluding egg shells, exuviae, growth of mature neuters and saliva used in mound-building) is thus calculated as 34,260 g (f.w.) $ha^{-1}$ $a^{-1}$, or 9136 g (d.w.) $ha^{-1}$ $a^{-1}$, with a calorific equivalent of 43,320 kcal $ha^{-1}$ $a^{-1}$.

TABLE 3.6.1 Timing of important events (in days after tandem formation) in six incipient colonies of Macrotermes bellicosus. Date of first laying in colonies 1, 3 and 6 are assumed since visibility was poor. First laying date and hatching date of colony 5 are exceptional in view of the first adult date and it is considered that the first eggs and hatchlings may have passed unobserved. Only colony 3 survived to the stage of the first fungus comb. This colony was provided with a piece of fungus comb from which to innoculate its own incipient combs.

| Colony number | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Copularium formation | 1-4 | 1-4 | 1-4 | 1-4 | 1-4 | 1-4 |
| First eggs laid | 6(?) | 6 | 6(?) | 6 | 15(?) | 6(?) |
| First eggs hatched | 33 | 33 | 33 | 36 | 44(?) | 36 |
| First adults present | 71 | - | 68 | 68 | 71 | 68 |
| First foraging | - | - | 75 | 75 | 77 | 79 |
| First fungus combs | - | - | 90-95 | - | - | - |

### 3.6.4 DISCUSSION

If the population of Macrotermes bellicosus on the study area was relatively stable and in equilibrium with the other elements of the ecosystem, then it would be expected that an amount equal to the annual production would be returned to the environment each year by death of individuals. Mortality can be divided into two major pathways, 1) death of entire colonies, and 2) death of functional groups such as foraging parties or alates. From the available data, it is possible to quantify the first of these pathways, while other sources offer some data on the second.

1) In the same way as returns of faeces to the environment were calculated, the age/height distribution of colonies on the study area (Figure 3.2.6) has been used to estimate colony mortality and return of termites to the environment. Once again the best fit (survivorship curve) was used, assuming this to be more representative of mortality over a long period of time. The calculations are given in Table 3.6.2, showing that about 6.6 colonies died $ha^{-1}$ $a^{-1}$, with an expected population of 390,731 individuals. In Table 3.2.2.4 it has been shown that the population of M. bellicosus (1,282,758 $ha^{-1}$) was equivalent to 4808.9433 kcal $ha^{-1}$ $a^{-1}$. Therefore, if it is assumed that the caste composition is similar in dying colonies, 390,731 individuals can be calculated as equivalent to 1465 kcal $ha^{-1}$ $a^{-1}$, or 3.4% of the annual production. Many young colonies died as a result of predation following mound damage by rain storms, while mortality of older colonies may have been due either to predation by subterranean Doryline ants or aardvarks (Orycteropus afer), or simply the result of ageing of the royal pair.

2) C. Longhurst has carried out studies on a major predator of termites at Mokwa, the Ponerine ant Megaponera foetens. He estimated

that mortality of Macrotermes bellicosus caused by this species was 142 individuals $m^{-2}$ $a^{-1}$ (pers. comm.). Attacks on Macrotermes bellicosus nests were a rare event, most of the termites being taken from foraging parties. If it is assumed that foraging parties of M. bellicosus contained workers and soldiers in the same proportions as found in nests (Table 3.2.16), and that Megaponera foetens is not caste-selective, then it can be calculated (Table 3.6.3) that the calorific equivalent of termites taken is equal to 10,040 kcal $ha^{-1}$ $a^{-1}$, i.e. 23.2% of the annual figure for production.

Wood and Sands (in press) consider that swarming alates suffer almost 100% mortality. This is supported by data in Figure 3.2.6, which suggests that in the region of 100-200 alate pairs per hectare succeed in founding colonies, representing only 0.7 - 1.4% of the estimated annual alate production. Therefore, taking 100% alate mortality as an approximation, returns of alates to the ecosystem are equivalent to 7986 kcal $ha^{-1}$ $a^{-1}$, or 18.4% of total annual production. These alates would generally be consumed by an array of opportunistic predators, both invertebrate and vertebrate, (see Wood and Sands, in press, for a full review of predators).

Hence, although it is not possible to quantify all the causes of mortality in Macrotermes bellicosus, it can be stated that losses of foragers to Megaponera foetens, and losses of whole colonies and alates to other predators, amounts to 19,491 kcal $ha^{-1}$ $a^{-1}$, or 45% of the annual production.

There are many other factors which have not been quantified, such as losses to predators from rain-damaged colonies which subsequently recover and the losses to many other predators which, although not as specialised as Megaponera foetens, undoubtedly take large numbers of foraging termites. Hence, two conclusions may be drawn. Firstly, the figures for mortality which are available support, in general terms, the estimated level of annual production. Secondly, a large proportion of the annual production is passed into the predatory food-chain, much of this via foraging parties which are vulnerable to attack despite the use of subterranean or mud-covered surface runways. The work of C. Longhurst suggests that ants are major predators.

TABLE 3.6.2 Calculation of mortality of _M. bellicosus_ individuals by death of entire colonies. The return of 390,731 inds. ha$^{-1}$ a$^{-1}$ is equivalent to 1,465 kcal ha$^{-1}$ a$^{-1}$. The population of nests in each rank is taken from Table 3.2.13, the biomass estimated from data in Table 3.2.20 and the calorific equivalent from data in Table 3.2.24.

| MOUND HEIGHT RANGE m | MEAN AGE FOR RANK, x (YEARS) | NUMBER OF COLONIES 6ha$^{-1}$ lx | NUMBER OF COLONIES DYING IN AGE INTERVAL, dx ($=1x_{n+1}-1x_n$) | NUMBER OF COLONIES DYING IN ONE YEAR | POPULATION OF NEST IN EACH RANK | MORTALITY OF INDIVIDUALS PER ANNUM |
|---|---|---|---|---|---|---|
| HYPOGEAL | ~ 0.5 | ~ 45 | 23.51 | 25.01 | ~ 10,000 | 250,100 |
| 0-0.5 | 1.44 | 21.49 | 15.40 | 9.87 | 46,525 | 459,202 |
| 0.51-1.0 | 3.00 | 6.09 | 2.95 | 2.20 | 157,152 | 345,734 |
| 1.01-1.5 | 4.34 | 3.14 | 1.23 | 1.04 | 403,098 | 419,222 |
| 1.51-2.0 | 5.52 | 1.91 | 0.68 | 0.60 | 626,609 | 375,965 |
| 2.01-2.5 | 6.65 | 1.23 | 0.42 | 0.37 | 659,500 | 244,015 |
| 2.51-3.0 | 7.80 | 0.81 | 0.29 | 0.23 | 629,000 | 144,670 |
| 3.01-3.5 | 9.08 | 0.52 | 0.22 | 0.13 | 577,500 | 75,075 |
| 3.51-4.0 | 10.76 | 0.30 | 0.16 | 0.03 | 454,000 | 13,620 |
| 4.01-4.5 | 15.89 | 0.14 | 0.12 | 0.03 | 419,500 | 12,585 |
| 4.51-5.0 | ~ 20.0 | 0.02 | 0.02 | 0.01 | ~ 419,500 | 4,195 |
| 5.01-5.5 | ~ 22.5 | 0 | 0 | 0 | - | 0 |
| TOTAL (6ha$^{-1}$) | | 80.65 | - | 39.520 | | 2,344,383 |
| TOTAL (1ha$^{-1}$) | | 13.44 | - | 6.587 | | 390,731 |

TABLE 3.6.3 Calculation of the calorific equivalent of predation of *Macrotermes bellicosus* individuals by *Megaponera foetens*, (142 individuals $m^{-2}$ $a^{-1}$, C. Longhurst, pers. comm.)

| CASTE | RELATIVE PROPORTIONS OF CASTES (From Table 3.2.16) | NUMBER OF CAPTIVES EXPECTED FROM EACH CASTE $m^{-2}$ $a^{-1}$ | BIOMASS PER INDIVIDUAL, (From Table 3.2.18) mg (d.w.) | EXPECTED CAPTIVE BIOMASS, mg $m^{-2}$ $a^{-1}$ (d.w.) | CALORIFIC EQUIVALENTS OF CASTES (From Table 3 2 23) kcal $g^{-1}$ (d.w.) | EXPECTED CAPTIVE CALORIFIC EQUIVALENTS kcal $m^{-2}$ $a^{-1}$ |
|---|---|---|---|---|---|---|
| MAJOR SOLDIERS | 0.65 | 2.24 | 8.767 | 19.64 | 5.0190 | 0.0986 |
| MINOR SOLDIERS | 0.96 | 3.31 | 1.498 | 4.96 | 4.8318 | 0.0240 |
| MAJOR WORKERS | 10.08 | 34.72 | 2.609 | 90.58 | 4.7918 | 0.4340 |
| MINOR WORKERS | 29.53 | 101.73 | 1.008 | 102.54 | 4.3632 | 0.4474 |
| TOTALS |  | 142.00 |  | 217.72 |  | 1.0040 |

# SECTION FOUR

# SYNTHESIS

## SECTION 4.1

## DISCUSSIONS

### 4.1.1 ENERGETIC EQUATIONS AND ASSESSMENT OF EXPERIMENTAL ERRORS

The energetic data gathered from a population of *Macrotermes bellicosus* can be expressed in the form of two important equations, in accordance with the First Law of Thermodynamics:

$$C = P + R + F \qquad 1)$$

and:

$$A = R + P = C - F \qquad 2)$$

where C = consumption, P = production, R = respiration, A = assimilation and F = faeces production, all terms being expressed in kilocalories per unit area per year, (Petrusewicz and Macfadyen 1970).

The values obtained for these factors are as follows:

Consumption (C) = 1,265,920 kcal $ha^{-1}$ $a^{-1}$ (Section 2.4, Table 2.4.7)
Production (P) = 43,320 kcal $ha^{-1}$ $a^{-1}$ (Section 3.6)
Respiration (R) = 95,321 kcal $ha^{-1}$ $a^{-1}$ (Section 3.5, Table 3.5.4)
Faeces production (F) = 976,574 kcal $ha^{-1}$ $a^{-1}$ (Section 3.4)

Hence, equations 1) and 2) can be re-written as:

$$\begin{array}{ccccccccc} C & & P & & R & & F & & \text{Error} \\ 1{,}265{,}920 & = & 43{,}320 & + & 95{,}321 & + & 976{,}574 & + & 150{,}715 \end{array} \qquad 3)$$

$$\text{and:}\quad \begin{array}{ccccc} A & & R & & P \\ 138{,}641 & = & 95{,}321 & + & 43{,}320 \end{array} \qquad 4)$$

$$\text{or:}\quad \begin{array}{ccccc} A & & C & & F \\ 289{,}356 & = & 1{,}265{,}920 & - & 976{,}574 \end{array} \qquad 5)$$

where the difference in calculated assimilation in equations 4) and 5) is equal to the error term in equation 3). This imbalance of 150,715 kcal $ha^{-1}$ $a^{-1}$ represents 11.91% of the estimate for consumption. Before considering the data further, the probable origins of this error are examined.

1) Un-measured parameters. The dynamics of the food stores have not been clarified to a satisfactory degree. These stores were invariably occupied by termitophiles of various kinds, notably dipterous larvae. Undoubtedly the comminuted and moist nature of the stores made them an excellent substrate for microbial activity, particularly at the high nest temperatures. If it is conservatively assumed that food stores respired at 120 $\mu l\ g^{-1}$ (d.w.) $hr^{-1}$ at 30°C, (old combs respired at 236 $\mu l\ g^{-1}\ hr^{-1}$), and that all food consumed, (240.518 kg $ha^{-1}\ a^{-1}$ (d.w.), passed through the stores and remained there for 10 days, then it can be calculated that about 35,000 kcals per year could be lost to food store respiration, (Rfs). This is considered to be a reasonable assumption and may be included in equation 3) to give:

$$\overset{\text{C}}{1{,}265{,}920} - \overset{\text{Rfs}}{35{,}000} = \overset{\text{P}}{43{,}320} + \overset{\text{R}}{95{,}321} + \overset{\text{F}}{976{,}574} + \overset{\text{Error}}{115{,}715} \qquad 6)$$

2) Measured parameters. Although considerable attention was given to the estimations of colony populations (Section 3.2), clearly not all the individuals were collected. Any errors here were probably minimal in comparison to those in the construction of the population/age model in Figure 3.2.7, and its use in area-specific population estimates. Some support for these estimates is derived from calculation of weight-specific consumption rates from population-independent baiting results, (Table 3.3.3), which agree reasonably with consumption rates from isolation tank experiments, where the population was accurately assessed. Field consumption measurements are perhaps slightly too high (see below), but this is probably due to overestimates in baiting rather than to underestimates of populations.

Respiration and production measurements were based on population extrapolations (Sections 3.5, 3.6) and some error was undoubtedly involved. Certain small, unquantified production parameters have already been discussed, (Section 3.6). However, annual production and respiration values are comparatively low and a small percentage error cannot possibly absorb the error factor in equation 6).

Conversely, both consumption (C) and faeces production (F) are large values. The estimates of consumption were based on large-scale field experiments in relatively uncontrolled conditions. The baiting results in particular, show considerable variation between plots (Table 2.4.4). The results were checked in isolation tank experiments (Section 3.3) and supported by food store calculations (Section 3.2). The synthesis of consumption data, (Table 3.3.3, Section 3.3.4.2) has shown a general agreement but suggested that the field data were close to the upper limit of the consumption range. Hence there is a possibility that the consumption value is a slight overestimate.

The calculations of annual faeces production, (Section 3.4), are perhaps the most tenuous of all the data. Although the standing crop biomass of fungus combs was calculated on a reasonable statistical basis, there is no doubt that the turnover rate, (based on one result), and the tardy realisation of dead comb accumulation, (and consequent assumptions), detract from the reliability of the final figure. The error of 115,715 kcal $ha^{-1}$ $a^{-1}$, representing only 11.85% of this estimate, is well within the bounds of subjective confidence limits.

I therefore conclude that the error is partly due to an overestimate of consumption, but mainly to an underestimate of faeces production. In further considerations, the assimilation (A) will be taken as the sum of respiration and production as given in equation 4), i.e. 138,641 kcal $ha^{-1}$ $a^{-1}$.

## 4.1.2 ECOLOGICAL EFFICIENCIES AND A CONSIDERATION OF THE ROLE OF THE FUNGUS COMBS

The assimilation efficiency of *Macrotermes bellicosus* cannot be accurately quantified due to the errors discussed in Section 4.1.1. When calculated from $\frac{C-F}{C}$ x 100, the value is equal to 22.86%, but when calculated as $\frac{R+P}{C}$ x 100, is equal to 10.95%. Hence, the assimilation efficiency can only be assigned to a range between these two values, both of which are low when compared with examples from other groups of termites, (50-60%, Wood, in press) and plant feeding terrestrial invertebrates in general (about 30%, Phillipson 1973).

Other measures of efficiency are concerned with the utilisation of assimilated food, i.e. the relationships between values for respiration (R), production (P), assimilation (A = R+P), and the biomass (B) of the population concerned.

The calorific production to biomass ratio for *Macrotermes bellicosus* can be calculated as equal to 7.46, (production = 43,320 kcal $ha^{-1}$ $a^{-1}$, biomass = 5,807 kcal $ha^{-1}$, Section 3.2.3.8). This value can be divided into two components:- production of alates (1.375) and production of neuters (6.085).

Comparable energetic data from termites are few and incomplete. Lepage (1974) and Josens (1972a, 1973), have provided the most complete studies, and Wood and Sands (in press), have used calorific data from Josens (1972a) and Matsumoto (1976) to calculate calorific production to biomass ratios. For Macrotermitinae the values given are 10.2 (*Ancistrotermes cavithorax*), 6.5 (*Macrotermes subhyalinus*, and 5.4 (*Odontotermes smeathmani*). For Nasutitermitinae the values are 3.3 (*Trinervitermes geminatus*), 1.5 (*idem*), and 3.9 *Trinervitermes* *trinervius*), with one value from the Rhinotermitidae of 3.4 (*Psammotermes hybostoma*).

Hence, while species other than Macrotermitinae show ratios similar to those of other invertebrates, (about 3:1, Phillipson 1973), the Macrotermitinae have ratios two to three times higher. Wood and Sands (in press) attribute this difference mainly to higher neuter production in the Macrotermitinae.

Wood and Sands (*loc. cit.*), have used population and biomass data from Josens (1972a, 1973) and Lepage (1974), to estimate annual respiration values for several species of termites. Their calculations have been shown to fit the regression of production and respiration data collected from a range of poikilotherms by McNeill and Lawton (1970). My own data for *Macrotermes bellicosus* are also in good agreement with the regression, which is reproduced in Figure 4.1.1.

Respiration and production data are frequently examined in comparison with the value for assimilation. Hence, in this study, the respiration loss, defined as:

$$\frac{R}{A} \times 100, \text{ is equal to: } \frac{95{,}321}{138{,}641} \times 100, \text{ i.e. } \underline{68.75\%}$$

and the net population production efficiency, defined as:

$$\frac{P}{A} \times 100, \text{ is equal to: } \frac{43{,}320}{138{,}641} \times 100, \text{ i.e. } \underline{31.25\%}$$

where assimilation (A) is equal to the sum of respiration (R) and production (P). The respiration loss and production efficiency are therefore complementary values, together adding up to 100%. In general, production efficiencies of homoiotherms are in the range 1-2%, while the value for insects is 20-60%, (McNeill and Lawton 1970, Wiegert and Evans 1967, Engelmann 1966). Respiration is a measure of the work done in maintenance of body processes and in the homoiotherms this includes maintenance of body temperature. The resulting low production efficiency of this group is largely offset by a high assimilation efficiency.

Production efficiencies calculated from the works of Josens (1972a, 1973) and Lepage (1974) by Wood and Sands (in press), can be compared with my data. For Macrotermitinae the values given are 55.6% (Ancistrotermes cavithorax), 30.4% (Macrotermes subhyalinus) and 42.3% (Odontotermes smeathmani). For Nasutitermitinae the values are 19.1% (Trinervitermes geminatus), 11.0% (idem), and 26.2% (Trinervitermes trinervius), with one value from the Rhinotermitidae of 33.5% (Psammotermes hybostoma). The calculated values from the Macrotermitinae are fairly consistent with my measured estimate of 31.25% for Macrotermes bellicosus and there is clearly an indication that the Macrotermitinae are more efficient producers (in terms of respiratory costs) than are the Nasutitermitinae.

It therefore appears that the Macrotermitinae have higher production to biomass ratios and higher production efficiencies than many other invertebrates including at least some other groups of termites. This is perhaps even more surprising in view of the relatively nutrient-poor, undecayed, plant litter which constitutes their main diet.

The nutrition of M. bellicosus and most other Macrotermitinae appears to be dependent in some way upon the symbiosis with the fungi Termitomyces spp. Since the effect of the fungal metabolism is presumably to transform the foodstuff into a form more suitable for production of termite tissue, it is pertinent to examine the production efficiency of M. bellicosus with inclusion of the estimate for fungal respiration (Rfc). Hence:-

$$\text{Production efficiency of termite/fungus system} = \frac{P}{A+Rfc} \times 100 = \frac{43,320}{138,641+546,856} \times 100 = \underline{6.32\%}$$

This figure approaches the very low level found in homoiotherms. However, unlike the case of the homoiotherms, the low efficiency is not offset by a high assimilation efficiency. What is it then, that offsets the very high energetic cost of the symbiosis?

There is no doubt that plant litter in general, is a very poor food source in terms of nutrient concentration and availability. No known vertebrates are capable of utilising it, and there are strong indications that the majority of invertebrate litter feeders require some degree of fungal breakdown before litter becomes palatable (Fittkau and Klinge 1973, Burges 1967, Section 2.5). This generalisation also extends to other groups of termites. Kovoor (1964a, b, 1966) has shown that Microcerotermes edentatus is able to digest wood more completely once it has been subjected to attack by certain fungi, and many other examples are reviewed by Sands (1969). The essential action of the fungi may be in the respiration of organic carbon and concentration of nutrients into fungal protoplasm. Hungate (1940) has shown that weight loss in rotted wood did not affect the percentage of nitrogen by volume and assumed that losses were due to decomposition of carbon compounds. The rotting of wood is particularly efficiently performed by "white-rot" fungi which are able to break down polyphenols (Walker 1975), and it appears that Termitomyces spp. also have this ability (Dr. M.J. Swift, pers. comm.).

There is evidence that this action of fungi in concentrating nutrients also occurs in the fungus combs of Macrotermes bellicosus. In Section 3.4.3 (Table 3.4.3) it has been shown that nutrients such as N, Ca and K (and perhaps others which are less easily quantified) are more concentrated in the middle-aged section of each comb. Since it has also been shown that the respiratory rate of young comb is very high (Section 3.5), nutrient concentration may be attributed to the carbon losses involved. However, respiratory losses continue in older comb but nutrient concentrations appear to be lower in old comb than in middle-aged comb. My own observations and those of Grassé and Noirot (1958) have shown that the fungal conidiophores and conidia grow mainly on the middle-aged section of combs. Matsumoto (1976) has shown that these nodules contain a very high proportion of nitrogen (7.3-7.4% in two spp. of Macrotermes). They are consumed by the termites (particularly larvae) and their high nitrogen content is undoubtedly of value in accelerating growth. However, removal of the nodules depletes the nutrients in the combs, resulting in lower nutrient levels in the older sections of combs than in the middle sections. Even so, nitrogen and other nutrient levels are higher in old comb than in food stores or litter and therefore the comb still represents a high quality food source. Nitrogen has been cited as a representative nutrient because of its importance as a constituent of amino-acids and the ease and accuracy with which it can be measured, but it should not be taken as an indication that other elements are not equally as important. However, there is considerable recent evidence of the importance of nitrogen in insect-plant relationships (e.g. Hill 1976, Tamm 1975, McNeill 1973, further bibliography in Hill loc. cit.), particularly in terms of limiting insect populations.

In answer to the question as to what benefits are gained from the high energetic cost of the termite/fungus symbiosis, it may therefore be stated that in dispersing organic carbon compounds which are in excess of the needs of the termites, a food source of high nutritional value is obtained. The effects of the symbiosis and its advantages are four-fold.

Firstly, by virtue of their fungal association, the Macrotermitinae are able to utilise a plentiful food resource (fresh plant litter) which is in little demand by other animals.

Secondly, the high quality diet of Macrotermes bellicosus permits the high production to biomass ratio discussed earlier in this section. The production appears to be largely offset by heavy predation on the foraging population (Section 3.6). This may be contrasted with another highly successful group of termites, the Nasutitermitinae. This subfamily feeds on all forms of plant debris except very fresh dead wood. Their production to biomass ratios are not as high as those of the Macrotermitinae but their losses to predation are probably lower since the development of the frontal gland in the soldiers renders them unpalatable to many predators, notably ants (Ohiagu 1976). Hence, it may be speculated that while the evolutionary strategy of the Macrotermitinae has been to meet predation pressure by production of vast numbers of expendable and quickly replaceable neuters, the strategy of the Nasutitermitinae has been avoidance of predation pressure by the development of chemical defences. This apparent difference is of some considerable interest since it renders the Macrotermitinae a more important link in the consumer food chain.

Thirdly, a peculiar feature of the Macrotermitinae that has not been previously explained, is the fact that they have a uniform, simplified digestive tube similar to that of the Kalotermitidae and Rhinotermitidae and in contrast to that of other Termitidae, (Noirot and Noirot-Timothée, 1969). I would like to suggest that this simplification has been permitted by the development of an external digestive mechanism in the form of fungus combs. A corollary may be that the time required for passage of food through the gut is shorter, allowing the high weight-specific consumption rates that have been recorded (Section 3.3.4.2).

Finally, extra energetic costs to the termites which result from the symbiosis, are only the need for building suitable nests to contain the fungus combs and perhaps some attention to "weeding" the cultures. For functions such as these, the highly developed social behaviour of the Isoptera is ideally suited. It is therefore perhaps not surprising that the most complex nests in the insect world are found in the Macrotermitinae, notably in those of Macrotermes bellicosus described earlier (Section 3.1). In view of the importance of the fungus combs which has become apparent in the last few sections, the structure of the nest of Macrotermes bellicosus may be briefly re-assessed. The facts that the combs occupy most of the space in the habitacle and also produce most of the heat which causes the high temperatures in the nest, suggest that they have more influence on nest structure than has previously been supposed. The nest temperatures are known to be optimal for growth of the fungus (M.J. Swift, pers. comm.) and it is the behaviour of the termites, in constructing the mound, that ensures the maintenance of these temperatures. The evolutionary development of the nest therefore seems to be a matter of co-adaptation between the termites and their fungal symbionts.

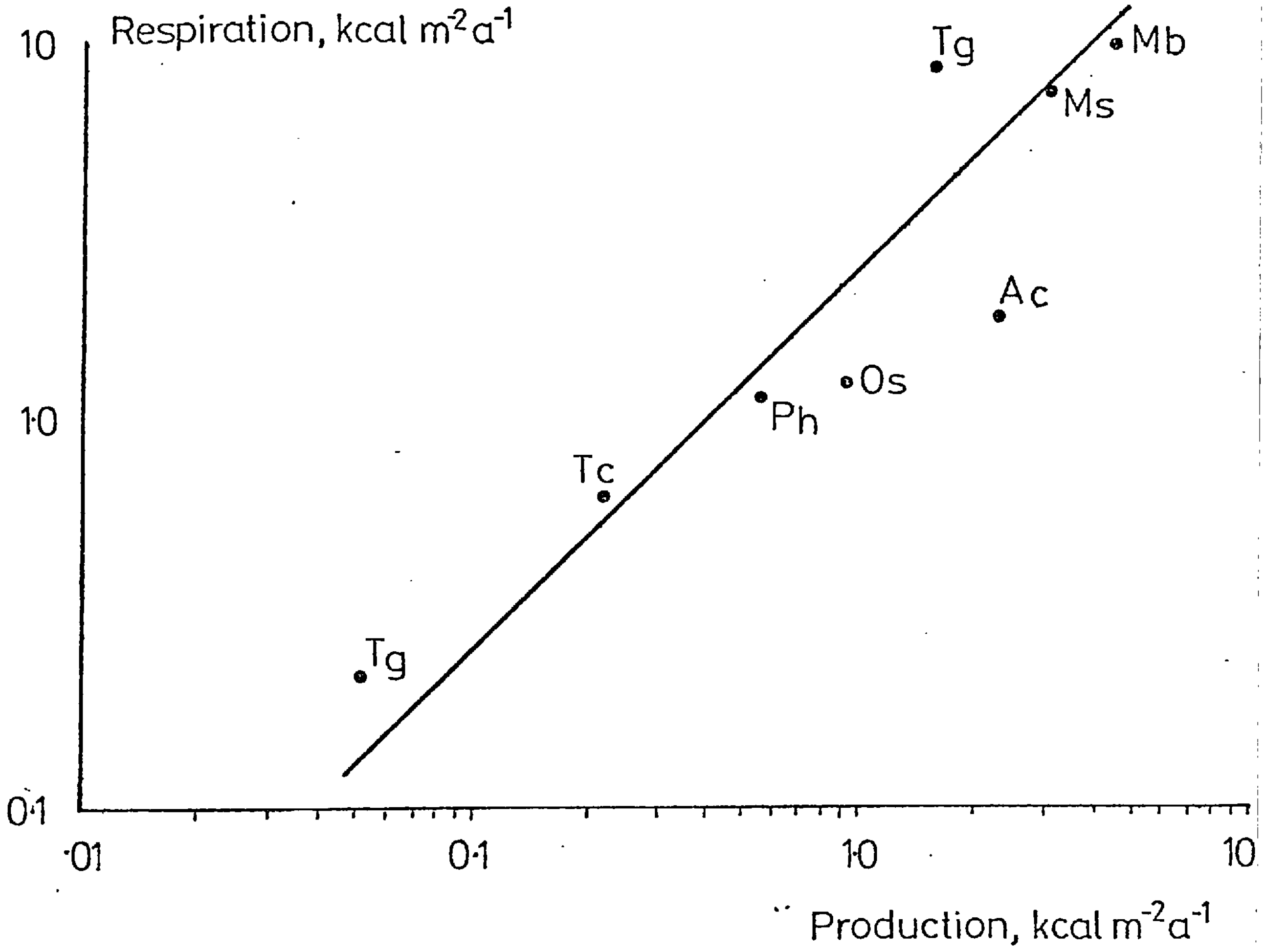


FIGURE 4.1.1 Double log plot of annual respiration and production data from termites. Tg = Trinervitermes geminatus, Tt = Trinervitermes trinervius, Ph = Psammotermes hybostoma, Ac = Ancistrotermes cavithorax, Os = Odontotermes smeathmani, Ms = Macrotermes subhyalinus, Mb = Macrotermes bellicosus (present study). The regression line is from a wide range of poikilotherms (McNeill and Lawton 1970). After Wood and Sands (in press).

## SECTION 4.2

## FINAL CONCLUSIONS

Many conclusions relevant only to individual sub-sections have been put forward immediately following them. In these final conclusions the major points pertaining to the role of Macrotermitinae as litter-feeders are brought together and emphasised by reference to the more important biological and ecological characteristics of *Macrotermes bellicosus*.

In Section Two, data on litter production, accumulation and decomposition have been described and the important role of the Macrotermitinae quantified (Fig. 2.2.4). It was suggested that this sub-family accelerates litter removal through its ability to feed on relatively fresh, undecayed plant litter. This is considered to be of particular importance in the savannas, where seasonality of rainfall slows down the fungal and microbial decomposition pathways which are of primary importance in temperate and rain forest ecosystems.

Data from Section Three are summarised in Figure 4.1.2. It has been found that by virtue of a symbiotic relationship with a white-rot fungus, *Termitomyces* sp. *Macrotermes bellicosus* is efficient in extracting nutrients from its low quality litter diet.

Foodstuffs are initially stored on top of the fungus combs where, facilitated by high nest temperatures and humidity, some moistening and microbial decay may occur. After seven to ten days the food is consumed and rapidly passes through the relatively unspecialised alimentary canal. Assimilation is low in this first passage and the large amounts of faeces produced are built into a system of combs upon which the fungus Termitomyces grows. The metabolism of the fungus results in release of large amounts of carbon dioxide, thereby concentrating valuable nutrients in the fungus combs. The high heat output from the combs is used to maintain an optimal nest temperature by construction of a highly complex nest system around the combs. Undoubtedly the fungus-termite symbiosis has considerably influenced the evolution of the nest-building behaviour.

After a time, the fungus produces nitrogen-rich nodules (consisting mainly of conidiophores and conidia) on the surface of the combs, upon which the termites, mainly larvae, begin to feed. After a further period of fungal degradation the termites consume the comb itself, which by this time is also rich in nutrients and is easily assimilable. The building and consumption of combs is a continuous process, at least in Macrotermes bellicosus.

As a result of this high quality diet, Macrotermes bellicosus is able to maintain a high production to biomass ratio and high production efficiency. The consequent high populations and fast turnover of this species and of other Macrotermitinae, renders the termite-fungus symbiosis an important link in the passage of nutrients from plant litter to the consumer food chain in Southern Guinea savanna.

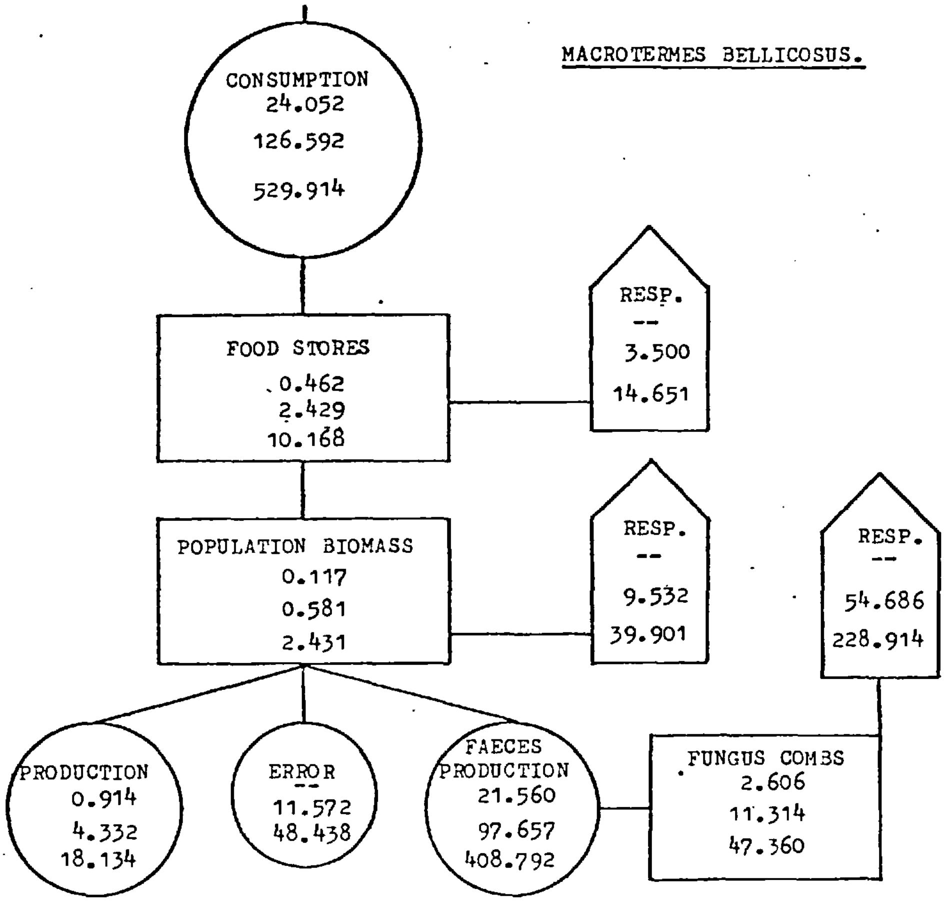


FIGURE 4.2.1 Flow diagram summarising data from Section 3 (energetics of Macrotermes bellicosus). In each compartment the upper figure is biomass (g $m^{-2}$, d.w.), the centre figure is the calorific equivalent (kcal $m^{-2}$) and the lower figure is the joule equivalent (kj $m^{-2}$). The text should be consulted for more precise values. Estimates of standing crops are in boxes, flux values in circles (flux $a^{-1}$), and energy losses through respiration in cones (loss $a^{-1}$).

# THE POPULATION ECOLOGY AND ENERGETICS OF *MACROTERMES BELLICOSUS* (SMEATHMAN), ISOPTERA.

## SUMMARY

1) This study was carried out at Mokwa (5°04'E, 9°18'N), in the Southern Guinea savanna climatic and vegetation zone of Nigeria. The climatic, edaphic and vegetational features of the area are described and an inventory of termite species is given.

2) The annual production of woody litter was estimated as 1.391 t ha$^{-1}$ a$^{-1}$ (7,598,256 kcal ha$^{-1}$ a$^{-1}$). This decomposed at a measured rate of 50.98% a$^{-1}$ (calculated rate 49.31% a$^{-1}$), resulting in a mean standing crop of wood of 2.821 t ha$^{-1}$ (15,412,251 kcal ha$^{-1}$). The annual production of leaf litter was estimated as 2.387 t ha$^{-1}$ a$^{-1}$ (11,238,932 kcal ha$^{-1}$ a$^{-1}$). This decomposed at a calculated rate of 264.3% a$^{-1}$, resulting in a mean leaf litter standing crop of 0.903 t ha$^{-1}$ (4,248,969 kcal ha$^{-1}$). Total annual litter production was thus 3.778 t ha$^{-1}$ a$^{-1}$ (18,837,188 kcal ha$^{-1}$ a$^{-1}$) and the mean total standing crop of litter was 3.724 t ha$^{-1}$ a$^{-1}$ (19,661,220 kcal ha$^{-1}$ a$^{-1}$), giving a calculated decomposition constant (k) of 95.81% a$^{-1}$.

3) Termites removed 835.464 kg ha$^{-1}$ a$^{-1}$ of wood litter (4,564,474 kcal ha$^{-1}$ a$^{-1}$), representing 60.1% of the annual wood fall. They also removed 68.44 kg ha$^{-1}$ a$^{-1}$ of leaf litter (322,195 kcal ha$^{-1}$ a$^{-1}$), representing 2.9% of the annual leaf fall. Total removal of litter by termites was thus 903.904 kg ha$^{-1}$ a$^{-1}$ (4,886,669 kcal ha$^{-1}$ a$^{-1}$), representing 23.9% (by weight) or 25.9% (by calorific values) of the total annual litter production.

4) A field method for quantitatively separating the role of the various termite species was developed, revealing that 860.635 kg $ha^{-1}$ $a^{-1}$ (4,650,273 kcal $ha^{-1}$ $a^{-1}$), or 95.2% of the litter taken by termites, was removed by the Macrotermitinae (fungus-growers).

5) The annual bush fire removed about 12.5 kg $ha^{-1}$ (68,293 kcal $ha^{-1}$) of wood litter, (0.9% of wood fall), and 1,173 kg $ha^{-1}$ (5,520,296 kcal $ha^{-1}$) of leaf litter (49.1% of leaf fall), with a total of 1,185.5 kg $ha^{-1}$ (5,588,589 kcal $ha^{-1}$), i.e. 31.4% (by weight) or 29.7% (by calorific values) of annual litter production.

6) It is concluded that the Macrotermitinae removed 34.45% of the annual litter fall available for biotic decomposition, most of this being relatively fresh woody litter. Their ability to feed on this undecomposed substrate is an important element in the high turnover rate of litter and distinguishes decomposition processes in savanna from the essentially fungal and microbial based patterns found in equatorial and temperate forests.

7) The structure and function of a previously undescribed nest of _Macrotermes bellicosus_ are discussed. The spiral base-plate and size of the nest suggest that it is the most advanced structure built by the Isoptera and possibly by the Insecta as a whole. The pattern is considered to be largely due to co-adaptation between the termites and their fungal symbionts.

8) From colony population counts and annual mound censuses, the population density of _M. bellicosus_ neuters (including larvae), has been estimated as 1,282,758 inds. $ha^{-1}$, equivalent to a biomass of 4,442.54 g $ha^{-1}$ (f.w.) or 1,043.56 g $ha^{-1}$ (d.w.), (4,809 kcal $ha^{-1}$). Alate production was estimated as 28,753 inds. $ha^{-1}$ $a^{-1}$, equivalent to a biomass of 2,219.73 g $ha^{-1}$ $a^{-1}$

(f.w.) or 1,038.31 g $ha^{-1}$ $a^{-1}$ (d.w.), (7,986 kcal $ha^{-1}$ $a^{-1}$). Allowing for the presence of alates for a limited period only, the mean biomass of neuters plus alates is calculated as 4,720.01 g $ha^{-1}$(f.w.) or 1,173.35 g $ha^{-1}$ (d.w.) (5,807 kcal $ha^{-1}$).

9) Field estimates of consumption by Macrotermes bellicosus were checked in feeding trials on colonies isolated in large concrete tanks. The estimate of 139.608 mg (d.w.) $g^{-1}$ (f.w.) $d^{-1}$ or 240.518 kg $ha^{-1}$ $a^{-1}$ (1,265,920 kcal $ha^{-1}$ $a^{-1}$), was well supported by the data.

10) Faeces production by M. bellicosus, as calculated from the standing crop biomass of fungus combs and their turnover rate, was estimated as 215.603 kg $ha^{-1}$ $a^{-1}$ (d.w.), (976,574 kcal $ha^{-1}$ $a^{-1}$). In the light of an assimilation value calculated from production and respiration data, the value for faeces production was considered to be under-estimated by up to 12%, although a small part of the error may have been due to a slight over-estimation of consumption.

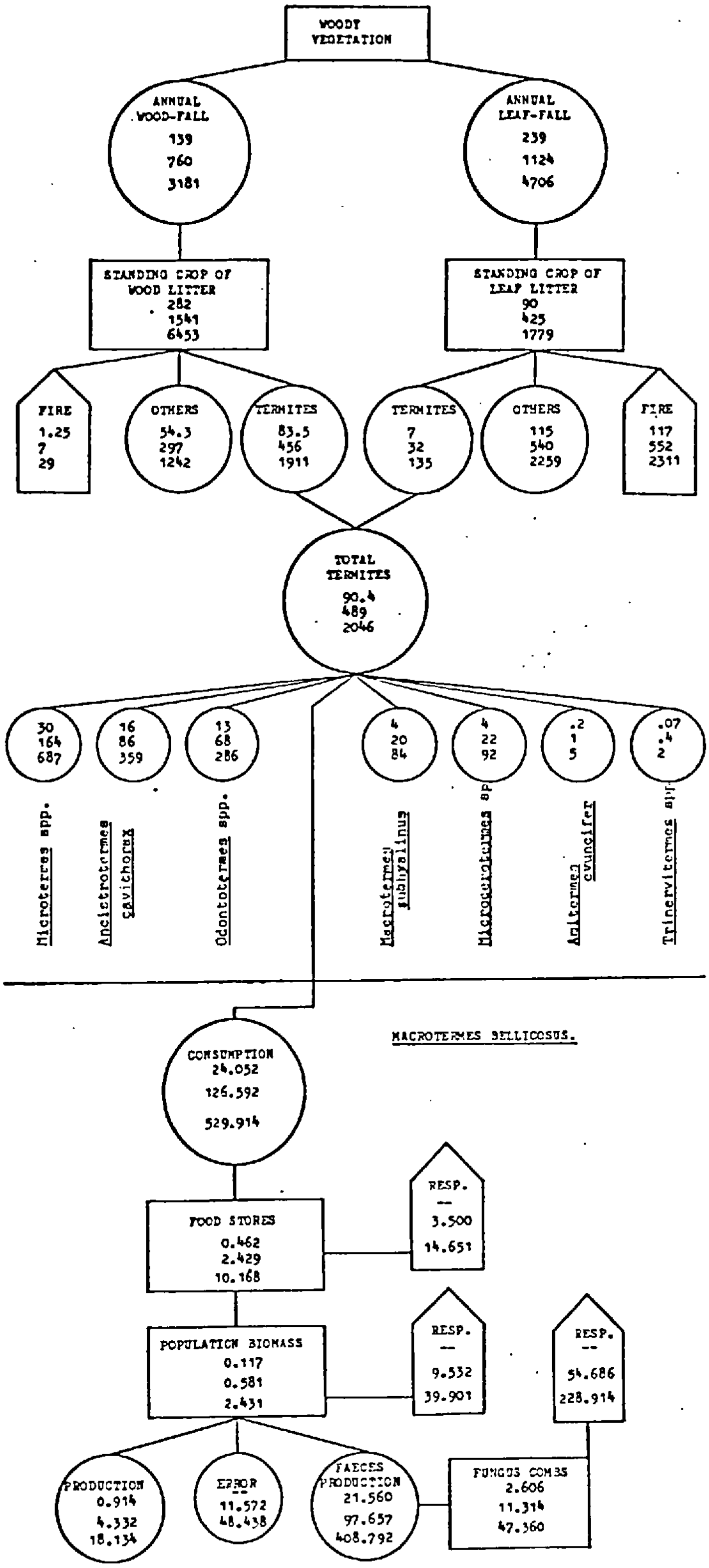
11) By extrapolation fron groups of individuals in Gilson respirometers, population respiration of M. bellicosus was estimated as 95,321 kcal $ha^{-1}$ $a^{-1}$. Respiration of fungus combs was estimated at the far greater value of 546,856 kcal $ha^{-1}$ $a^{-1}$. Calculations showed that heat production in nests was mainly due to the metabolism of the fungus combs.

12) Production due to growth of alates and neuters was estimated from alate production, larval populations and larval development time as 34,260 g $ha^{-1}$ $a^{-1}$ (f.w.), 9,136 g $ha^{-1}$ $a^{-1}$ (d.w.), (43,320 kcal $ha^{-1}$ $a^{-1}$). The production estimate was supported, in general terms, by incomplete mortality data.

13) A consideration of ecological efficiencies showed that the production to biomass ratio (7.46) and the net population production

efficiency (31.25%) of *M. bellicosus*, are high in comparison with other invertebrates and non-Macrotermitinae termites.

14) It is concluded that the symbiosis between *Macrotermes bellicosus* and the fungus *Termitomyces* sp. permits decomposition of faeces inside the nest and concentration of nutrients within the fungus combs. This is facilitated by the metabolism of the fungus which oxidises the organic carbon, thus lowering the carbon : nitrogen ratio of the substrate, which is re-consumed by the termites. Heat evolved by the combs is used to create an homoeostatic microclimate which is optimal for fungal and termite metabolism. The resulting high quality diet of the termites permits a high production to biomass ratio and high production efficiency, which render the termite-fungus symbiosis an important link in the passage of nutrients from plant litter to the consumer food chain.



Summary of the data concerning litter dynamics, consumption by termites and the energetics of *Macrotermes bellicosus* in Southern Guinea savanna. In each compartment the upper figure is biomass (g $m^{-2}$, d.w.), the centre figure is the calorific equivalent (kcal $m^{-2}$) and the lower figure is the joule equivalent (kj $m^{-2}$). Estimates of standing crops are in boxes, flux values in circles (flux $a^{-1}$), and energy losses through fire or respiration in cones (loss $a^{-1}$).

"Science tells us what we can know, but what we can know is little, and if we forget how much we cannot know we become insensitive to many things of very great importance."

Bertrand Russell
in "A History of Western Philosophy."

## ACKNOWLEDGEMENTS

It is a very great pleasure to express my gratitude to Dr. T.G. Wood, Dr. W.A. Sands and Dr. N. Waloff for supervising my research, critically reading the manuscript and giving freely of their assistance and advice at all stages of the study.

I would also like to thank those who have helped in so many ways during my most enjoyable stay in Nigeria, in particular the Director of I.A.R., Samaru, Zaria; Dr. H.A. van Rheenen and Dr. C.M. Yaqub, the former Officers-in-Charge of the A.R.S., Mokwa, and also Prof. H. Caswell of I.A.R., Samaru.

For permission to use the land which constituted my study area I am very grateful to the Chief of Zugurma.

For technical assistance, without which this work would not have been possible, I would like to thank Samson Ananaba, Kayode Akinyemi, Amadu Ailla, Mm. Lawal, Mm. Bagudu Agaie, Alan Broodbank, Paul Ridout and the many other people who have helped me, particularly from the staff and work-force of the A.R.S., Mokwa and Silwood Park, Ascot.

For valuable discussions and advice I would like to thank Chris Longhurst, Sean Murphy, Martin Birley, Robin Taylor, Matthew Cock, Bob Lamb, Michael Pearce, John Mumford and Tom Bellows.

For facilities at the Imperial College Field Station, Silwood Park, I would like to thank Prof. T.R.E. Southwood F.R.S., Dr. S. McNeill and Mr. K.H. Fisher.

For permission to use unpublished data I am grateful to Mr. C. Longhurst, Dr. T.G. Wood, Dr. R.A. Johnson, Dr. C.E. Ohiagu, Dr. W.L. Nutting, Dr. N. Abo-Khatwa and Dr. M.J. Swift.

This study was financed through a Research Fellowship with the Centre for Overseas Pest Research. I am grateful to the Director, Dr. P.T. Haskell and to Dr. R.F. Chapman of the Division of Biology.

Finally, I would like to record my indebtedness to my family and to Dorothy Byrne of the Waltham Forest Guardian.

# APPENDICES

## APPENDIX 2.1.1

Minor wood fall
23.5.74 - 22.5.75.

Wood fall g

| WEEK NUMBER AND STARTING DATE | 1 Ad | 2 Cc | 3 Cg | 4 Ch | 5 Ea | 6 Ec | 7 Ee | 8 Ff | 9 Gc | 10 Hc | 11 Gf | 12 He | 13 Jd | 14 Lb | 15 Lf | 16 Lg | TOTAL g | TOTAL kg ha$^{-1}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 23 May | 348 | 124 | 71 | 189 | 177 | 442 | 182 | 50 | 154 | 294 | 134 | 685 | 112 | 407 | 97 | 161 | 3627 | 22.669 |
| 2 31 " | 415 | 286 | 50 | 384 | 186 | 456 | 180 | 169 | 206 | 292 | 278 | 319 | 516 | 488 | 117 | 2023 | 6365 | 39.781 |
| 3 6 June | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 4 13 " | 98 | 201 | 171 | 349 | 231 | 397 | 376 | 230 | 196 | 385 | 295 | 602 | 2175 | 539 | 113 | 493 | 6851 | 42.819 |
| 5 20 " | 199 | 575 | 78 | 42 | 117 | 3725 | 350 | 254 | 161 | 387 | 363 | 544 | 1326 | 750 | 450 | 1324 | 10645 | 66.531 |
| 6 27 " | 207 | 109 | 87 | 200 | 33 | 231 | 117 | 91 | 196 | 371 | 107 | 160 | 110 | 130 | 49 | 103 | 2301 | 14.381 |
| 7 4 July | 127 | 148 | 53 | 92 | 29 | 110 | 105 | 152 | 259 | 73 | 168 | 162 | 124 | 203 | 42 | 329 | 2176 | 13.600 |
| 8 11 " | 421 | 97 | 248 | 79 | 111 | 188 | 339 | 62 | 86 | 302 | 498 | 163 | 496 | 161 | 164 | 562 | 3977 | 24.856 |
| 9 18 " | 81 | 55 | 23 | 73 | 53 | 213 | 135 | 50 | 43 | 114 | 88 | 265 | 159 | 212 | 84 | 394 | 2042 | 12.763 |
| 10 25 " | 36 | 25 | 27 | 17 | 51 | 123 | 176 | 40 | 106 | 124 | 952 | 650 | 22 | 517 | 37 | 300 | 3203 | 20.019 |
| 11 1 Aug | 58 | 29 | 50 | 27 | 87 | 109 | 60 | 90 | 260 | 309 | 2239 | 177 | 70 | 38 | 78 | 198 | 3879 | 24.244 |
| 12 8 " | 130 | 9 | 90 | 88 | 33 | 130 | 52 | 59 | 38 | 285 | 57 | 90 | 516 | 139 | 108 | 103 | 1927 | 12.044 |
| 13 15 " | 42 | 175 | 55 | 61 | 119 | 71 | 388 | 39 | 219 | 75 | 82 | 75 | 28 | 92 | 83 | 60 | 1664 | 10.400 |
| 14 22 " | 196 | 53 | 178 | 71 | 49 | 119 | 126 | 211 | 102 | 155 | 40 | 52 | 25 | 226 | 72 | 82 | 1757 | 10.981 |
| 15 29 " | 179 | 415 | 101 | 52 | 79 | 98 | 81 | 71 | 66 | 367 | 117 | 102 | 42 | 156 | 148 | 611 | 2685 | 16.781 |
| 16 5 Sept | 117 | 53 | 91 | 401 | 110 | 1809 | 85 | 37 | 18 | 151 | 29 | 245 | 81 | 118 | 154 | 141 | 3640 | 22.750 |
| 17 12 " | 91 | 72 | 84 | 182 | 50 | 126 | 100 | 439 | 33 | 139 | 81 | 228 | 55 | 193 | 65 | 236 | 2174 | 13.588 |
| 18 19 " | 44 | 82 | 126 | 85 | 160 | 194 | 124 | 234 | 48 | 359 | 245 | 154 | 128 | 124 | 64 | 464 | 2635 | 16.469 |
| 19 26 " | 582 | 14 | 43 | 47 | 90 | 353 | 139 | 135 | 53 | 255 | 93 | 68 | 296 | 72 | 122 | 814 | 3176 | 19.850 |
| 20 3 Oct | 98 | 177 | 138 | 123 | 89 | 519 | 103 | 231 | 258 | 155 | 96 | 113 | 146 | 300 | 50 | 472 | 3068 | 19.175 |
| 21 10 " | 24 | 34 | 81 | 46 | 158 | 133 | 98 | 514 | 327 | 158 | 128 | 113 | 302 | 266 | 53 | 190 | 2625 | 16.406 |
| 22 17 " | 117 | 209 | 56 | 98 | 249 | 378 | 45 | 130 | 239 | 183 | 67 | 82 | 112 | 113 | 167 | 67 | 2312 | 14.450 |
| 23 24 " | 172 | 39 | 23 | 71 | 55 | 89 | 88 | 122 | 143 | 59 | 55 | 146 | 80 | 69 | 35 | 87 | 1333 | 8.331 |
| 24 31 " | 52 | 24 | 34 | 83 | 23 | 49 | 59 | 51 | 34 | 54 | 55 | 102 | 35 | 170 | 49 | 210 | 1084 | 6.775 |
| 25 7 Nov | 46 | 27 | 46 | 87 | 134 | 175 | 95 | 245 | 207 | 194 | 57 | 57 | 247 | 83 | 246 | 110 | 2056 | 12.850 |
| 26 14 " | 33 | 15 | 45 | 51 | 31 | 35 | 49 | 52 | 43 | 53 | 21 | 38 | 20 | 88 | 44 | 66 | 684 | 4.275 |
| 27 21 " | 53 | 65 | 31 | 117 | 127 | 84 | 175 | 148 | 30 | 29 | 43 | 48 | 86 | 81 | 54 | 60 | 1231 | 7.694 |
| 28 28 " | 39 | 22 | 32 | 39 | 27 | 192 | 140 | 84 | 51 | 135 | 88 | 60 | 49 | 83 | 49 | 84 | 1174 | 7.338 |
| 29 5 Dec | 26 | 26 | 32 | 47 | 16 | 116 | 124 | 89 | 47 | 56 | 61 | 44 | MAJOR | 55 | 98 | 45 | 882 | 5.513 |
| 30 12 " | 55 | 33 | 29 | 155 | 51 | 119 | 80 | 117 | 58 | 379 | 468 | 97 | 400 | 136 | 141 | 105 | 2423 | 15.144 |
| 31 19 " | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 32 26 " | 181 | 72 | 69 | 53 | 44 | 36 | 239 | 118 | 117 | 63 | 106 | 74 | 347 | 54 | 80 | 97 | 1750 | 10.938 |
| 33 2 Jan | 265 | 77 | 207 | 129 | 76 | 116 | 44 | 303 | 50 | 100 | 281 | 104 | 367 | 309 | 71 | 116 | 2615 | 16.344 |
| 34 9 " | 417 | 135 | 183 | 70 | 108 | 146 | 75 | 322 | 78 | 219 | 121 | 61 | 320 | 227 | 152 | 57 | 2691 | 16.819 |
| 35 16 " | 629 | 146 | 382 | 263 | 151 | 102 | 122 | 493 | 232 | 99 | 284 | 117 | 438 | 173 | 54 | 176 | 3861 | 24.131 |
| 36 23 " | 219 | 163 | 99 | 197 | 85 | 145 | 143 | 196 | 109 | 197 | 195 | 68 | 206 | 101 | 57 | 96 | 2185 | 13.663 |
| 37 30 " | 206 | 215 | 139 | 315 | 336 | 171 | 130 | 306 | 131 | 104 | 196 | 75 | 139 | 183 | 38 | 279 | 2963 | 18.519 |
| 38 6 Feb | 163 | 124 | 115 | 148 | 64 | 205 | 159 | 194 | 87 | 166 | 232 | 145 | 114 | 59 | 40 | 104 | 2119 | 13.244 |
| 39 13 " | 240 | 387 | 194 | 436 | 238 | 273 | 351 | 482. | 239 | 283 | 277 | 278 | 790 | 229 | 218 | 232 | 5147 | 32.169 |
| 40 20 " | 323 | 205 | 141 | 222 | 203 | 135 | 187 | 148 | 366 | 142 | 102 | 115 | 284 | 252 | 59 | 265 | 3149 | 19.681 |
| 41 27 " | 219 | 97 | 198 | 338 | 59 | 181 | 183 | 197 | 228 | 119 | 156 | 124 | 329 | 132 | 55 | 106 | 2721 | 17.006 |
| 42 6 Mar | 200 | 119 | 195 | 78 | 69 | 161 | 199 | 129 | 337 | 118 | 111 | 57 | 105 | 103 | 72 | 115 | 2168 | 13.550 |
| 43 13 " | 182 | 88 | 167 | 349 | 100 | 407 | 169 | 252 | 306 | 305 | 212 | 220 | 255 | 128 | 383 | 284 | 3807 | 23.794 |
| 44 20 " | 79 | 75 | 136 | 207 | 59 | 90 | 95 | 138 | 186 | 225 | 233 | 149 | 110 | 94 | 23 | 189 | 2088 | 13.050 |
| 45 27 " | 192 | 68 | 206 | 135 | 90 | 65 | 104 | 282 | 209 | 82 | 182 | 92 | 149 | 176 | 116 | 126 | 2275 | 14.219 |
| 46 3 Apr | 131 | 74 | 108 | 136 | 39 | 167 | 151 | 132 | 126 | 117 | 164 | 112 | 136 | 126 | 57 | 129 | 1905 | 11.906 |
| 47 10 " | 117 | 72 | 85 | 76 | 103 | 75 | 138 | 105 | 78 | 309 | 94 | 181 | 584 | 55 | 58 | 628 | 2758 | 17.238 |
| 48 17 " | 192 | 182 | 114 | 404 | 64 | 213 | 195 | 212 | 126 | 273 | 145 | MAJOR | MAJOR | 450 | 79 | 204 | 2853 | 17.831 |
| 49 24 " | 88 | 169 | 179 | 143 | 54 | 141 | 112 | 92 | 1997 | 234 | 160 | 532 | 463 | 203 | 89 | 151 | 4807 | 30.044 |
| 50 1 May | 63 | 74 | 138 | 81 | 223 | 202 | 233 | 199 | 195 | 202 | 193 | 4004 | 384 | 503 | 31 | 175 | 6900 | 43.125 |
| 51 8 " | 117 | 38 | 77 | 63 | 55 | 64 | 47 | 121 | 139 | 34 | 72 | 232 | 132 | 102 | 48 | 93 | 1434 | 8.963 |
| 52 15 " | 203 | 76 | 125 | 452 | 52 | 416 | 279 | 56 | 119 | 104 | 301 | 2330 | 151 | 456 | 162 | 274 | 5556 | 34.725 |
| TOTALS | 8512 | 5849 | 5430 | 7651 | 4997 | 14294 | 7526 | 8673 | 9136 | 9297 | 10823 | 14711 | 13561 | 10124 | 4975 | 13790 | 149349 | 933.431 kg ha$^{-1}$ a$^{-1}$ |

## APPENDIX 2.1.2 Minor wood fall in size classes with overall size class totals including major falls.

| WEEK NUMBER | WEIGHT IN EACH SIZE CLASS g | | | | TOTAL WEIGHT g | % IN EACH SIZE CLASS | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | 1 | 2 | 3 | 4 |
| 1 (22 May) | 1252 | 874 | 678 | 823 | 3627 | 34.5 | 24.1 | 18.7 | 22.7 |
| 2 | 2260 | 1012 | 1267 | 1826 | 6365 | 35.5 | 15.9 | 19.9 | 28.7 |
| 3 | | | | | | | | | |
| 4 | 1905 | 1747 | 891 | 2308 | 6851 | 27.8 | 25.5 | 13.0 | 33.7 |
| 5 | 2310 | 2470 | 1863 | 4002 | 10645 | 21.7 | 23.2 | 17.5 | 37.6 |
| 6 | 1270 | 435 | 596 | 0 | 2301 | 55.2 | 18.9 | 25.9 | 0 |
| 7 | 975 | 570 | 631 | 0 | 2176 | 44.8 | 26.2 | 29.0 | 0 |
| 8 | 1396 | 1038 | 728 | 815 | 3977 | 35.1 | 26.1 | 18.3 | 20.5 |
| 9 | 847 | 205 | 582 | 408 | 2042 | 41.5 | 10.0 | 28.5 | 20.0 |
| 10 | 1083 | 343 | 452 | 1325 | 3203 | 33.8 | 10.7 | 14.1 | 41.4 |
| 11 | 737 | 400 | 400 | 2342 | 3879 | 19.0 | 10.3 | 10.3 | 60.4 |
| 12 | 501 | 322 | 351 | 753 | 1927 | 26.0 | 16.7 | 18.2 | 39.1 |
| 13 | 271 | 474 | 270 | 649 | 1664 | 16.3 | 28.5 | 16.2 | 39.0 |
| 14 | 738 | 180 | 300 | 539 | 1757 | 42.0 | 10.2 | 17.1 | 30.7 |
| 15 | 811 | 561 | 580 | 733 | 2685 | 30.2 | 20.9 | 21.6 | 27.3 |
| 16 | 870 | 728 | 699 | 1343 | 3640 | 23.9 | 20.0 | 19.2 | 36.9 |
| 17 | 741 | 289 | 520 | 624 | 2174 | 34.1 | 13.3 | 23.9 | 28.7 |
| 18 | 1115 | 369 | 561 | 590 | 2635 | 42.3 | 14.0 | 21.3 | 22.4 |
| 19 | 845 | 572 | 753 | 1006 | 3176 | 26.6 | 18.0 | 23.7 | 31.7 |
| 20 | 507 | 764 | 966 | 831 | 3068 | 16.5 | 24.9 | 31.5 | 27.1 |
| 21 | 706 | 442 | 549 | 928 | 2625 | 26.9 | 16.8 | 20.9 | 35.4 |
| 22 | 719 | 391 | 453 | 749 | 2312 | 31.1 | 16.9 | 19.6 | 32.4 |
| 23 | 685 | 223 | 425 | 0 | 1333 | 51.4 | 16.7 | 31.9 | 0 |
| 24 | 597 | 203 | 0 | 284 | 1084 | 55.1 | 18.7 | 0 | 26.2 |
| 25 | 543 | 193 | 543 | 777 | 2056 | 26.4 | 9.4 | 26.4 | 37.8 |
| 26 | 395 | 135 | 154 | 0 | 684 | 57.8 | 19.7 | 22.5 | 0 |
| 27 | 485 | 185 | 561 | 0 | 1231 | 39.4 | 15.0 | 45.6 | 0 |
| 28 | 770 | 193 | 211 | 0 | 1174 | 65.6 | 16.4 | 18.0 | 0 |
| 29 | 446 | 193 | 243 | 0 | 882 | 50.6 | 21.8 | 27.6 | 0 |
| 30 | 475 | 691 | 550 | 707 | 2423 | 19.6 | 28.5 | 22.7 | 29.3 |
| 31 | | | | | | | | | |
| 32 | 508 | 343 | 333 | 566 | 1750 | 29.0 | 19.6 | 19.0 | 32.4 |
| 33 | 1783 | 513 | 319 | 0 | 2615 | 68.2 | 19.6 | 12.2 | 0 |
| 34 | 1657 | 447 | 240 | 347 | 2691 | 61.6 | 16.6 | 8.9 | 12.9 |
| 35 | 2977 | 463 | 421 | 0 | 3861 | 77.1 | 12.0 | 10.9 | 0 |
| 36 | 1388 | 404 | 394 | 0 | 2186 | 63.5 | 18.5 | 18.0 | 0 |
| 37 | 1834 | 619 | 510 | 0 | 2963 | 61.9 | 20.9 | 17.2 | 0 |
| 38 | 1490 | 398 | 231 | 0 | 2119 | 70.3 | 18.8 | 10.9 | 0 |
| 39 | 3314 | 371 | 1251 | 211 | 5147 | 64.4 | 7.2 | 24.3 | 4.1 |
| 40 | 2349 | 460 | 340 | 0 | 3149 | 74.6 | 14.6 | 10.8 | 0 |
| 41 | 1850 | 389 | 482 | 0 | 2721 | 68.0 | 14.3 | 17.7 | 0 |
| 42 | 1730 | 254 | 184 | 0 | 2168 | 79.8 | 11.7 | 8.5 | 0 |
| 43 | 1926 | 481 | 700 | 700 | 3807 | 50.6 | 12.6 | 18.4 | 18.4 |
| 44 | 896 | 290 | 211 | 691 | 2088 | 42.9 | 13.9 | 10.1 | 33.1 |
| 45 | 1430 | 312 | 221 | 312 | 2275 | 62.9 | 13.7 | 9.7 | 13.7 |
| 46 | 1294 | 301 | 310 | 0 | 1905 | 67.9 | 15.8 | 16.3 | 0 |
| 47 | 632 | 519 | 507 | 1100 | 2758 | 22.9 | 18.8 | 18.4 | 39.9 |
| 48 | 1001 | 502 | 548 | 802 | 2853 | 35.1 | 17.6 | 19.2 | 28.1 |
| 49 | 1154 | 889 | 889 | 1875 | 4807 | 24.0 | 18.5 | 16.5 | 39.0 |
| 50 | 2546 | 1111 | 1145 | 2098 | 6900 | 36.9 | 16.1 | 16.6 | 30.4 |
| 51 | 165 | 165 | 465 | 639 | 1434 | 11.5 | 11.5 | 32.4 | 44.6 |
| 52 | 1450 | 972 | 917 | 2217 | 5556 | 26.1 | 17.5 | 16.5 | 39.9 |
| TOTALS | 59639 | 26405 | 27395 | 35920 | 149349 | 39.93 | 17.68 | 18.34 | 24.05 |

Total for major falls (size class 4) = 73172 g

| SIZE-CLASS | TOTAL FALL g | TOTAL FALL kg $ha^{-1}$ | % OF TOTAL |
|---|---|---|---|
| 1 | 59629 | 372.681 | 26.797 |
| 2 | 26405 | 165.031 | 11.866 |
| 3 | 27395 | 171.219 | 12.311 |
| 4 | 109092 | 681.825 | 49.025 |
| | 222521 | 1390.756 | 100.000 |

## APPENDIX 2.1.3 Leaf fall records 3.10.74 - 2.10.75 ( 16 0.25m$^2$ samples collected fortnightly. Study area burnt on 31.12.74.

| | Leaf fall g | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| WEEK NUMBER AND STARTING DATE | Ad 1 | Cc 2 | Cg 3 | Ch 4 | Ea 5 | Ec 6 | Ee 7 | Ff 8 | Gc 9 | Hc 10 | Gf 11 | He 12 | Jd 13 | Lb 14 | Lf 15 | Lg 16 | TOTAL g | TOTAL kg ha$^{-1}$ |
| 2 3-17 Oct | 1.122 | 2.705 | 0.462 | 0.71 | 0 | 0.806 | 1.049 | 0.994 | 0 | 2.276 | 1.652 | 0.592 | 2.575 | 0.337 | 1.767 | 1.264 | 18.311 | 45.778 |
| 4 17-31 " | 0.537 | 0.689 | 1.398 | 1.398 | 0 | 0.543 | 0.959 | 0.671 | 0.389 | 2.024 | 0.250 | 0.896 | 0.660 | 0.558 | 1.372 | 1.703 | 14.040 | 35.118 |
| 6 1-14 Nov | 2.758 | 4.394 | 5.099 | 6.080 | 0.183 | 2.445 | 3.107 | 2.443 | 5.256 | 19.160 | 4.552 | 6.904 | 2.008 | 6.742 | 2.764 | 2.318 | 76.213 | 190.533 |
| 8 14-28 " | 1.594 | 4.170 | 4.829 | 2.310 | 0 | 0.996 | 3.465 | 5.653 | 4.396 | 17.443 | 4.964 | 3.494 | 1.431 | 0.713 | 0.777 | 3.640 | 59.880 | 149.700 |
| 10 28-12 Dec | 2.220 | 2.165 | 4.216 | 1.593 | 0.680 | 1.259 | 4.925 | 3.458 | 4.970 | 5.262 | 10.168 | 2.200 | Net burnt | 2.220 | 3.417 | 1.719 | 50.472 | 134.592 |
| 13 12- 2 Jan | 10.987 | 7.731 | 6.200 | 5.853 | 3.428 | 4.954 | 10.371 | 7.538 | 8.649 | 4.939 | 10.008 | 6.941 | " | 9.211 | 8.974 | 11.965 | 117.749 | 313.997 |
| 15 2-16 | 52.762 | 3.664 | 4.468 | 1.455 | 1.474 | 4.011 | 5.523 | 11.950 | 7.762 | 9.817 | 13.893 | 11.630 | " | 5.534 | 6.950 | 25.773 | 166.666 | 444.443 |
| 17 16-30 | 7.145 | 6.225 | 0.849 | 1.763 | 1.410 | 1.968 | 9.463 | 2.952 | 8.911 | 5.824 | 1.387 | 3.637 | " | 0.781 | 4.381 | 32.415 | 89.111 | 237.629 |
| 19 30-13 Feb | 5.242 | 4.153 | 1.064 | 2.852 | 2.902 | 2.581 | 19.242 | 0.866 | 0.553 | 2.351 | 9.227 | 1.803 | " | 10.960 | 9.812 | 15.598 | 89.206 | 237.883 |
| 21 13-27 | 2.205 | 1.545 | 1.072 | 4.008 | 0.967 | 1.980 | 9.190 | 0.972 | 6.727 | 2.745 | 1.631 | 0.984 | " | 2.642 | 3.404 | 10.851 | 50.923 | 135.795 |
| 23 27-13 Mar | 1.181 | 0.875 | 2.000 | 0.931 | 0.418 | 0 | 1.031 | Net stolen | 0.452 | 2.724 | 1.552 | 1.970 | " | 2.203 | 1.640 | 4.677 | 21.654 | 61.869 |
| 25 13-27 | 2.527 | 2.066 | 0 | 2.206 | 0 | 0 | 2.215 | " | 1.975 | 1.853 | 2.524 | 2.066 | " | 0.260 | 5.573 | 1.715 | 24.980 | 71.371 |
| 27 27-10 Apr | 0.371 | 0.131 | 1.962 | 2.009 | 0 | 2.773 | 1.356 | " | 4.569 | 0.724 | 0 | 0.875 | " | 0 | 3.012 | 0.313 | 18.095 | 51.700 |
| 29 10-24 | 0 | 0.799 | 3.005 | 0 | 0 | 1.693 | 0 | 0 | 0 | 0 | 4.164 | 2.462 | 0 | 0 | 0 | 0 | 12.123 | 30.308 |
| 31 24-8 May | 3.013 | 1.009 | 0.162 | 0.162 | 0 | 0 | 0 | 0.485 | 0 | 0 | 0.873 | 2.449 | 1.255 | 0 | 0 | 0.385 | 9.793 | 24.483 |
| 33 8-22 | 0.342 | 0 | 0.233 | 0 | 0 | 0 | 0.898 | 0 | 0 | 0.294 | 0 | 2.152 | 0 | 0 | 0 | 1.665 | 5.584 | 13.960 |
| 35 22-5 June | 0.428 | 0 | 0 | 0 | 1.473 | 0 | 1.736 | 0 | 1.199 | 1.379 | 0 | 1.283 | 0 | 1.324 | 1.113 | 1.267 | 11.202 | 28.005 |
| 37 5-19 | 0 | 0 | 1.217 | 0 | 0 | 0 | 0.851 | 0.490 | 0 | 0.388 | 0.392 | 0.692 | 0 | 0 | 0 | 0.815 | 4.845 | 12.113 |
| 39 19- 3 July | 1.009 | 0 | 0 | 0 | 0.547 | 0.630 | 0 | 0.618 | 0.373 | 0 | 0.391 | 0.532 | 1.057 | 0.903 | 1.190 | 0.881 | 8.131 | 20.328 |
| 41 3-17 | 0.751 | 0 | 0 | 0 | 0 | 0.230 | 0.592 | 0 | 0 | 0 | 0 | 1.009 | 0 | 0 | 1.826 | 0.414 | 4.822 | 12.055 |
| 43 17-31 | 2.256 | 1.352 | 0 | 0 | 0 | 1.394 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.100 | 1.623 | 6.725 | 16.813 |
| 45 31-14 Aug | 4.206 | 0.287 | 0 | 0 | 0 | 1.413 | 1.004 | 0.321 | 0 | 0.818 | 0.587 | 2.855 | 0 | 0 | 2.680 | 1.451 | 15.622 | 39.055 |
| 47 14-28 | 4.732 | 0 | 0 | 0 | 0 | 0 | 0.493 | 0 | 0 | 0.165 | 0.407 | 2.751 | 0 | 0 | 1.664 | 1.667 | 11.879 | 29.698 |
| 49 28-11 Sept | 1.796 | 0 | 0 | 0 | 0 | 0 | 0.782 | 0.733 | 0 | 0 | 0.247 | 0 | 0 | 0 | 0 | 0.158 | 3.716 | 9.290 |
| 51 11-25 | 2.122 | 0.929 | 0.159 | 0 | 0 | 0.360 | 1.259 | 0.458 | 0.413 | 0.196 | 0.844 | 0 | 0 | 0 | 1.134 | 0.816 | 8.690 | 21.725 |
| 52 25- 2 Oct | 0.265 | 0.461 | 0 | 0.434 | 0 | 0.823 | 0.643 | 0 | 1.028 | 0.834 | 0.655 | 0.241 | 0.573 | 0 | 1.025 | 0.662 | 7.644 | 19.110 |
| | 111.571 | 45.350 | 38.395 | 33.764 | 13.482 | 30.859 | 80.154 | 40.602 | 57.622 | 81.221 | 70.368 | 60.418 | (9.559) | 44.388 | 64.575 | 125.755 | 908.083 | 2387.351 kg ha$^{-1}$ a$^{-1}$ |

APPENDIX 2.2.1 Standing dead items found on the study area, (d.b.h. > 5.0 cm), with calculation of volume (V).

| MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) | MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) | MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) | MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) | MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) | MAP SQUARE NO. | D.B.H. (m) | HEIGHT (m) | V (cc) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ab | .20 | 6 | 94248 | Cd | .07 | 1.5 | 3770 | Ed | .06 | 2 | 2827 | Gh | .22 | 10 | 190066 | Ic | .08 | 3.5 | 8796 | Kf | .19 | 16 | 226823 |
| Ab | .07 | 4 | 7697 | Cd | .15 | 2 | 3848 | Ed | .13 | 3.5 | 23228 | Gh | .30 | 4 | 141372 | Ic | .07 | 2 | 3848 | Lh | .16 | 4 | 40212 |
| Ac | .32 | 4 | 160850 | Cd | .20 | 4 | 35343 | Ed | .07 | 2.5 | 4811 | Gg | .16 | 5.5 | 55292 | Ic | .17 | 8.0 | 90792 | Lg | .17 | 6 | 68094 |
| Ac | .13 | 4.4 | 29201 | Cd | .20 | 8 | 125664 | Ed | .20 | 10 | 157080 | Gg | .30 | 10 | 353429 | Id | .12 | 2 | 11310 | Lg | .09 | 4 | 12723 |
| Ad | .13 | 2.5 | 16592 | Ce | .23 | 8 | 166190 | Ed | .12 | 2 | 11310 | Gf | .09 | 4 | 12723 | Id | .12 | 4.5 | 25447 | Lf | .19 | 5 | 70882 |
| Ad | .2 | 3 | 47124 | Ce | .15 | 8 | 70686 | Ed | .10 | 4 | 15708 | Ge | .05 | 2 | 723823 | Id | .17 | 8 | 90792 | Lf | .12 | 3.5 | 19792 |
| Ae | .14 | 5 | 38485 | Cf | .13 | 2.5 | 16592 | Ee | .08 | 2 | 5027 | Ge | .05 | 2 | 2827 | Ie | .07 | 4 | 7697 | Le | .07 | 2.5 | 4811 |
| Ae | .14 | 6 | 46181 | Cf | .10 | 5 | 19535 | Ee | .10 | 4 | 15708 | Ge | .07 | 5 | 9621 | Ie | .14 | 8 | 61575 | Ld | .30 | 15 | 530144 |
| Ae | .10 | 1.2 | 4712 | Cf | .10 | 2 | 7854 | Ef | .20 | 10 | 157080 | Gd | .09 | 5.5 | 17495 | If | .18 | 8 | 114511 | Lc | .12 | 4 | 22619 |
| Ae | .20 | 5 | 78540 | Cf | .13 | 6 | 39820 | Ef | .08 | 1 | 2513 | Gc | .10 | 2 | 7854 | If | .14 | 4 | 30788 | Lb | .18 | 6 | 76341 |
| Ae | .10 | 5 | 19635 | Cg | .20 | 8 | 125664 | Ef | .08 | 2 | 5027 | Gc | .10 | 3 | 11781 | Ig | .05 | 2.5 | 2454 | | | | |
| Af | .11 | 3 | 14255 | Cg | .15 | 3 | 26507 | Ef | .07 | 3 | 5773 | Gc | .07 | 5.5 | 10583 | Ig | .25 | 6 | 147262 | | | | |
| Af | .18 | 7 | 89064 | Cg | .18 | 2 | 25447 | Ef | .15 | 8 | 70686 | Gc | .07 | 1 | 1924 | Ig | .09 | 4 | 12723 | | | | |
| Af | .15 | 3 | 26507 | Ch | .23 | 10 | 207738 | Eg | .10 | 3 | 11781 | Gb | .40 | 8 | 502655 | Ig | .07 | 1.5 | 2886 | | | | |
| Af | .12 | 4 | 22619 | Ch | .17 | 8 | 113490 | Eg | .15 | 3 | 26507 | Gb | .08 | 2 | 5027 | Ih | .17 | 2.5 | 28373 | | | | |
| Ag | .14 | 5 | 38485 | Dh | .12 | 2 | 11310 | Eg | .28 | 1 | 30788 | Gb | .10 | 2.5 | 9817 | Jh | .08 | 2 | 5027 | | | | |
| Ah | .13 | 6 | 39820 | Dg | .23 | 1 | 661250 | Eg | .13 | 7 | 46456 | Ga | .05 | 2.5 | 2454 | Jh | .07 | 2 | 3848 | | | | |
| Ah | .08 | 4 | 10053 | Df | .13 | 1.5 | 9955 | Eh | .15 | 7 | 61850 | Ga | .08 | 4.5 | 11310 | Jg | .09 | 3 | 9543 | | | | |
| Bh | .10 | 3.5 | 13744 | De | .08 | 1 | 2513 | Eh | .15 | 2 | 17671 | Ga | .08 | 2 | 5027 | Jg | .16 | 6.5 | 65345 | | | | |
| Bh | .11 | 3 | 14255 | De | .15 | 8 | 70686 | Fc | .13 | 4 | 26546 | Hb | .22 | 5 | 95033 | Jd | .09 | 2.5 | 7952 | | | | |
| Bh | .11 | 4 | 19007 | De | .14 | 8 | 61575 | Fd | .08 | 1.5 | 3770 | He | .09 | 2 | 6362 | Jd | .11 | 4 | 19007 | | | | |
| Bf | .10 | 3 | 11781 | De | .13 | 5 | 33183 | Fd | .06 | 4 | 5655 | Hf | .12 | 6 | 33929 | Jc | .22 | 7 | 133046 | | | | |
| Bd | .11 | 2.5 | 11879 | Dc | .13 | 1.5 | 9955 | Fe | .16 | 7.5 | 75398 | Hf | .07 | 6 | 11545 | Jc | .16 | 7.5 | 75398 | | | | |
| Bd | .22 | 2.5 | 47517 | Dc | .10 | 5 | 19635 | Fe | .13 | 5 | 33183 | Hf | .17 | 10 | 113490 | Jb | .13 | 3.5 | 23228 | | | | |
| Bd | .12 | 2.5 | 9817 | Dc | .15 | 3 | 26507 | Fe | .08 | 7 | 17593 | Hf | .20 | 6 | 94248 | Ka | .08 | 3 | 7540 | | | | |
| Bd | .14 | 5 | 28274 | Dc | .15 | 3 | 26507 | Fe | .13 | 6 | 39820 | Hg | .05 | 3 | 2945 | Kb | .25 | 1 | 24544 | | | | |
| Bc | .25 | 6 | 46181 | Dc | .10 | 2 | 7854 | Fe | .12 | 3.5 | 19792 | Hg | .20 | 10 | 157080 | Kb | .09 | 2 | 6362 | | | | |
| Bb | .09 | 3 | 73631 | Db | .14 | 6 | 46181 | Fe | .12 | 3.5 | 19792 | Hh | .07 | 2 | 3848 | Kb | .13 | 4 | 26546 | | | | |
| Ba | .07 | 2.5 | 7952 | Da | .10 | 2 | 7854 | Ff | .05 | 2 | 1963 | Hh | .14 | 2.5 | 19242 | Kb | .13 | 4 | 26546 | | | | |
| Ca | .11 | 4 | 7697 | Ea | .07 | 4 | 7697 | Ff | .18 | 8 | 101788 | Ia | .17 | 6 | 68094 | Kc | .17 | 2 | 22698 | | | | |
| Ca | .12 | 2 | 9503 | Ea | .08 | 2 | 5027 | Ff | .12 | 1 | 5655 | Ia | .24 | 14 | 316673 | Kc | .20 | 3.5 | 54978 | | | | |
| Cb | .15 | 4.5 | 25447 | Eb | .07 | 2 | 3848 | Ff | .10 | 5 | 19635 | Ib | .07 | 2 | 3848 | Ke | .11 | 5.5 | 26134 | | | | |
| Cc | .13 | 2 | 17671 | Ec | .08 | 2 | 5027 | Fh | .20 | 8 | 125664 | Ib | .15 | 14 | 123700 | Kf | .09 | 2 | 6362 | | | | |
| Cc | .08 | 9 | 59730 | Ed | .12 | 7 | 39584 | Gh | .09 | 8 | 25447 | Ib | .11 | 4 | 19007 | Kf | .2 | 16 | 251327 | | | | |

APPENDIX 3.2: The populations of 19 *Macrotermes bellicosus* colonies. Results from counts of volumetric samples of each colony, summarised in Tables 3.2.15 &16 . Key: MS = major soldier, mS = minor soldier, MW = major worker, mW = minor worker, L = larvae, N = alate nymphs.

Colony One : Entire population counted

Colony Two : " " "

Colony Three :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 2 | 6 | 88 | 125 | 320 |
| 2 | 1 | 4 | 96 | 134 | 361 |
| 3 | 2 | 5 | 96 | 147 | 346 |
| 4 | 2 | 6 | 96 | 166 | 355 |
| 5 | 1 | 8 | 88 | 145 | 362 |
| 6 | 3 | 7 | 89 | 139 | 350 |
| 7 | 2 | 8 | 91 | 142 | 366 |
| 8 | 1 | 8 | 99 | 138 | 367 |
| 9 | 1 | 5 | 91 | 137 | 338 |
| 10 | 2 | 6 | 92 | 142 | 349 |
| 11 | 1 | 5 | 95 | 146 | 353 |
| 12 | 2 | 5 | 92 | 152 | 360 |
| MEAN | 1.667 | 6.083 | 92.75 | 142.75 | 352.25 |
| X106.25 | 177 | 646 | 9855 | 15167 | 37427 |

Sample : 12 x 4.8cc

Total volume :
510cc (106.25 x 4.8

Colony Four :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 5 | 9 | 61 | 269 | 381 |
| 2 | 4 | 5 | 59 | 233 | 397 |
| 3 | 3 | 8 | 55 | 252 | 362 |
| 4 | 5 | 6 | 52 | 231 | 358 |
| 5 | 6 | 3 | 52 | 201 | 369 |
| MEAN | 4.6 | 6.2 | 55.8 | 237.2 | 373.4 |
| X82 | 377.2 | 508.4 | 4575.6 | 19450.4 | 30618.8 |

Sample : 5 x 5cc

Total volume :
410cc (82 x 5)

APPENDIX 3.2: (Cont'd)

Colony Five :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 10 | 33 | 259 | 719 | 1827 |
| 2 | 10 | 24 | 307 | 477 | 1824 |
| 3 | 8 | 26 | 306 | 710 | 1895 |
| 4 | 5 | 21 | 245 | 789 | 1617 |
| 5 | 15 | 18 | 270 | 887 | 2146 |
| MEAN | 9.6 | 24.4 | 277.4 | 716.4 | 1865.8 |
| X372 | 357 | 908 | 10319 | 26650 | 69408 |
| | | | From fungus combs | | 4600 |
| | | | | | 74008 |

Sample: 5 x 21.75cc

Total volume :
808.75cc (372 x 21.7

Colony Six :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 6 | 11 | 46 | 133 | 605 |
| 2 | 44 | 7 | 49 | 142 | 614 |
| 3 | 5 | 4 | 49 | 153 | 652 |
| 4 | 6 | 13 | 46 | 149 | 619 |
| 5 | 3 | 4 | 50 | 133 | 657 |
| 6 | 5 | 5 | 51 | 167 | 596 |
| 7 | 6 | 3 | 49 | 146 | 641 |
| 8 | 8 | 3 | 47 | 165 | 611 |
| MEAN | 5.375 | 6.25 | 48.375 | 148.5 | 624.375 |
| X172 | 924.5 | 1075 | 8320.5 | 25542 | 107392.5 |

Sample : 8 x 5cc

Total volume :
860cc (172 x 5)

APPENDIX 3.2: (Cont'd)

Colony Seven :

1) From fungus combs

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | - | 3 | 50 | 138 | 834 |
| 2 | - | 6 | 62 | 103 | 852 |
| 3 | - | 8 | 47 | 143 | 879 |
| 4 | - | 6 | 65 | 126 | 848 |
| 5 | - | 10 | 52 | 148 | 855 |
| 6 | - | 4 | 56 | 123 | 817 |
| MEAN | - | 37 | 55.33 | 130.17 | 847.5 |
| X48.96 | 52 | 302 | 2709 | 6373 | 41494 |

Sample : 6 x 4.8cc

Total volume:
235cc (48.96 x 4.8)

2) From the rest of the nest

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 1 | 12 | 79 | 283 | 472 |
| 2 | 1 | 7 | 75 | 245 | 431 |
| 3 | 1 | 7 | 79 | 235 | 442 |
| 4 | 1 | 8 | 81 | 255 | 415 |
| 5 | 0 | 8 | 79 | 231 | 449 |
| 6 | 2 | 7 | 91 | 236 | 435 |
| 7 | 1 | 5 | 75 | 231 | 429 |
| 8 | 0 | 11 | 62 | 262 | 417 |
| 9 | 0 | 17 | 67 | 241 | 438 |
| 10 | 0 | 6 | 81 | 269 | 415 |
| MEAN | 0.7 | 8.8 | 76.9 | 248.8 | 434.3 |
| X416.25 | 291 | 3663 | 32010 | 103563 | 180777 |

Sample : 10 x 4.8cc

Total volume:
1998cc (416.25 x 4.8

3) Overall totals

| MS | mS | MW | mW | L |
|---|---|---|---|---|
| 343 | 3965 | 34719 | 109936 | 222271 |

Colony Eight:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 7 | 79 | 331 | 151 |
| 2 | 7 | 11 | 51 | 230 | 104 |
| 3 | 8 | 6 | 63 | 203 | 105 |
| 4 | 6 | 3 | 85 | 280 | 144 |
| 5 | 5 | 11 | 58 | 259 | 128 |
| 6 | 6 | 6 | 67 | 274 | 125 |
| 7 | 6 | 8 | 81 | 308 | 139 |
| 8 | 4 | 5 | 76 | 299 | 139 |
| 9 | 3 | 11 | 56 | 326 | 129 |
| 10 | 7 | 11 | 47 | 320 | 146 |
| 11 | 7 | 9 | 72 | 282 | 129 |
| 12 | 5 | 9 | 72 | 281 | 158 |
| 13 | 5 | 7 | 88 | 316 | 181 |
| 14 | 7 | 7 | 76 | 314 | 138 |
| 15 | 5 | 11 | 78 | 297 | 157 |
| 16 | 3 | 12 | 60 | 297 | 135 |
| 17 | 9 | 4 | 58 | 306 | 150 |
| 18 | 6 | 6 | 67 | 290 | 106 |
| 19 | 3 | 4 | 80 | 292 | 107 |
| 20 | 5 | 12 | 67 | 391 | 121 |
| MEAN | 5.5 | 8.00 | 69.05 | 294.8 | 134.6 |
| X460 | 2530 | 3680 | 31763 | 135608 | 61916 |
| EXTRAS | 25 | 75 | 500 | 500 | 516 |
| TOTAL | 2555 | 3755 | 32263 | 136108 | 62432 |

Sample : 20 x 5cc

Total volume :
2300cc (460 x 5)

Colony Nine:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 13 | 59 | 163 | 278 |
| 2 | 1 | 10 | 46 | 177 | 223 |
| 3 | 4 | 3 | 54 | 166 | 236 |
| 4 | 4 | 6 | 51 | 168 | 239 |
| 5 | 3 | 6 | 47 | 148 | 275 |
| 6 | 3 | 8 | 52 | 168 | 238 |
| 7 | 3 | 6 | 36 | 162 | 228 |
| 8 | 4 | 8 | 47 | 172 | 279 |
| 9 | 6 | 5 | 50 | 147 | 277 |
| 10 | 3 | 6 | 46 | 164 | 222 |
| 11 | 4 | 5 | 53 | 162 | 225 |
| 12 | 4 | 2 | 54 | 163 | 234 |
| 13 | 2 | 4 | 56 | 166 | 269 |
| 14 | 5 | 4 | 48 | 157 | 271 |
| 15 | 3 | 6 | 55 | 169 | 237 |
| 16 | 1 | 2 | 57 | 149 | 262 |
| 17 | 2 | 6 | 55 | 139 | 248 |
| 18 | 5 | 6 | 51 | 165 | 276 |
| 19 | 2 | 11 | 54 | 163 | 262 |
| 20 | 1 | 8 | 38 | 157 | 247 |
| 21 | | | | | 249 |
| 22 | | | | | 252 |
| 23 | | | | | 270 |
| 24 | | | | | 264 |
| 25 | | | | | 286 |
| MEAN | 3.15 | 6.25 | 50.45 | 161.25 | 253.88 |
| X874.17 | 2754 | 5464 | 44102 | 140960 | 221934 |
| EXTRAS | 370 | 107 | 861 | 753 | 1135 |
| TOTAL | 3124 | 5571 | 44963 | 141713 | 223069 |

Sample : 20 (larvae 25
x 4.8cc

Total volume:
4196 cc

APPENDIX 3.2: (Cont'd)

Colony Ten :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 4 | 7 | 49 | 150 | 456 |
| 2 | 4 | 10 | 61 | 200 | 486 |
| 3 | 4 | 8 | 65 | 226 | 435 |
| 4 | 5 | 10 | 63 | 200 | 521 |
| 5 | 4 | 18 | 52 | 217 | 546 |
| 6 | 4 | 11 | 56 | 176 | 523 |
| 7 | 7 | 9 | 55 | 221 | 429 |
| 8 | 5 | 8 | 42 | 197 | 519 |
| 9 | 5 | 9 | 59 | 160 | 444 |
| 10 | 5 | 14 | 40 | 206 | 496 |
| 11 | 5 | 11 | 49 | 182 | 410 |
| 12 | 0 | 10 | 59 | 215 | 543 |
| 13 | 2 | 7 | 47 | 188 | 505 |
| 14 | 3 | 16 | 56 | 188 | 460 |
| 15 | 5 | 15 | 49 | 199 | 448 |
| 16 | 6 | 13 | 54 | 202 | 520 |
| 17 | 3 | 10 | 53 | 166 | 451 |
| 18 | 7 | 7 | 62 | 197 | 448 |
| 19 | 3 | 14 | 52 | 198 | 466 |
| 20 | 3 | 20 | 55 | 216 | 502 |
| MEAN | 4.2 | 11.35 | 53.9 | 195.2 | 480.4 |
| X550 | 2310 | 6243 | 29645 | 107360 | 264220 |

Sample : 20 x 5cc

Total volume :
2750cc

Colony Eleven :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 1 | 7 | 96 | 374 | 629 |
| 2 | 1 | 2 | 47 | 325 | 324 |
| 3 | 0 | 7 | 78 | 217 | 356 |
| 4 | 3 | 2 | 75 | 211 | 446 |
| 5 | 2 | 3 | 66 | 165 | 432 |
| 6 | 0 | 4 | 79 | 209 | 434 |
| 7 | 1 | 3 | 69 | 226 | 377 |
| 8 | 0 | 4 | 74 | 238 | 386 |
| 9 | 0 | 1 | 78 | 168 | 347 |
| 10 | 1 | 4 | 90 | 222 | 382 |
| 11 | 1 | 2 | 70 | 203 | 410 |
| 12 | 1 | 5 | 76 | 188 | 415 |
| 13 | 1 | 4 | 69 | 203 | 432 |
| 14 | 0 | 7 | 78 | 195 | 409 |
| 15 | 1 | 3 | 92 | 211 | 378 |
| 16 | 0 | 3 | 77 | 196 | 474 |
| 17 | 0 | 4 | 77 | 231 | 461 |
| MEAN | 0.767 | 3.824 | 75.94 | 222.47 | 417.18 |
| X1108.5 | 848 | 4239 | 84179 | 246608 | 462444 |

Sample : 17 x 4.8cc

Total volume :
5321cc (1108.5 x 4.8)

APPENDIX 3.2: (Cont'd)

Colony Twelve:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 2 | 4 | 52 | 211 | 399 |
| 2 | 1 | 3 | 50 | 215 | 365 |
| 3 | 2 | 5 | 54 | 218 | 382 |
| 4 | 3 | 3 | 60 | 214 | 372 |
| 5 | 3 | 5 | 52 | 221 | 396 |
| 6 | 2 | 3 | 61 | 201 | 399 |
| 7 | 4 | 3 | 66 | 210 | 325 |
| 8 | 1 | 5 | 50 | 200 | 359 |
| 9 | 4 | 6 | 56 | 213 | 389 |
| 10 | 2 | 4 | 56 | 229 | 358 |
| 11 | 2 | 4 | 59 | 203 | 363 |
| 12 | 0 | 6 | 60 | 208 | 320 |
| 13 | 2 | 5 | 51 | 225 | 329 |
| 14 | 2 | 6 | 49 | 201 | 349 |
| 15 | 5 | 4 | 56 | 201 | 376 |
| 16 | 2 | 4 | 60 | 205 | 369 |
| 17 | 4 | 4 | 55 | 222 | 385 |
| 18 | 3 | 1 | 52 | 205 | 336 |
| 19 | 2 | 5 | 67 | 209 | 363 |
| 20 | 1 | 4 | 58 | 216 | 384 |
| MEAN | 2.35 | 4.2 | 56.2 | 211.35 | 366.05 |
| X866.67 | 2037 | 3640 | 48707 | 183171 | 317246 |

Sample : 20 x 4.8cc

Total volume :
4160cc (866.67 x 4.8)

Colony Thirteen :

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 3 | 35 | 80 | 646 |
| 2 | 2 | 2 | 36 | 101 | 585 |
| 3 | 2 | 2 | 39 | 92 | 606 |
| 4 | 1 | 2 | 37 | 76 | 613 |
| 5 | 3 | 2 | 33 | 83 | 608 |
| 6 | 3 | 1 | 38 | 80 | 699 |
| 7 | 2 | 2 | 34 | 99 | 592 |
| 8 | 3 | 1 | 33 | 87 | 632 |
| 9 | 3 | 2 | 35 | 88 | 501 |
| 10 | 2 | 2 | 33 | 84 | 627 |
| 11 | 3 | 2 | 34 | 89 | 610 |
| 12 | 3 | 3 | 37 | 81 | 599 |
| 13 | 2 | 3 | 32 | 90 | 608 |
| 14 | 1 | 3 | 39 | 80 | 577 |
| 15 | 1 | 3 | 38 | 81 | 593 |
| 16 | 2 | 2 | 31 | 92 | 624 |
| 17 | 3 | 2 | 37 | 90 | 600 |
| 18 | 1 | 2 | 30 | 79 | 581 |
| 19 | 2 | 1 | 33 | 84 | 608 |
| 20 | 2 | 3 | 36 | 98 | 677 |
| MEAN | 2.2 | 2.15 | 35 | 86.7 | 609.3 |
| X707.5 | 1557 | 1521 | 24763 | 61340 | 431080 |

Sample : 20 x 4.8cc

Total volume :
3396 cc (707.5 x 4.8)

APPENDIX 3.2: (Cont'd)

Colony Fourteen:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 3 | 34 | 217 | 396 |
| 2 | 3 | 2 | 31 | 150 | 469 |
| 3 | 4 | 0 | 45 | 137 | 388 |
| 4 | 10 | 3 | 31 | 147 | 322 |
| 5 | 6 | 3 | 43 | 184 | 334 |
| 6 | 4 | 2 | 36 | 166 | 316 |
| 7 | 5 | 5 | 43 | 136 | 333 |
| 8 | 3 | 3 | 45 | 184 | 318 |
| 9 | 8 | 3 | 45 | 180 | 343 |
| 10 | 2 | 3 | 37 | 138 | 288 |
| 11 | 3 | 3 | 47 | 177 | 413 |
| 12 | 2 | 3 | 33 | 160 | 327 |
| 13 | 2 | 2 | 47 | 190 | 329 |
| 14 | 8 | 2 | 40 | 186 | 414 |
| 15 | 7 | 2 | 40 | 194 | 361 |
| MEAN | 4.667 | 2.600 | 39.80 | 169.733 | 352.733 |
| X900 | 4200 | 2340 | 35820 | 152760 | 317460 |

Sample : 15 x 5cc

Total volume :
4,500cc (900 x 5)

Colony Fifteen:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 10 | 2 | 56 | 124 | 274 |
| 2 | 5 | 2 | 59 | 146 | 281 |
| 3 | 2 | 5 | 61 | 159 | 173 |
| 4 | 2 | 3 | 54 | 162 | 256 |
| 5 | 2 | 3 | 57 | 160 | 204 |
| 6 | 6 | 4 | 51 | 167 | 268 |
| 7 | 7 | 5 | 52 | 150 | 192 |
| 8 | 4 | 5 | 51 | 154 | 189 |
| 9 | 4 | 4 | 50 | 181 | 253 |
| 10 | 5 | 4 | 56 | 191 | 258 |
| 11 | 5 | 5 | 55 | 155 | 187 |
| 12 | 5 | 4 | 50 | 177 | 178 |
| 13 | 4 | 6 | 58 | 174 | 205 |
| 14 | 4 | 2 | 57 | 165 | 181 |
| 15 | 5 | 3 | 57 | 182 | 177 |
| 16 | 3 | 2 | 56 | 175 | 199 |
| 17 | 5 | 3 | 59 | 156 | 206 |
| 18 | 4 | 2 | 52 | 170 | 183 |
| 19 | 3 | 2 | 60 | 166 | 197 |
| 20 | 3 | 3 | 52 | 165 | 188 |
| MEAN | 4.4 | 3.45 | 55.25 | 163.95 | 212.45 |
| X1072.1 | 4717 | 3699 | 59234 | 175771 | 227768 |

Sample : 20 x 4.8cc

Total volume :
5146cc (1072.1 x 4.8)

APPENDIX 3.2: (cont'd)

Colony Sixteen:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 2 | 2 | 66 | 191 | 509 |
| 2 | 2 | 2 | 67 | 250 | 508 |
| 3 | 5 | 3 | 53 | 273 | 498 |
| 4 | 3 | 4 | 61 | 236 | 483 |
| 5 | 2 | 9 | 51 | 245 | 512 |
| 6 | 4 | 2 | 66 | 249 | 576 |
| 7 | 2 | 2 | 61 | 223 | 532 |
| 8 | 3 | 2 | 59 | 267 | 499 |
| 9 | 4 | 6 | 58 | 298 | 490 |
| 10 | 3 | 3 | 59 | 247 | 518 |
| 11 | 3 | 0 | 58 | 245 | 500 |
| 12 | 1 | 3 | 59 | 221 | 569 |
| 13 | 5 | 3 | 71 | 234 | 498 |
| 14 | 6 | 3 | 62 | 247 | 502 |
| 15 | 5 | 2 | 69 | 268 | 485 |
| 16 | 5 | 3 | 53 | 266 | 498 |
| 17 | 3 | 2 | 59 | 229 | 485 |
| 18 | 5 | 5 | 61 | 277 | 501 |
| MEAN | 3.50 | 3.11 | 60.72 | 248.11 | 509.06 |
| X870 | 3045 | 2706 | 52826 | 215856 | 442882 |

Sample : 18 x 5cc

Total volume : 4350cc (870 x 5)

Colony Seventeen:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 1 | 29 | 53 | 680 |
| 2 | 2 | 1 | 23 | 51 | 600 |
| 3 | 2 | 2 | 23 | 51 | 598 |
| 4 | 2 | 1 | 20 | 50 | 622 |
| 5 | 3 | 3 | 21 | 54 | 611 |
| 6 | 3 | 3 | 24 | 56 | 554 |
| 7 | 2 | 1 | 23 | 60 | 587 |
| 8 | 3 | 1 | 27 | 50 | 602 |
| 9 | 2 | 2 | 25 | 57 | 651 |
| 10 | 1 | 2 | 24 | 54 | 608 |
| 11 | 2 | 1 | 25 | 58 | 589 |
| 12 | 1 | 1 | 28 | 53 | 611 |
| 13 | 3 | 1 | 20 | 50 | 691 |
| 14 | 1 | 2 | 23 | 53 | 698 |
| 15 | 3 | 2 | 25 | 59 | 653 |
| 16 | 2 | 2 | 20 | 55 | 654 |
| 17 | 3 | 2 | 21 | 50 | 685 |
| 18 | 2 | 3 | 23 | 61 | 555 |
| MEAN | 2.22 | 1.72 | 23.6 | 54.17 | 625 |
| X509.6 | 1131 | 877 | 12027 | 27605 | 318500 |

Sample : 18 x 4.8cc

Total volume : 2446cc (509.6 x 4.8)

APPENDIX 3.2: (Cont'd)

Colony Eighteen:

| | MS | mS | MW | mW | L | N |
|---|---|---|---|---|---|---|
| 1 | 6 | 5 | 51 | 100 | 140 | 4 |
| 2 | 9 | 3 | 55 | 153 | 115 | 7 |
| 3 | 5 | 8 | 50 | 170 | 118 | 11 |
| 4 | 8 | 5 | 54 | 139 | 115 | 16 |
| 5 | 5 | 0 | 49 | 97 | 100 | 10 |
| 6 | 5 | 8 | 51 | 178 | 92 | 14 |
| 7 | 3 | 9 | 42 | 80 | 77 | 10 |
| 8 | 5 | 4 | 40 | 130 | 81 | 6 |
| 9 | 8 | 4 | 58 | 178 | 131 | 7 |
| 10 | 7 | 2 | 44 | 83 | 97 | 8 |
| 11 | 2 | 2 | 40 | 78 | 126 | 13 |
| 12 | 6 | 3 | 48 | 162 | 144 | 14 |
| 13 | 4 | 9 | 52 | 167 | 78 | 10 |
| 14 | 5 | 3 | 48 | 147 | 135 | 8 |
| 15 | 5 | 6 | 45 | 104 | 91 | 3 |
| 16 | 9 | 7 | 50 | 142 | 105 | 14 |
| 17 | 9 | 5 | 60 | 144 | 163 | 15 |
| 18 | 7 | 4 | 47 | 171 | 138 | 11 |
| 19 | 6 | 5 | 45 | 104 | 90 | 7 |
| 20 | 6 | 6 | 51 | 88 | 65 | 5 |
| MEAN | 6 | 4.9 | 49 | 130.75 | 110.05 | 9.65 |
| X1600 | 9600 | 7840 | 78400 | 209200 | 176080 | 15440 |

Sample : 20 x 5cc

Total volume : 8000cc (1600 x 5)

Colony Nineteen:

| | MS | mS | MW | mW | L |
|---|---|---|---|---|---|
| 1 | 3 | 6 | 87 | 219 | 103 |
| 2 | 5 | 3 | 112 | 235 | 80 |
| 3 | 4 | 6 | 130 | 198 | 75 |
| 4 | 7 | 6 | 98 | 167 | 62 |
| 5 | 6 | 10 | 117 | 149 | 53 |
| 6 | 3 | 4 | 120 | 152 | 49 |
| 7 | 4 | 7 | 142 | 144 | 79 |
| 8 | 3 | 3 | 104 | 149 | 61 |
| 9 | 3 | 5 | 115 | 158 | 79 |
| 10 | 3 | 9 | 110 | 178 | 76 |
| 11 | 7 | 6 | 100 | 186 | 74 |
| 12 | 9 | 4 | 99 | 126 | 68 |
| 13 | 3 | 14 | 90 | 170 | 50 |
| 14 | 5 | 2 | 96 | 168 | 53 |
| 15 | 4 | 9 | 108 | 144 | 82 |
| 16 | 5 | 6 | 125 | 170 | 53 |
| 17 | 9 | 7 | 81 | 185 | 62 |
| 18 | 3 | 6 | 101 | 199 | 69 |
| 19 | 4 | 5 | 104 | 164 | 97 |
| 20 | 4 | 6 | 114 | 191 | 45 |
| MEAN | 4.7 | 6.2 | 107.65 | 172.6 | 68.5 |
| X1460 | 6862 | 9052 | 157169 | 251996 | 100010 |

Sample : 20 x 5cc

Total volume : 7,300cc (1460 x 5)

APPENDIX 3.5.1 Summary of respirometry data at 24°C corrected to S.T.P. Data for castes of <u>Macrotermes</u> <u>bellicosus</u> in $\mu l\ O_2\ hr^{-1}g^{-1}$ wet weight and for fungus combs in $\mu l\ O_2\ hr^{-1}g^{-1}$ dry weight.

| CASTE OR COMB | | $O_2$ consumption, $\mu l\ g^{-1}hr^{-1}$ fresh wt. (termites) or dry wt. (fungus combs) | | | Log wet weight per individual, mg | | |
|---|---|---|---|---|---|---|---|
| | | ONE | TWO | THREE | ONE | TWO | THREE |
| MAJOR SOLDIERS | 1 | 163.218 | 245.847 | 130.515 | 1.5911 | 1.6848 | 1.5984 |
| | 2 | 198.258 | 172.194 | 271.969 | 1.6163 | 1.6687 | 1.6378 |
| | 3 | 167.415 | | 334.859 | 1.5948 | | 1.6028 |
| | 4 | 233.219 | | 232.068 | 1.5721 | | 1.6135 |
| | 5 | 227.942 | | 232.371 | 1.5399 | | 1.6096 |
| | 6 | 243.479 | | 189.701 | 1.5984 | | 1.5881 |
| | $\bar{x}$ | 205.589 | 209.021 | 231.914 | | | |
| | s.d. | 34.656 | 52.081 | 69.665 | | | |
| MINOR SOLDIERS | 1 | 296.896 | 358.482 | 350.765 | 0.9890 | 0.9243 | 0.9332 |
| | 2 | 242.604 | 301.203 | 358.703 | 0.9777 | 0.9408 | 0.9685 |
| | 3 | 196.896 | 212.839 | 317.842 | 0.9890 | 0.9901 | 0.9432 |
| | 4 | 297.102 | | 306.824 | 0.9661 | | 0.9743 |
| | 5 | 279.522 | | 285.180 | 1.0414 | | 0.9720 |
| | 6 | 256.668 | | 277.053 | 1.0212 | | 0.9848 |
| | $\bar{x}$ | 244.948 | 290.841 | 316.061 | | | |
| | s.d. | 41.656 | 73.372 | 33.426 | | | |
| MAJOR WORKERS | 1 | 251.394 | 340.271 | 231.431 | 1.2041 | 1.0563 | 1.0607 |
| | 2 | 258.426 | | 310.710 | 1.2553 | | 1.1629 |
| | 3 | 315.561 | | 238.327 | 1.2347 | | 1.1089 |
| | 4 | 250.515 | | 270.425 | 1.2218 | | 1.1341 |
| | 5 | 264.579 | | 265.152 | 1.1903 | | 1.1206 |
| | 6 | 297.981 | | | 1.2131 | | |
| | $\bar{x}$ | 273.076 | 340.271 | 263.209 | | | |
| | s.d. | 27.170 | | 31.389 | | | |
| MINOR WORKERS | 1 | 398.187 | 363.175 | 341.797 | 0.8751 | 0.6893 | 0.8274 |
| | 2 | 338.415 | 192.877 | 371.803 | 0.8129 | 0.7459 | 0.7825 |
| | 3 | 369.180 | 508.281 | 439.001 | 0.8751 | 0.7067 | 0.7657 |
| | 4 | 327.867 | 350.133 | 407.839 | 0.8513 | 0.7210 | 0.8500 |
| | 5 | 338.415 | | 475.841 | 0.8129 | | 0.8055 |
| | 6 | 297.102 | | 349.145 | 0.8865 | | 0.7882 |
| | $\bar{x}$ | 344.861 | 353.617 | 397.571 | | | |
| | s.d. | 34.894 | 128.921 | 53.043 | | | |
| LARVAE | 1 | 159.796 | 154.049 | 140.053 | 0.5643 | 0.5449 | 0.3968 |
| | 2 | 163.308 | 147.973 | 138.225 | 0.5948 | 0.5382 | 0.3010 |
| | 3 | 175.600 | 177.372 | 230.604 | 0.5229 | 0.6057 | 0.2472 |
| | 4 | 170.332 | 162.977 | 159.974 | 0.4260 | 0.6335 | 0.4060 |
| | 5 | 204.574 | 156.683 | 149.413 | 0.4771 | 0.6128 | 0.4356 |
| | 6 | 162.430 | 157.052 | 170.698 | 0.5229 | 0.5246 | 0.3778 |
| | $\bar{x}$ | 172.673 | 159.351 | 164.828 | | | |
| | s.d. | 16.674 | 10.078 | 34.478 | | | |
| NEW FUNGUS COMB | 1 | 390.372 | 303.962 | 415.882 | | | |
| | 2 | 447.105 | 590.006 | 434.363 | | | |
| | 3 | 474.120 | 593.809 | 458.636 | | | |
| | $\bar{x}$ | 473.199 | 495.926 | 436.294 | | | |
| | s.d. | 42.744 | 166.256 | 21.442 | | | |
| OLD FUNGUS COMB | 1 | 128.323 | 94.307 | 150.367 | | | |
| | 2 | 129.674 | 176.282 | 286.825 | | | |
| | 3 | 129.674 | 294.360 | 215.569 | | | |
| | $\bar{x}$ | 129.224 | 188.316 | 217.587 | | | |
| | s.d. | 0.780 | 100.568 | 68.251 | | | |

APPENDIX 3.5.2 Summary of respirometry data at 27°C corrected to S.T.P. Data for castes of <u>Macrotermes</u> <u>bellicosus</u> in $\mu l$ $O_2$ $hr^{-1}g^{-1}$ wet weight and for fungus combs in $\mu l$ $hr^{-1}g^{-1}$ dry weight.

| CASTE OR COMB | | $O_2$ consumption, $\mu l$ $g^{-1}hr^{-1}$ fresh wt. (termites) or dry wt. (fungus combs) | | | Log wet weight per individual, mg | | |
|---|---|---|---|---|---|---|---|
| | | ONE | TWO | THREE | ONE | TWO | THREE |
| MAJOR SOLDIERS | 1 | 220.872 | 295.741 | 208.796 | 1.6467 | 1.7081 | 1.5775 |
| | 2 | 230.400 | 315.469 | 229.454 | 1.6021 | 1.6696 | 1.5955 |
| | 3 | 339.428 | 279.188 | 203.842 | 1.5721 | 1.6662 | 1.5840 |
| | 4 | 236.661 | 358.013 | 285.518 | 1.5836 | 1.6875 | 1.6229 |
| | 5 | 247.355 | 253.514 | 244.023 | 1.6163 | 1.7822 | 1.5955 |
| | 6 | 282.764 | 276.051 | 343.072 | 1.5643 | 1.6135 | 1.5899 |
| | $\bar{x}$ | 259.580 | 296.329 | 252.451 | | | |
| | s.d. | 44.582 | 36.633 | 53.243 | | | |
| MINOR SOLDIERS | 1 | 289.105 | 449.262 | 368.672 | 1.0414 | 1.0139 | 0.9823 |
| | 2 | 247.681 | 366.775 | | 1.0700 | 1.0000 | |
| | 3 | 371.953 | 475.691 | | 1.0000 | 0.9566 | |
| | 4 | 264.941 | 511.913 | | 1.0414 | 0.9408 | |
| | 5 | 283.064 | 578.484 | | 1.0792 | 0.9031 | |
| | 6 | | | | | | |
| | $\bar{x}$ | 291.349 | 476.425 | 368.672 | | | |
| | s.d. | 47.893 | 78.162 | | | | |
| MAJOR WORKERS | 1 | 353.830 | 443.998 | 389.777 | 1.1950 | 1.0388 | 1.0911 |
| | 2 | 321.036 | 473.902 | 367.999 | 1.1663 | 1.0620 | 1.0893 |
| | 3 | 346.063 | 433.221 | 404.926 | 1.1809 | 1.0981 | 1.0713 |
| | 4 | 334.844 | 432.677 | 370.323 | 1.1950 | 1.0870 | 1.0354 |
| | 5 | 373.679 | 483.529 | 358.750 | 1.1712 | 1.1044 | 1.0569 |
| | 6 | 351.241 | 548.728 | 362.561 | 1.2175 | 1.0620 | 1.0407 |
| | $\bar{x}$ | 346.782 | 469.343 | 375.722 | | | |
| | s.d. | 17.882 | 44.307 | 17.891 | | | |
| MINOR WORKERS | 1 | 440.993 | 590.474 | 460.190 | 0.8325 | 0.7559 | 0.7634 |
| | 2 | 418.555 | 600.965 | 330.050 | 0.8129 | 0.7619 | 0.7782 |
| | 3 | 428.048 | 777.703 | 512.133 | 0.8195 | 0.7796 | 0.7474 |
| | 4 | 465.157 | 521.194 | 440.014 | 0.8451 | 0.7275 | 0.7348 |
| | 5 | 460.842 | 640.569 | 501.129 | 0.8195 | 0.7396 | 0.8062 |
| | 6 | 424.596 | 599.908 | | 0.8195 | 0.7760 | |
| | $\bar{x}$ | 439.699 | 621.802 | 448.703 | | | |
| | s.d. | 19.533 | 85.644 | 72.557 | | | |
| LARVAE | 1 | 235.008 | 240.599 | 175.377 | 0.7877 | 0.5237 | 0.5024 |
| | 2 | 230.688 | 246.920 | 193.503 | 0.6990 | 0.4271 | 0.5407 |
| | 3 | 222.048 | 260.346 | 223.438 | 0.6690 | 0.4895 | 0.5051 |
| | 4 | 241.920 | 254.232 | 197.186 | 0.7482 | 0.5298 | 0.4732 |
| | 5 | 197.856 | 274.787 | 176.860 | 0.8062 | 0.4502 | 0.4968 |
| | 6 | | 240.213 | 213.645 | | 0.4838 | 0.5246 |
| | $\bar{x}$ | 225.504 | 252.850 | 196.668 | | | |
| | s.d. | 17.052 | 13.299 | 19.291 | | | |
| NEW FUNGUS COMB | 1 | 591.508 | 110.221 | 118.642 | | | |
| | 2 | 636.702 | 456.630 | 226.445 | | | |
| | 3 | 620.751 | 188.025 | 222.642 | | | |
| | $\bar{x}$ | 616.320 | 251.625 | 189.243 | | | |
| | s.d. | 22.920 | 181.751 | 61.172 | | | |
| OLD FUNGUS COMB | 1 | 237.932 | 189.010 | 98.606 | | | |
| | 2 | 261.858 | 283.496 | 38.885 | | | |
| | 3 | 179.446 | 256.625 | 90.525 | | | |
| | $\bar{x}$ | 226.412 | 243.044 | 76.005 | | | |
| | s.d. | 42.397 | 48.685 | 32.400 | | | |

Note: fungus comb figures at 27°C omitted from further calculations

APPENDIX 3.5.3 Summary of respirometry data at 30°C corrected to S.T.P. Data for castes of *Macrotermes bellicosus* in μl $O_2$ $hr^{-1}g^{-1}$ wet weight and for fungus combs in μl $O_2$ $hr^{-1}g^{-1}$ dry weight.

| CASTE OR COMB | | $O_2$ consumption, μl $g^{-1}hr^{-1}$ fresh wt. (termites) or dry wt. (fungus combs) | | | Log wet weight per individual, mg | | |
|---|---|---|---|---|---|---|---|
| | | ONE | TWO | THREE | ONE | TWO | THREE |
| MAJOR SOLDIERS | 1 | 195.829 | 319.250 | 239.584 | 1.6467 | 1.6860 | 1.6030 |
| | 2 | 381.150 | 286.291 | 195.900 | 1.6199 | 1.6335 | 1.5980 |
| | 3 | 253.788 | 348.685 | 187.468 | 1.6564 | 1.6458 | 1.5970 |
| | 4 | 323.507 | 263.140 | 385.190 | 1.6812 | 1.6590 | 1.6103 |
| | 5 | 435.514 | 363.800 | 330.835 | 1.6721 | 1.6571 | 1.6398 |
| | 6 | | 310.147 | 321.626 | | 1.6516 | 1.5860 |
| | $\bar{x}$ | 317.958 | 315.219 | 276.767 | | | |
| | s.d. | 96.016 | 37.606 | 80.731 | | | |
| MINOR SOLDIERS | 1 | 595.500 | 460.601 | 501.835 | 1.0107 | 0.9307 | 0.9370 |
| | 2 | 673.654 | 447.174 | 670.645 | 0.9420 | 0.9256 | 0.9307 |
| | 3 | 524.991 | 419.901 | 597.086 | 0.9777 | 0.9457 | 0.9345 |
| | 4 | 561.520 | 388.309 | 475.737 | 1.0512 | 0.9408 | 0.9697 |
| | 5 | 352.543 | 517.991 | 547.894 | 1.0414 | 0.9685 | 0.9708 |
| | 6 | 568.316 | | 375.171 | 1.0000 | | 0.9614 |
| | $\bar{x}$ | 546.087 | 446.795 | 528.061 | | | |
| | s.d. | 107.100 | 48.486 | 102.263 | | | |
| MAJOR WORKERS | 1 | 500.356 | 500.096 | 567.396 | 1.2512 | 1.0852 | 1.0816 |
| | 2 | 475.720 | 529.195 | 395.845 | 1.856 | 1.0923 | 1.1145 |
| | 3 | 474.871 | 514.240 | 455.324 | 1.2086 | 1.1472 | 1.1589 |
| | 4 | 435.794 | 608.962 | 483.037 | 1.1950 | 1.0780 | 1.0992 |
| | 5 | 508.001 | 472.610 | 450.725 | 1.2305 | 1.0969 | 1.0670 |
| | 6 | | 558.386 | | | 1.0470 | |
| | $\bar{x}$ | 478.948 | 530.581 | 470.465 | | | |
| | s.d. | 28.248 | 47.907 | 62.731 | | | |
| MINOR WORKERS | 1 | 666.008 | 654.468 | 502.088 | 0.8633 | 0.7686 | 0.7649 |
| | 2 | 620.135 | 744.115 | 688.282 | 0.8808 | 0.7774 | 0.7505 |
| | 3 | 543.680 | 602.331 | 881.621 | 0.8195 | 0.7723 | 0.7210 |
| | 4 | 600.597 | 633.270 | 697.106 | 0.8751 | 0.7853 | 0.8109 |
| | 5 | 631.179 | 595.858 | 647.997 | 0.8751 | 0.7364 | 0.7767 |
| | 6 | 637.125 | 744.204 | 612.090 | 0.8325 | 0.7474 | 0.8062 |
| | $\bar{x}$ | 616.454 | 662.374 | 671.531 | | | |
| | s.d. | 41.619 | 66.808 | 124.796 | | | |
| LARVAE | 1 | 270.193 | 300.847 | 247.735 | 0.6368 | 0.5635 | 0.4951 |
| | 2 | 278,663 | 228.137 | 261.640 | 0.6021 | 0.6428 | 1.0374 |
| | 3 | 274.428 | 268.244 | 309.650 | 0.6301 | 0.5407 | 0.3110 |
| | 4 | 293.062 | 316.045 | 266.332 | 0.5798 | 0.2520 | 0.3667 |
| | 5 | 250.712 | 271.305 | 292.696 | 0.6690 | 0.3291 | 0.3450 |
| | 6 | 307.461 | 263.954 | 265.843 | 0.5315 | 0.3814 | 0.4723 |
| | $\bar{x}$ | 279.087 | 274.755 | 273.983 | | | |
| | s.d. | 19.527 | 30.757 | 22.753 | | | |
| NEW FUNGUS COMB | 1 | 801.392 | 748.856 | 999.198 | | | |
| | 2 | | 746.100 | 846.298 | | | |
| | 3 | | 366.731 | 1074.681 | | | |
| | $\bar{x}$ | 801.392 | 620.562 | 973.392 | | | |
| | s.d. | | 219.829 | 116.358 | | | |
| OLD FUNGUS COMB | 1 | 222.826 | 160.580 | 336.146 | | | |
| | 2 | 212.402 | 161.889 | 243.151 | | | |
| | 3 | 224.129 | 146.017 | 337.629 | | | |
| | $\bar{x}$ | 219.786 | 156.162 | 305.642 | | | |
| | s.d. | 6.428 | 8.810 | 54.124 | | | |

APPENDIX 3.5.4 Summary of respirometry data at 34°C corrected to S.T.P. Data for castes of Macrotermes bellicosus in $\mu l$ $O_2$ $hr^{-1}g^{-1}$ wet weight and for fungus combs in $\mu l$ $O_2$ $hr^{-1}g^{-1}$ dry weight.

| CASTE OR COMB | | $O_2$ consumption, $\mu l$ $g^{-1}hr^{-1}$ fresh wt. (termites) or dry wt. (fungus combs) | | | Log wet weight per individual, mg | | |
|---|---|---|---|---|---|---|---|
| | | ONE | TWO | THREE | ONE | TWO | THREE |
| MAJOR SOLDIERS | 1 | 371.622 | 371.234 | 244.190 | 1.6267 | 1.7138 | 1.5899 |
| | 2 | 452.395 | 259.449 | 267.012 | 1.6163 | 1.6506 | 1.6392 |
| | 3 | 469.319 | 430.339 | 382.049 | 1.5873 | 1.6650 | 1.6304 |
| | 4 | 450.530 | 407.836 | 362.161 | 1.5894 | 1.6872 | 1.6163 |
| | 5 | 453.024 | | 472.951 | 1.6092 | | 1.6152 |
| | 6 | 317.834 | | 468.027 | 1.6267 | | 1.6042 |
| | $\bar{x}$ | 419.121 | 367.214 | 366.065 | | | |
| | s.d. | 60.462 | 75.860 | 96.702 | | | |
| MINOR SOLDIERS | 1 | 646.570 | 676.355 | 586.951 | 0.9420 | 0.9217 | 0.9857 |
| | 2 | 638.270 | 623.348 | 601.132 | 1.0000 | 0.9879 | 0.9673 |
| | 3 | 574.360 | 550.221 | 531.793 | 0.9890 | 0.9281 | 0.9638 |
| | 4 | 749.490 | 770.129 | 600.833 | 0.9542 | 0.9408 | 0.9542 |
| | 5 | 652.380 | 478.531 | | 0.9420 | 0.9256 | |
| | 6 | 702.180 | 712.688 | | 0.9294 | 0.8648 | |
| | $\bar{x}$ | 660.542 | 635.212 | 580.177 | | | |
| | s.d. | 59.717 | 107.528 | 32.927 | | | |
| MAJOR WORKERS | 1 | 525.390 | 695.803 | 669.730 | 1.1950 | 1.1430 | 1.0453 |
| | 2 | 654.870 | 726.391 | 620.584 | 1.1712 | 1.1335 | 1.1038 |
| | 3 | 658.190 | 659.432 | 625.680 | 1.1614 | 1.0828 | 1.1260 |
| | 4 | 720.440 | 648.625 | 628.595 | 1.1903 | 1.1260 | 1.1095 |
| | 5 | | 649.743 | 665.142 | | 1.1287 | 1.0923 |
| | 6 | | 630.385 | | | 1.0792 | |
| | $\bar{x}$ | 639.723 | 668.397 | 641.946 | | | |
| | s.d. | 81.971 | 35.717 | 23.501 | | | |
| MINOR WORKERS | 1 | 802.610 | 715.586 | 1000.973 | 0.8808 | 0.7882 | 0.7193 |
| | 2 | 849.920 | 829.677 | 941.694 | 0.8573 | 0.7868 | 0.7882 |
| | 3 | 877.310 | 809.032 | 703.462 | 0.8451 | 0.7796 | 0.8041 |
| | 4 | 971.930 | 949.292 | 732.336 | 0.8451 | 0.7574 | 0.8176 |
| | 5 | 827.510 | 838.355 | 887.526 | 0.8865 | 0.7604 | 0.7664 |
| | 6 | 862.370 | 894.782 | 817.727 | 0.8451 | 0.7679 | 0.8122 |
| | $\bar{x}$ | 865.275 | 839.454 | 847.286 | | | |
| | s.d. | 58.511 | 79.361 | 117.409 | | | |
| LARVAE | 1 | 481.605 | 390.528 | 330.000 | 0.5339 | 0.3802 | 0.4388 |
| | 2 | 326.863 | 417.677 | 442.953 | 0.5229 | 0.2967 | 0.4105 |
| | 3 | 398.855 | 678.881 | 386.556 | 0.5721 | 0.1271 | 0.4482 |
| | 4 | 376.513 | 485.329 | 321.875 | 0.4150 | 0.1523 | 0.4430 |
| | 5 | 429.473 | 595.530 | 340.998 | 0.4150 | 0.0887 | 0.4683 |
| | 6 | 387.270 | 381.895 | 358.458 | 0.4960 | 0.0198 | 0.4810 |
| | $\bar{x}$ | 400.096 | 491.640 | 363.473 | | | |
| | s.d. | 52.138 | 121.351 | 45.235 | | | |
| NEW FUNGUS COMB | 1 | 1348.646 | 996.405 | 660.276 | | | |
| | 2 | 1384.271 | 818.518 | 676.744 | | | |
| | 3 | 1332.106 | 1146.844 | | | | |
| | $\bar{x}$ | 1355.008 | 987.322 | 668.510 | | | |
| | s.d. | 26.658 | 164.251 | 11.645 | | | |
| OLD FUNGUS COMB | 1 | 264.276 | 184.022 | 303.526 | | | |
| | 2 | 303.174 | 456.514 | 340.657 | | | |
| | 3 | 261.292 | 171.278 | 256.851 | | | |
| | $\bar{x}$ | 276.247 | 270.605 | 300.345 | | | |
| | s.d. | 23.367 | 161.128 | 41.993 | | | |

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## PLATE 1

A leaf trap on the edge of one of the wood litter collection quadrats. The plate also shows the general appearance of Southern Guinea savanna during the dry season at Mokwa. In the wet season the leaf trap would be obscured by tall grasses. (Ref. Section 2.1.)

## PLATE 2

Comparison of two sets of logs ( $>$ 2.0 cm diameter). The logs on the left were suspended off the ground for one year and unavailable to termites. Those on the right were left on the ground during the same period and have been heavily attacked. (Ref. Section 2.3.)

## PLATE 3

Samson Ananaba of the A.R.S. Mokwa demonstrating the structure of a Macrotermes bellicosus nest of thetype that lacks a spiral base-plate. Because of the reduced "cellar" in this type of nest, the mounds were invariably small in comparison to the spiral plate type nests. (Ref. Section 3.1., Figures 3.1.1., 3.1.2.)

## PLATE 4

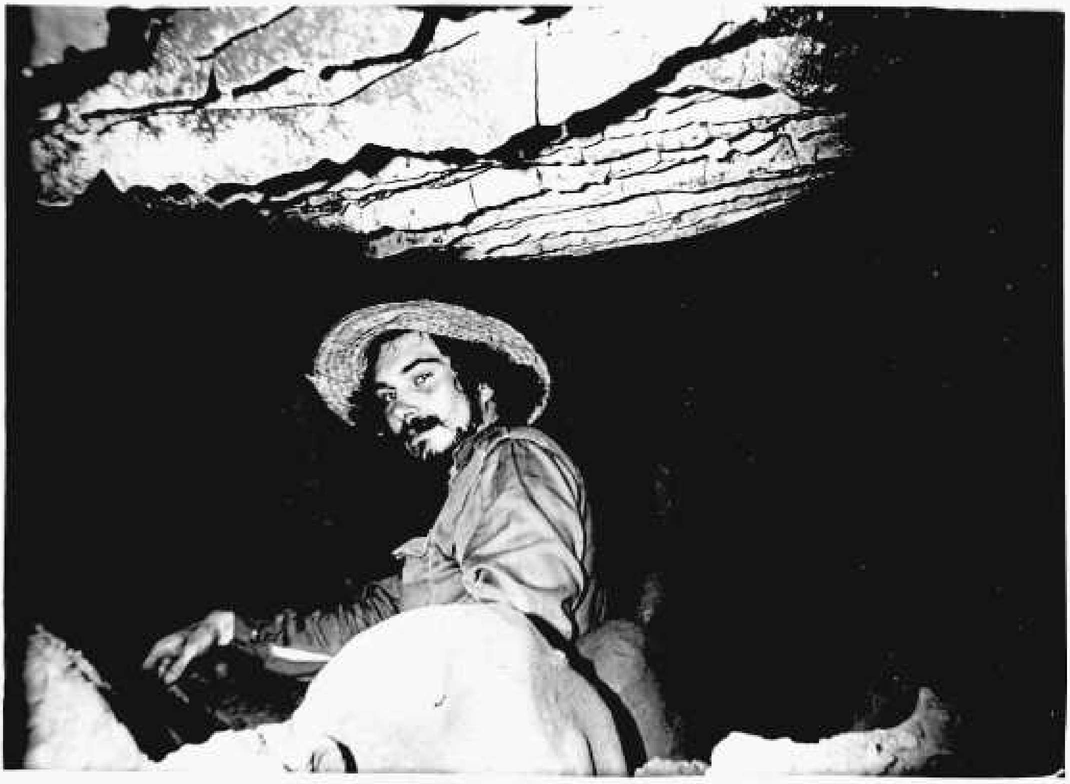
The endoecie extracted from a very small Macrotermes bellicosus nest of the spiral plate type. The idiotheque has been removed to reveal the comminuted food stores on top of the faecal fungus combs. (Ref. Section 3.1., Figures 3.1.1., 3.1.2.)

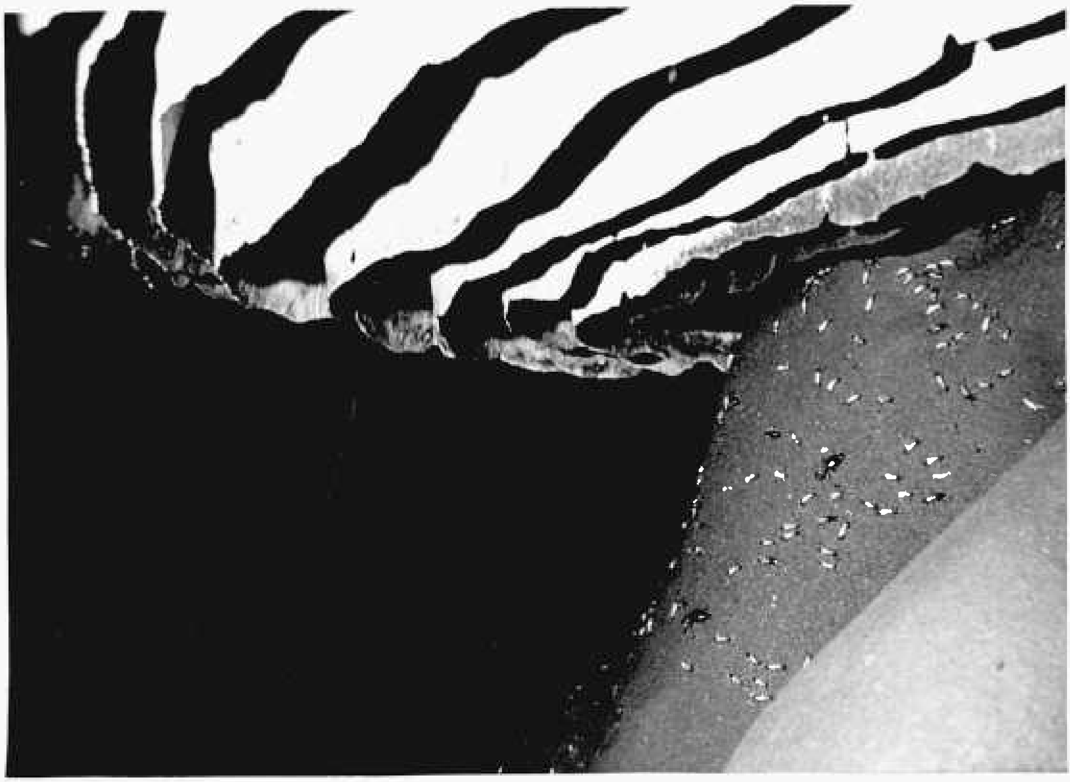
## PLATE 5

The author sitting in the cellar of a very large Macrotermes bellicosus nest of the spiral plate type. The mound was about 6 m high and the base-plate almost 3 m across. White mineral deposits are clearly visible on the vanes of the spiral plate. The supporting pillar is on the right, with channels leading down into the deep galleries. (Ref. Section 3.1., Figure 3.1.1.) (Photograph by Chris Longhurst.)

## PLATE 5

A close-up photograph of the central section of a spiral base-plate. The extraordinary regularity of the spirals is clearly shown and the size of the structures can be compared to the workers and soldiers on the pillar. (Ref. Section 3.1., Figure 3.1.1.)



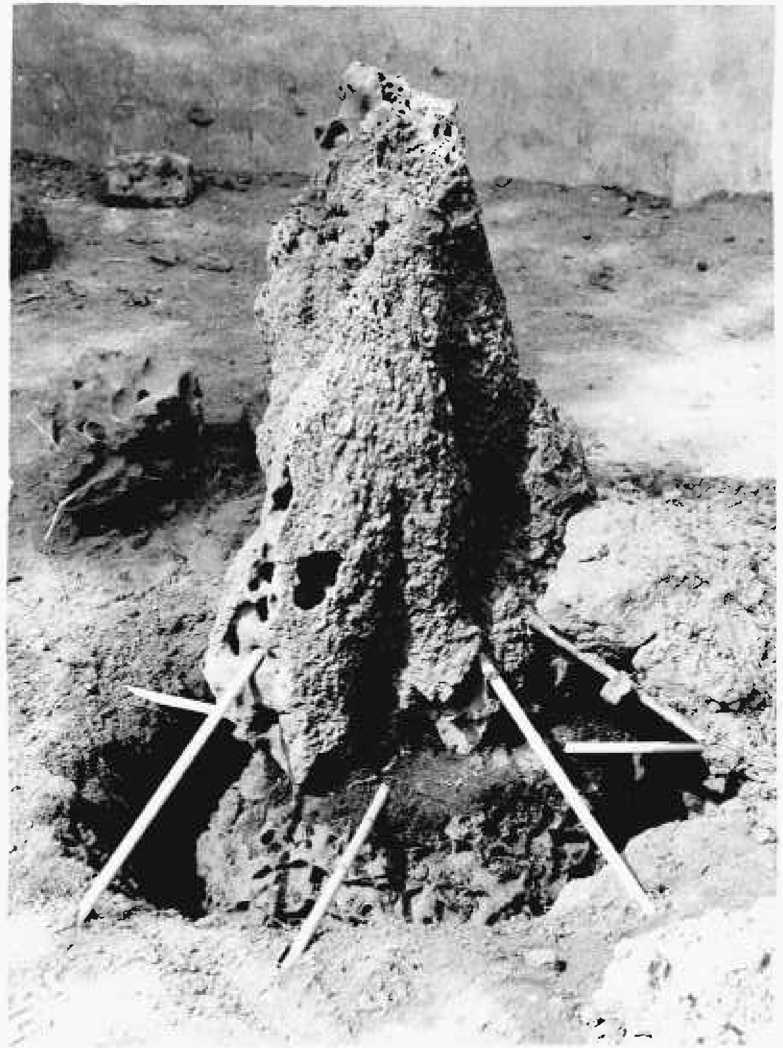


## PLATE 7

Another view of the spiral base-plate, this time from below, pillar on the left. Once again, the vanes and mineral deposits are clearly seen. It is believed that the evaporation which causes these depositions, helps to cool the endoecie from below. (Ref. Section 3.1.)

## PLATE 8

The three concrete isolation tanks used for estimation of the consumption rate of *Macrotermes bellicosus*. Mounds are visible in the central and near tanks. The walls extend for about a metre underground and are sealed by a concrete floor. The roof is in the process of construction. (Ref. Section 3.3.)



## PLATE 9

The above-ground portion of a spiral plate type nest of *Macrotermes bellicosus*. These "cathedral-type" mounds are aptly named with their graceful spires and buttresses attaining heights of over 6 m. (Ref. Section 3.1.)

## PLATE 10

The mound of a *Macrotermes bellicosus* colony in the process of reconstruction in one of the isolation tanks. The endoecie is visible in the artificial habitacle. The termites very quickly reconstructed the nest and built foraging galleries to all parts of the tanks. (Ref. Section 3.3.)