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THE ROLE OF TERMITES IN THE ECOLOGY OF TSAVO NATIONAL PARK, KENYA

A thesis submitted for the degree of

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by

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ABSTRACT

Tsavo National Park lies in an area of very dry country in South Eastern Kenya. Elephants live there in large numbers and in the early 1970's, they had a mean population density of about 1 km^{-2}. They have inflicted widespread destruction on the woodlands which originally covered the Park, leading to a complete change in the appearance of the habitat. This caused considerable anxiety about the future of the Park and all its animal populations so research was begun to try to elucidate the root causes of the "elephant problem" and to predict its consequences. The purpose of the present study was to find out what happens to dead wood in Tsavo and to gauge the importance of termites in the ecology of the area.

Section 1 gives a brief introduction to the history of Tsavo and sets out the main questions posed when this study was begun. In Section 2 the environment of the study area is described in terms of its topography and geology, the soils and their origins, the floristic and structural composition of the vegetation during this study, the climate and its variations in time and space and the role of fire in shaping the habitat. The species of termites found in the study area are listed in Section 3, followed by brief descriptions of their natural history.

Section 4 contains all the information on the turnover of dead wood. The standing crop and rates of wood fall and removal were measured directly at one site and extended by means of an index to measure consumption of dead wood by termites at other sites. Consumption is found to be related to rainfall. The results are discussed in relation to similar studies made elsewhere. A model is constructed relating the consumption of dead wood by termites to rainfall and comparing this with the consumption of grass and browse by large herbivorous mammals. A method is described for measuring the relative importance of different termite species as consumers of dead wood.

Section 5 gives the results of experiments on spatial and temporal patterns in the foraging activity of six species of termites leading to a discussion of their feeding strategies and the differences which allow them to coexist.

In Section 6 the feeding habits and species composition of the termite faunas of different sites are related to rainfall and discussed in relation to other studies. The importance of Macrotermitinae as removers of dead wood is shown to decline with increasing rainfall, even over the small range of rainfall experienced in Tsavo.

It is difficult to estimate populations of termites directly especially for species which nest underground. Section 7 gives the results of a brief survey of the chambers found in the walls of a ditch while Section 8 sets out the results of an aerial census of the distribution of mounds of Macrotermes subhyalinus.

The main results of the work were as follows:

Termites are responsible for removing almost all of the dead wood which disappears from the surface of the ground in Tsavo, at least when the climate is in a dry phase. At the main study site (mean rainfall 350 mm yr^{-1}.) the mean standing crop of dead wood on the ground was 316.7 g m^{-2} dry weight. Annual dead wood litter fall was 30.8 g m^{-2} dry weight and 28.1 g m^{-2} yr^{-1}. dry weight disappeared. An average piece of dead wood took about ten years to decompose completely. Studies at eight other sites, with mean rainfall varying between 200 and 500 mm yr^{-1}. indicate that consumption (C) (g m^{-2} yr^{-1}.) of dead wood by termites in Tsavo can be related to rainfall (AP) (mm yr^{-1}.) by the equation

$$C = 0.39\ AP - 101.78$$

using the data from several other studies in Africa as well a more general result was obtained

$$C = 0.13\ AP - 12.94$$

The fungus growing termites, Macrotermitinae, were the most important consumers of dead wood at all nine experimental sites, but their importance declined as rainfall increased. The percentage of total consumption eaten by Macrotermitinae (MC) was related to total consumption by termites (C) ($g\ m^{-2}\ yr^{-1}$.) by

$$MC = 100.4 - 0.18\ C$$

Some differences in food preferences and foraging strategies between species were noted. The Macrotermitinae foraged most intensively on dead wood during the rains whereas other termites ate most dead wood during the long dry season. Differences in resource exploitation between different species of Macrotermitinae are more subtle and probably depend on the ability of some species, eg. Microtermes allaudanus to hold a monopoly in restricted "favourable" sites while other species forage widely but less intensively eg. Odontotermes mediocris.

Macrotermes subhyalinus mounds never occurred at the high densities observed in other parts of Africa (table 8.7). Their distribution was related to soil types, rainfall and damage to trees by elephants. Subterranean nest chambers of other species occurred at a density of 0.77 chambers m^{-2} in a limited ditch sample.

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PLATES

1 Soldiers of Kalotermitidae

2 Soldiers of Rhinotermitidae and Termitidae

3 Soldiers of Microcerotermes sp. I and Amitermes spp.

4 Soldiers of Trinervitermes

5 Soldiers and workers of Macrotermes subhyalinus

6 Soldiers of Odontotermes sp.

7 Soldiers of Microtermes spp. and Synacanthotermes zanzibarensis

SECTION 1

GENERAL INTRODUCTION

Tsavo National Park was gazetted in 1948. It lies in South Eastern Kenya and covers 21,000 km^2 of semi-arid bushland. For administrative convenience the Park is divided into two sections, Tsavo East and Tsavo West, separated by the Nairobi-Mombasa railway line (Figure 1.1). The area has never been permanently settled although it was used by nomadic pastoralists and elephant hunters before it became a National Park. Observations made in the area by early explorers have been compiled by Corfield (1974) and the early development of the Park was described by Sheldrick (1973).

Initially almost all of Tsavo was covered with low woodlands dominated by *Commiphora*, *Acacia* and *Terminalia* trees. About ten years after the Park was gazetted it became apparent that elephants were killing the trees by ring barking and pushing them over. In some areas the destruction was extensive and the stark forms of dead trees dominated the landscape. The change in the vegetation was so dramatic that some people predicted that the vegetation would never recover and Tsavo would become a desert (Glover, 1963).

Tsavo Research Project was set up in 1966 to investigate the ecology of the area and particularly the relationship between elephants and their environment. A laboratory was built at the headquarters of Tsavo East near Voi town. The most intensive research has been carried out in Tsavo East south of the Galana River. The soils and vegetation have been investigated by Van Wijngaarden (in prep.). The flora was catalogued by Greenway (1969). Work on the distribution, number and habits of the large herbivores has been reviewed by Cobb (1976) and Phillipson (1975) considered the large mammal populations in relation to a theoretical estimate of

vegetation production and carrying capacity. The avifauna has been investigated by Lack (in prep.) and Smeenk (1974). The decomposition of elephant dung was studied by Anderson and Coe (1974), Coe (1977) and Kingston (1977). The climate of the region has been described by Cobb (1976) and Tyrrell and Coe (1974). Because there is such a wealth of background knowledge on this area, and it is well provided with roads, all the experimental work for the present study was done in Tsavo East south of the Galana River. This area is referred to as the study area and as Southern Tsavo East.

The purpose of the present study was to investigate the role of termites in the ecology of Tsavo. The National Parks Authorities were particularly concerned to know how long it took dead wood produced by elephant damage to disappear. I soon realised that the potential scope of the research was enormous even when restricted to decomposition of dead wood in its various forms. I therefore decided to restrict experimental work to an investigation of the decomposition of dead wood at the surface of the ground and the habits of the termite species involved. The main objectives of the study were:

1. To measure the standing crop, rate of production and rate of disappearance of dead wood.
2. To measure consumption of dead wood by termites and relate this to the overall rate of disappearance.
3. To measure the populations of termites and relate these to the importance of individual species as consumers of dead wood.
4. To work out the feeding preferences and strategies of the different species of termites present and see how they share out the available resources.

No means of measuring subterranean termite populations could be devised which would have been practicable with the resources available to me.

In Section 2 the habitat of Tsavo is described, followed in Section 3 by a list of the termite species found in Tsavo and brief notes on the natural history of each species. Section 4 contains all the information about dead wood production, standing crop and disappearance and the importance of different termite species which attack the wood. In Section 5 seasonal changes in termite activity are described and the spatial relationships of foraging are discussed. The taxonomic composition of the Tsavo termite fauna is discussed in relation to its recorded food preferences in Section 6 and Sections 7 and 8 contain observations on subterranean and mound nests respectively.

Termites are social insects which have been intensively studied because of their importance as pests of timber, stored products, agriculture and forestry (Harris, 1961). Reviews of work on the biology of termites may be found in Krishna and Weesner (1969, 1970). The ecological relationships of termites have come under increasing scrutiny during the last ten years. Their importance as soil animals was reviewed by Lee and Wood (1971b) and as decomposers by Wood (1976). Their energetic relationships have been reviewed and compared with ants in Brian (1978). Termites have been included in studies of ecosystems conducted under the auspices of the International Biological Programme (I.B.P.) and other agencies (Josens, 1972; Lepage, 1974; Haverty and Nutting, 1975b; Matsumoto, 1976; Collins, 1977b; Wood, Johnson, Ohiagu, Collins and Longhurst, 1977; Matsumoto and Abe, in press).

Figure 1.1

A Map of Southern Kenya showing the position of Tsavo National Park

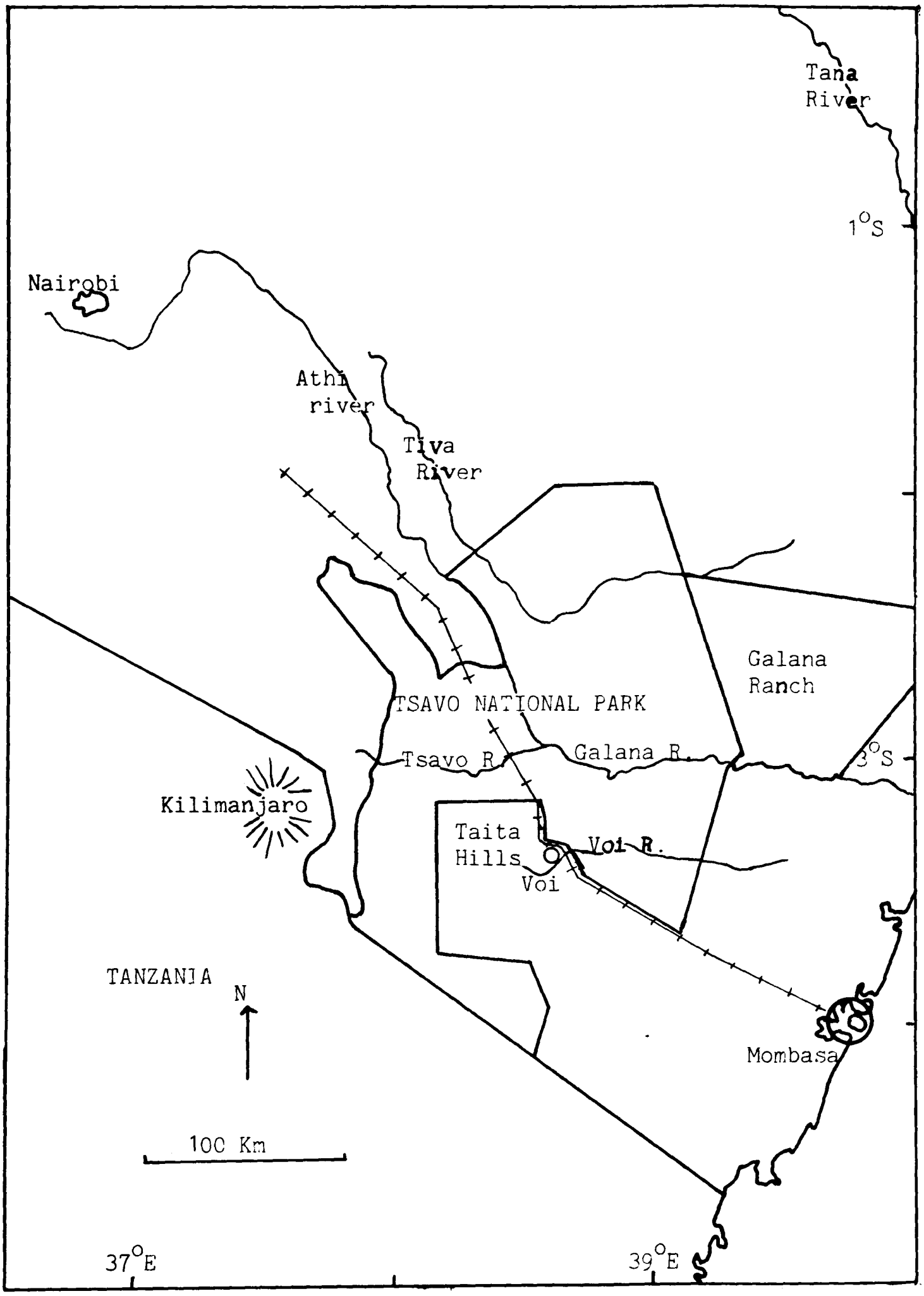


Table 1.1

Abbreviations used in the Text

a	regression constant
b	regression coefficient
d	normal distribution statistic
$\log_{10}$	logarithm to base 10
ln	logarithm to base e
N	sample size
N.S.	not significant
p	probability
r	correlation coefficient
S.E.	standard error
t	student's t
AE	annual evapotranspiration
AP	annual precipitation, or rainfall
C	consumption
D	disappearance of dead wood
DC	decomposition constant
F	dead wood litter fall
f.p.	foraging party
HQ	headquarters
LF	total litter fall from woody vegetation
LHB	large herbivore biomass
LHC	large herbivore consumption
LHE	large herbivore energy expenditure
LHP	large herbivore production
NAAP	net above-ground annual primary production
P	production
S	standing crop of dead wood

SECTION 2

TSAVO: CLIMATIC AND EDAPHIC BACKGROUND

2.1 INTRODUCTION

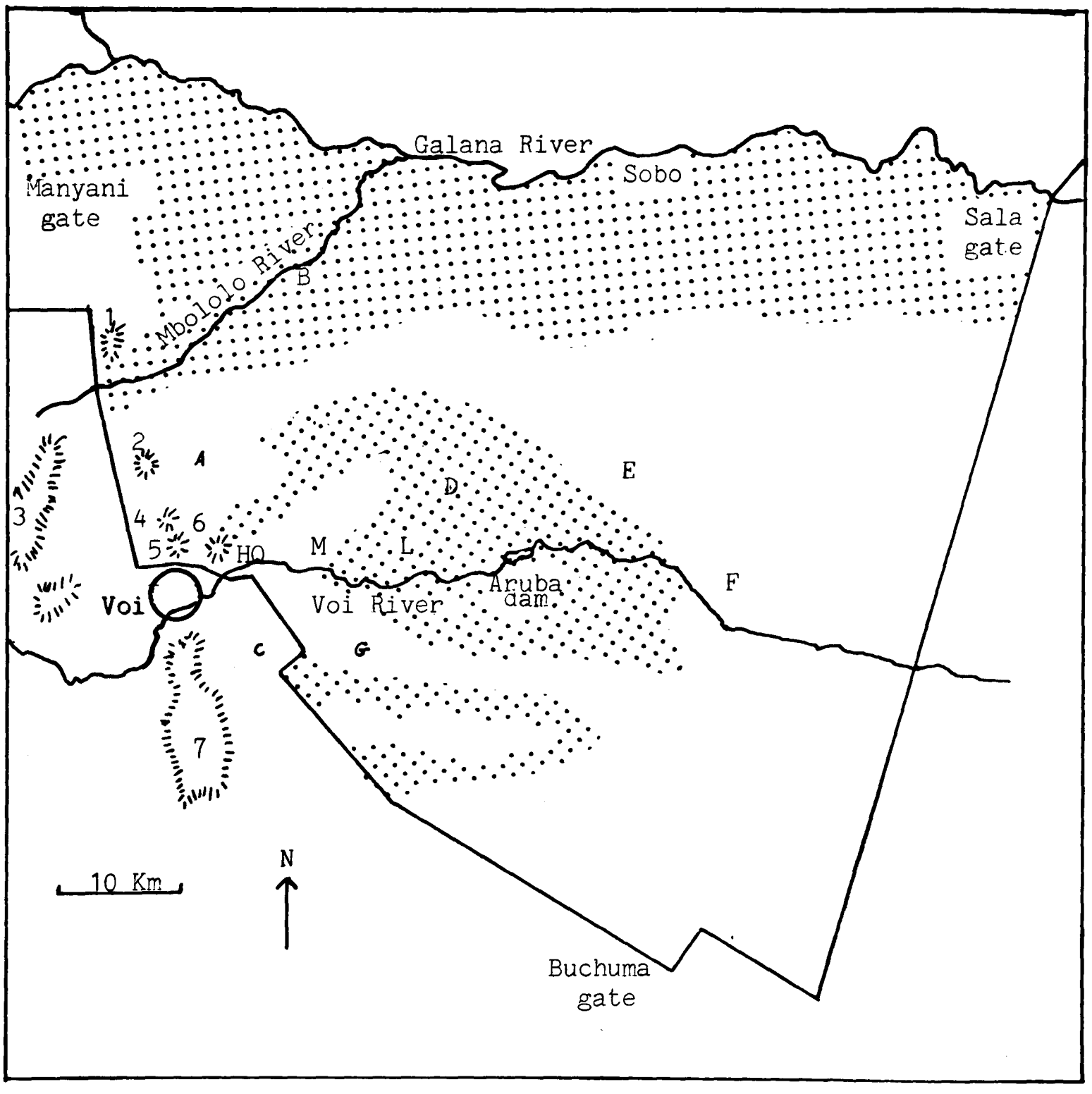
A considerable amount of work has been done in the last few years to describe the climate, soils and vegetation of the Tsavo ecosystem. These studies were made either to stand on their own such as the soil maps of W. van Wijngaarden, or as part of other studies such as the analysis of climate used to investigate the factors affecting the distribution and numbers of large mammals (Cobb, 1976). Some of these studies were very extensive covering areas up to 40,000 km^2 in and around the Tsavo National Parks, ranging from Kilimanjaro in the west to Galana Ranch in the east, the Usambara mountains in the south to the featureless bush to the north of Tsavo East. The experimental work for the present study was confined to the part of Tsavo East National Park south of the Galana River (Figure 2.1) and only this area will be described here. A detailed description of each experimental site is given in Section 4.1, pp.34.

2.2 GEOLOGY AND TOPOGRAPHY

Most of Tsavo East south of the Galana River is a peneplain with very low relief rising gently from 300 m in the north east to 600 m in the west. The underlying rocks are part of the Precambrian basement system which extends through much of Kenya and Tanzania (Parkinson, 1947) composed of gneisses, schists, migmatites and crystalline limestones. To the east of a line south of Sobo (Figure 2.1) the basement is covered by a band of Carboniferous-Permian sedimentary sandstones known as the Taru grits. The flat relief is broken in the west by hills which rise abruptly from the plain. The hills, Manga, Irima, Makingali and Mzinga (Figure 2.1) are outliers of the Taita Hills which rise to about 2,500 m

Figure 2.1

A Map of Southern Tsavo East showing major physical features, the Distribution of Different Soil Types, Places Named in the Text and the Location of the Experimental Sites Used in this Study.



Hills: 1 Manga, 2 Irima, 3 Taita, 4 Makingali, 5 Voi, 6 Mzinga, 7 Sagala.

Dissected erosional plain

Sedimentary basement plain

Sites: M main study site, A - G wooden disc transect sites, L subsidiary quadrat study site.

on the western edge of the study area. The hills are formed from the basement system rocks and have an important influence on the rainfall and fluvial water supply to this side of the study area. In the north the relief increases where the plain is dissected by a series of storm water channels draining into the Galana river. Limestone ridges are exposed between the stream beds.

2.3 SOILS

A detailed survey of the soils of Tsavo East has recently been made by W. van Wijngaarden; the brief description which follows has been taken from his unpublished preliminary reports and soil map. Three groups of soils can be identified on the basis of their origins and development; (i) erosional and (ii) sedimentary soils derived from the basement system and (iii) alluvial soils.

The basement erosional soils are derived from the underlying rocks. They are typically deep well drained red sandy clays or sandy loams (rhodic ferralsols) over gravel. These soils are very infertile and cover about 60% of the study area. A very similar soil is derived from the Taru grits in the East. In the dissected plain a calcic cambisol occurs on areas of exposed limestone. The soil is a thin stony yellowish brown sandy loam with low fertility.

The sedimentary basement soils are derived from the basement rocks but have been transported. They include very deep well drained red sandy clay to clay (ferric luvisols), very deep moderately drained brown friable sandy clay (chromic luvisols) and very deep imperfectly drained reddish brown sandy clay to clay (calcic luvisols). The chromic luvisols have a higher cation exchange capacity than the ferric luvisols, but both have a much higher base saturation than the rhodic ferralsols of the erosional plain.

The alluvial deposits in southern Tsavo East are mostly brown sandy clays or sandy loams occupying the bottoms of shallow valleys. They range from deep well drained soils often with saline or alkaline subsoil to poorly drained deep black calcareous clays in bottom lands. All these alluvial soils are potentially much more fertile than the erosional or sedimentary soils, but they cover less than 10% of the study area.

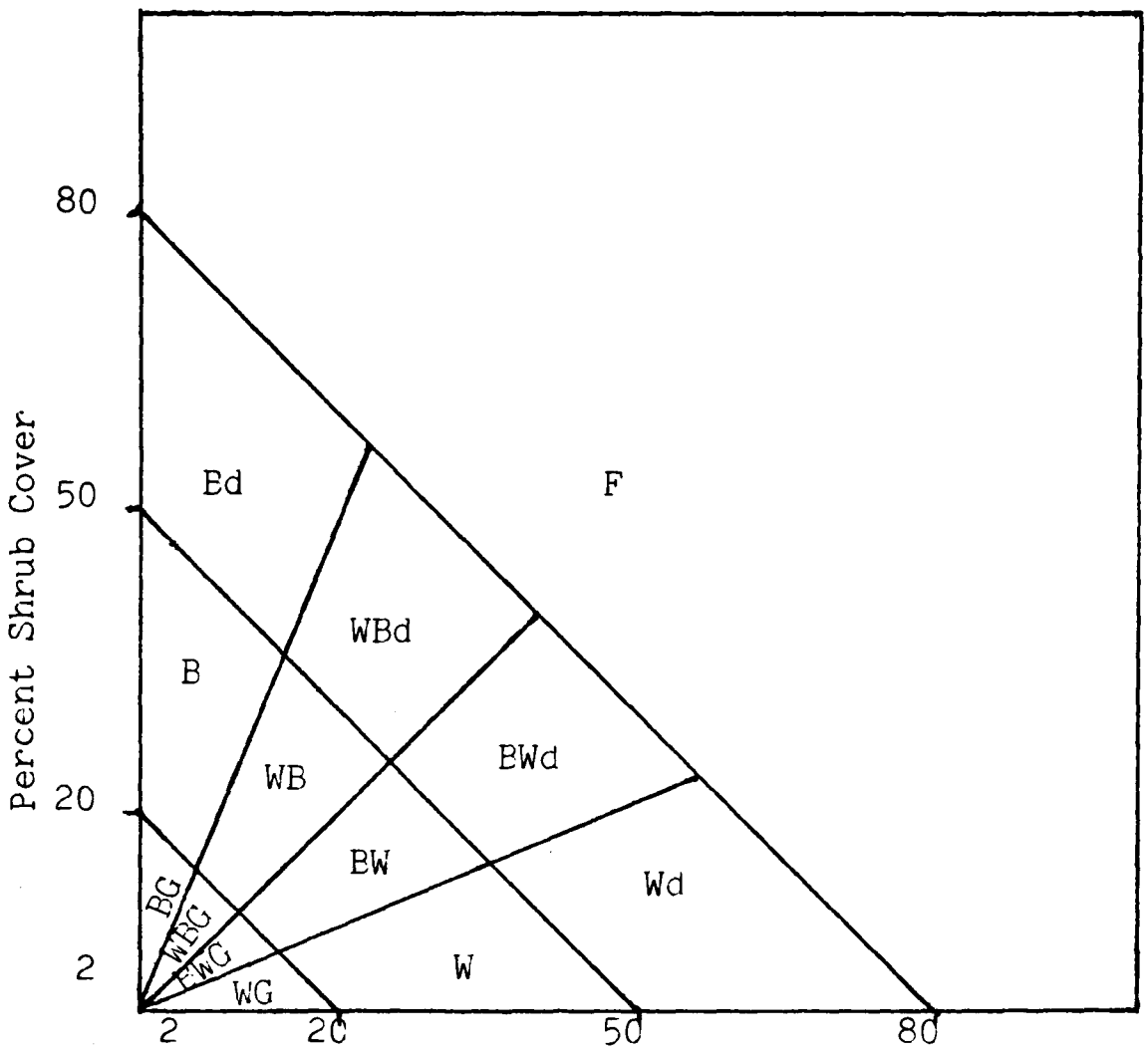
2.4 VEGETATION

A number of schemes for classifying the vegetation of East Africa have been published, notably those of Pratt, Greenway and Gwynne (1966) and Greenway (1973). Greenway (1969) used the latter scheme to describe the vegetation of Tsavo East; however this approach is not entirely satisfactory in the Tsavo context because the present vegetation structure depends not only on the variations in climate, soil and topography but also on the modifications to the basic picture brought about by elephants and in some cases by fire. Van Wijngaarden (in prep.) has classified the vegetation on two bases, the first by floristic associations, the second by habitat structure. He recognises sixteen floristic associations in southern Tsavo East ranging from the very restricted riverine forest to groupings associated with the common soil types. Structural variation is classified according to the cover of trees and shrubs in a scale from grassland (< 2% tree and shrub cover) through various combinations such as wooded bushed grassland (2-10% tree cover, 2-15% shrub cover) to forest (> 80% tree cover). This classification is summarised in Figure 2.2 and van Wijngaarden's report is reproduced in Appendix A.

In most of the sixteen floristic associations the commonest trees and shrubs were the same, the species used for floristic determination being sparser. This is partly because the whole of southern Tsavo East has suffered from a high level of elephant damage (Cobb, 1976) and the few

Figure 2.2

Classification of Vegetation Structure According to the Cover of Woody Plants. (After van Wijngaarden, in prep.).



F = forest B = bushland W = woodland G = grassland

d = dense

tree species relatively immune to elephants, such as Delonix elata, Platycelyphium voense and Melia volkensii have survived better than locally characteristic species. The exception to this is in areas where elephant activity has been restricted, on steep hill slopes and outside the Park boundaries. Mature Commiphora spp. trees dominate these areas as they did much of the Park thirty years ago. Recent drastic reduction of the elephant population and improved rainfall have led to extensive regeneration of young Commiphora spp. inside the Park since the present study was completed.

Most of the study area is covered by bushed grassland and wooded bushed grassland, with bushland and wooded bushland restricted to small areas with high rainfall near Buchuma and Voi. Outside the Park boundaries the vegetation is dominated by Commiphora woodland which is sometimes dense where rainfall is relatively high due to the proximity of the Taita and Sagala hills. Small areas of grassland occur on the less well drained alluvial soils of the study area.

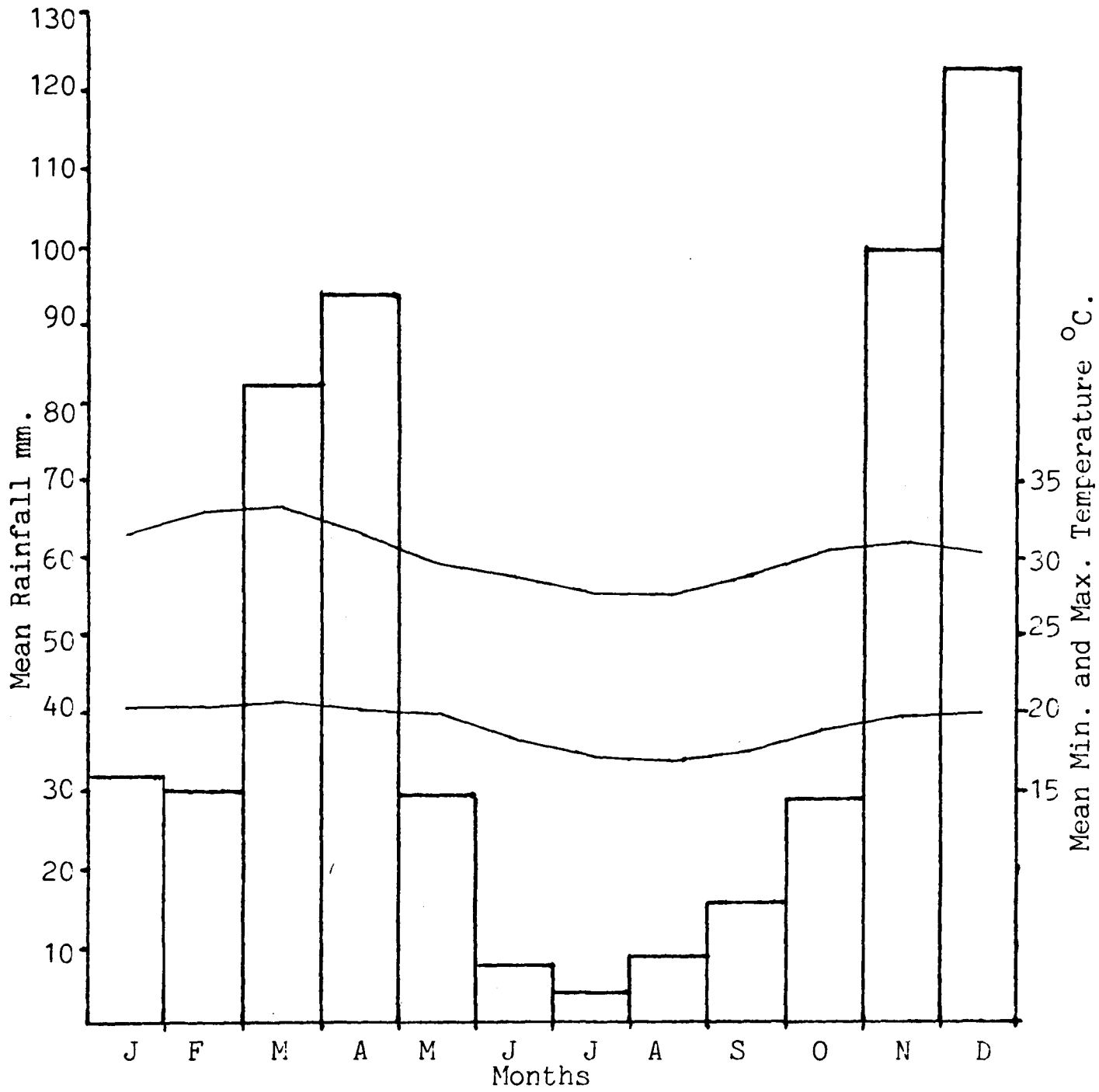
2.5 CLIMATE

From a biological point of view, rainfall is the most important climatic variable in arid environments such as Tsavo. Rainfall has been recorded at Voi station since 1904; the annual mean is 549 mm but precipitation is very unevenly distributed seasonally and from year to year. The mean rainfall for each month is shown in Figure 2.3 which reveals that there are two rainy seasons each year in March-April and November-December separated by two and six month dry seasons. Mean monthly maximum and minimum temperatures only fluctuate by about $5^{o}C$ and are also plotted in Figure 2.3.

Cobb (1976) made an exhaustive analysis of spatial and temporal patterns in the distribution of rainfall for the whole Tsavo region from

Figure 2.3

Mean monthly rainfall at Voi Town for 67 years (1904 - 1970) and monthly mean maximum and minimum air temperatures (1938 - 1970). (From reports of the East African Meteorological Department).



Kilimanjaro to the coast. He found the rainfall to be governed by two opposing trends; it declines with increasing distance from the coast, but increases with altitude. Superimposed on these major trends are subsidiary influences, notably orogenic rainfall in the Taita and Chyulu hills and associated rain shadows to the west of them, and a presumed descending wind system over north-eastern Tsavo East causing a major rainfall trough. He used trend surface analysis to plot the spatial pattern of the mean rainfall data for 1970-1974 from over 50 raingauges in the region (Figure 2.4). From this figure it can be seen that the rainfall at Voi town is not representative of the rainfall of southern Tsavo East. Most of the study area receives less than 400 mm annually and this declines in the north east to 200 mm.

Cobb (1976) used Fourier analysis to detect periodic phenomena in the long term rainfall data for the region. He demonstrated cyclical events with periodicities of 3.5, 4 and 5 years and a peak at 36 years which, due to the length of the data series, is less reliable but supports suggestions of a 40-50 year cycle (Phillipson, 1975). Some of the fluctuations which occur lead to severe droughts such as the one in 1970-1971 when 6000 elephants died (Corfield, 1973).

Monthly rainfall at the Tsavo Research Centre during the period of the present study is given in Table 2.1. The totals for 1975 (335.4 mm) and 1976 (298.0 mm) were both substantially less than the five year mean for 1970-1974 quoted by Cobb (1976) as 426 mm. This reflects the generally dry conditions which prevailed during the present study. The rainfall at 14 stations in the study area for each year from 1972-1976 are given in Table 2.2. The mean of the five years is also given and has been plotted for each raingauge position in Figure 2.5. Kingston (1977) compared the five year mean rainfall of 1970-1974 with long term data from 34 raingauges in the Tsavo region. He concluded that rainfall was significantly below the

long term average by 17%. There is no significant difference between the five year means for 1970-1974 and 1972-1976 for the raingauges given in Table 2.2, indicating that rainfall was still about 17% below the "expected" level.

Soil temperature is an important component of the climate for all soil animals, which includes most species of termites. The temperature of the soil from the surface down to 180 cm was recorded by Glover (1972). The annual means at three times of day at seven depths are given in Table 2.3, with the maximum and minimum temperatures recorded at each depth.

2.6 FIRE

Annual fires are an important feature of many African savanna ecosystems (Trapnell, Friend, Chamberlain and Birch, 1976). They were of little importance in the woodlands of Tsavo until elephants opened these up sufficiently for extensive stands of grass to grow. Fires, usually starting from the railway on the western edge of the study area, could then spread through the grasses and cause further damage to the woodlands. The importance of fire has declined recently, partly because in the very dry period since 1970 grass production has been low and little was left to be burned. No fires were reported in the study area during the period of the present investigation.

Figure 2.4

Distribution of Mean Annual Rainfall (1970 - 1974) analysed by Trend Surface Analysis (after Cobb (1976) figure 2.3.5).

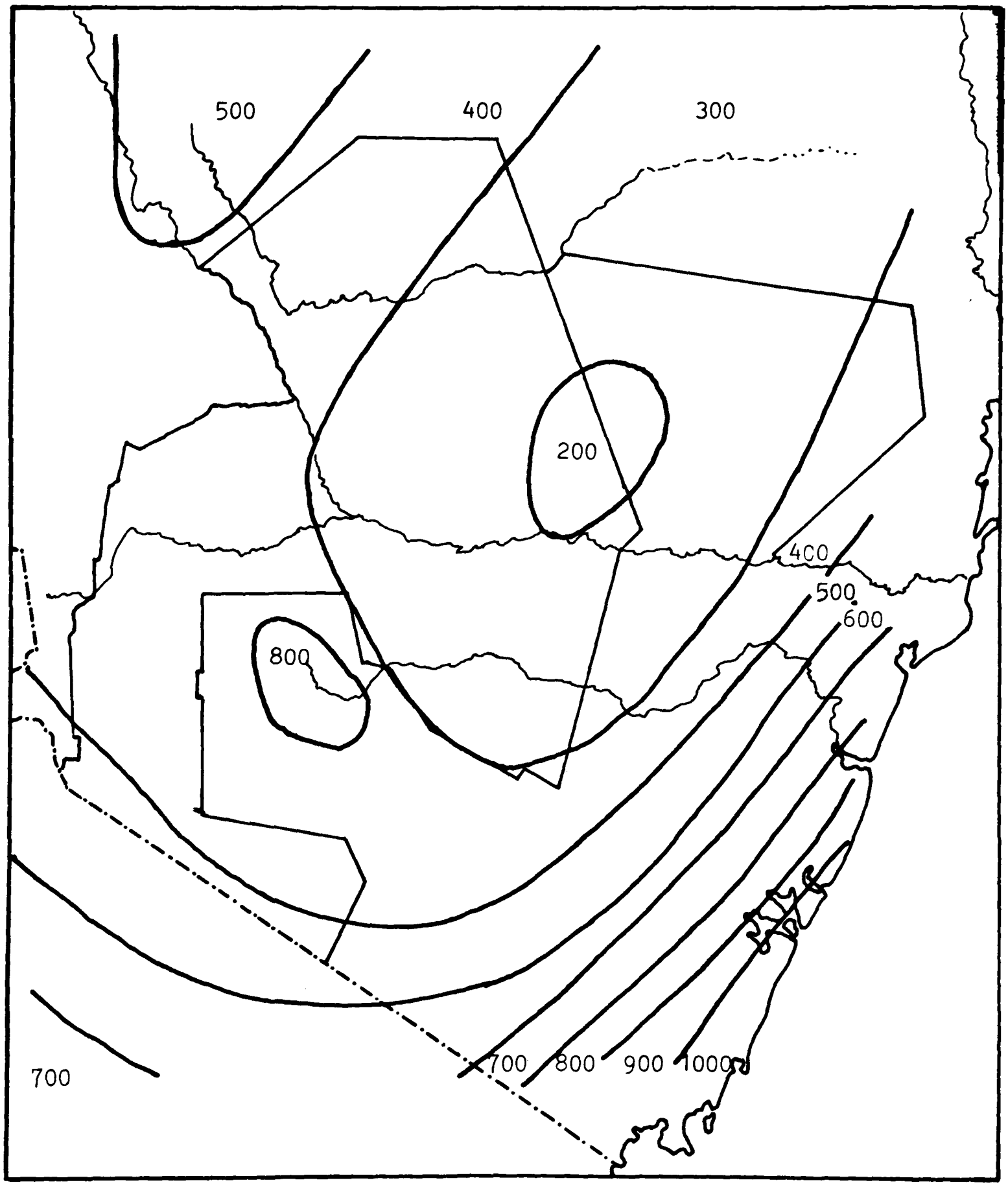


Table 2.1

Monthly Rainfall at Research Centre

during Period of Study

m m

Month	1975	1976	1977
January	7.9	0.0	9.5
February	0.0	0.0	35.2
March	32.8	3.6	22.1
April	19.4	45.95	70.2
May	9.2	12.90	
June	0.0	1.0	
July	1.0	0.0	
August	0.0	1.8	
September	20.3	45.3	
October	0.4	6.4	
November	90.8	102.5	
December	153.6	78.6	
Total	335.4	298.05	

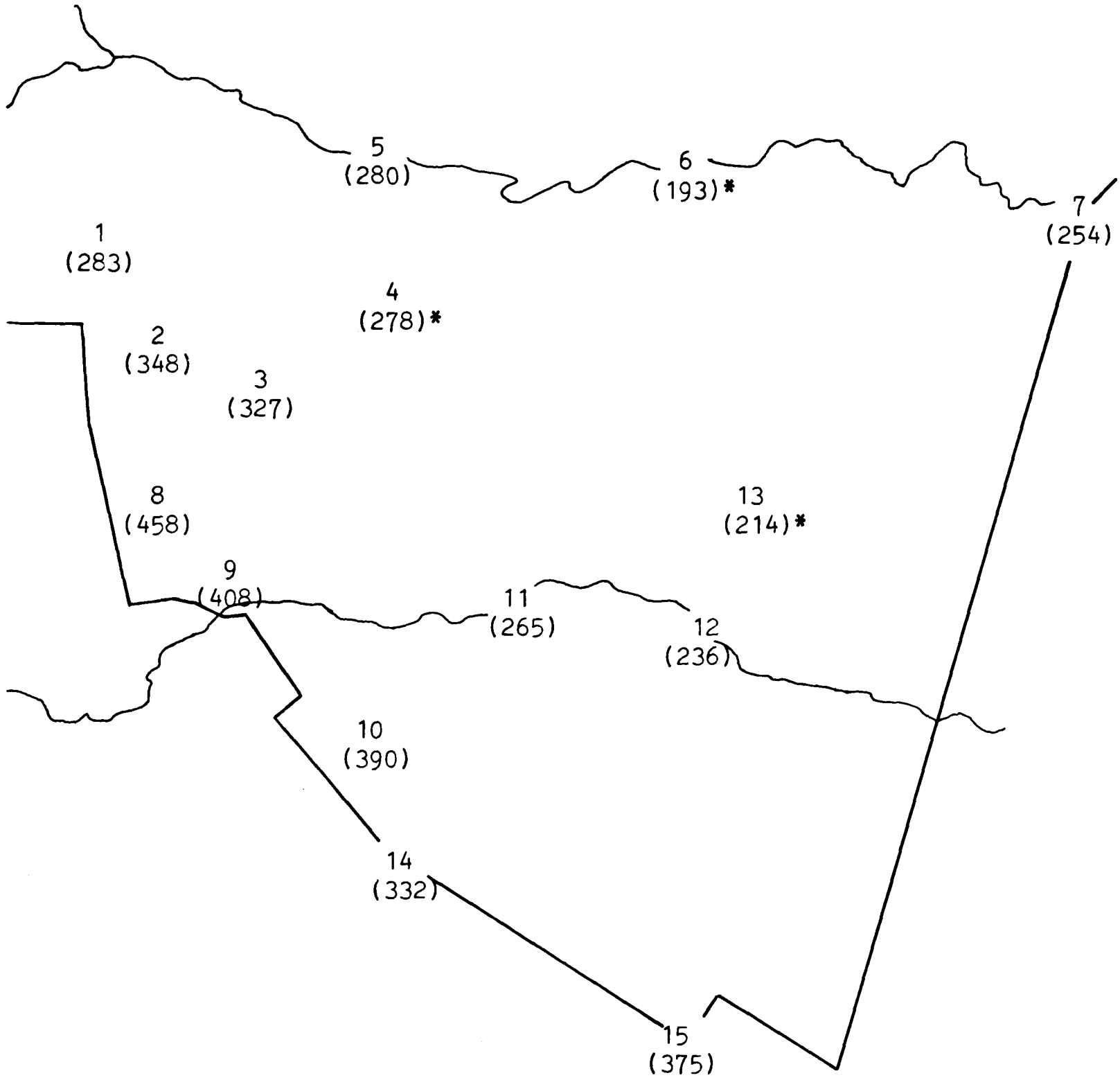
Table 2.2

Rainfall records for the five years 1972-1976 at raingauges in southern Tsavo East and the five year means. Experimental sites close to these raingauges are indicated. One month's records were missing from bracketed figures and that month estimated by interpolation.

Location	1972	1973	1974	1975	1976	5 yr. Mean	Experimental sites
Research Centre	590	472	344	335	298	408	
Manyani Gate	277	467	247	253	169	283	
Aruba Lodge	311	299	226	123	365	265	D
Buchuma Gate	641	308	354	295	278	375	
Sala Gate	373	244	280	179	192	254	
Lugards Falls	409	198	342	238	214	280	
Irimia Exclosure	759	473	233	266	559	458	A
Mudanda Rock	413	298	330	239	459	348	
Buffalo Wallows	542	288	309	220	276	327	B
Punda Milia	467	179	221	193	(329)	(278)	
Ndara Borehole	676	499	309	194	270	390	G
Mukwaju	364	201	237	189	188	236	F
Sala Cross Roads	386	225	118	104	236	214	E
Sobo	238	168	170	175	(216)	(193)	

Figure 2.5

Five year mean rainfall at 15 sites in Southern Tsavo East (1972 - 1976).mm yr^{-1}



* 1 month missing from the records and estimated by interpolation.

1	Manyani gate	8	Irima exclosure
2	Mudanda	9	Tsavo Research Centre
3	Buffalo Wallows	10	Ndara exclosure
4	Punda Milia	11	Aruba lodge
5	Lugards Falls	12	Mukwaju
6	Sobo	13	Sala - Mukwaju cross roads
7	Sala gate	14	Maungu
		15	Buchuma gate

Table 2.3

Soil Temperatures in Tsavo East

after Glover (1972)

^{o}C

	Annual Mean					
$Depth_{cm}$	08.00h	14.00h	18.00h	Max	Min	Range
0	23.9	47.1	29.8	78.9	19.1	59.8
10	26.0	33.3	32.9	-	22.2	-
20	28.2	29.1	30.4	36.3	23.6	12.7
30	28.8	28.9	29.1	34.2	25.0	9.2
60	28.9	29.0	28.9	32.8	25.3	7.5
90	28.9	29.2	28.9	32.5	26.4	6.1
180	28.9	28.9	28.9	32.0	27.0	5.0

SECTION 3

SYSTEMATIC LIST AND NATURAL HISTORY OF TERMITES IN SOUTHERN TSAVO EAST

3.1 INTRODUCTION

Because of the economic importance of termites the African termite fauna has received a lot of attention. Keys are available for identification of genera (Bouillon and Mathot, 1965) and for identification of species within several important genera, notably Amitermes (Sands, 1957 and 1959); Coptotermes (Harris, 1966a); Ancistrotermes (Harris, 1966b); Cubitermes in East Africa (Williams, 1966) and Macrotermes (Ruelle, 1970). Keys have also been compiled for two subfamilies of the Termitidae, Nasutitermitinae (Sands, 1965a) and the soldierless termites Apicotermitinae (Sands, 1972a). However some genera are still in need of revision, notably Odontotermes, Microtermes and Microcerotermes and the specific names used for members of these genera may eventually be reduced to synonyms. Final identification of many species has been made by Dr. W.A. Sands and Dr. R.M.C. Williams at the British Museum (Natural History) and each species collected has been compared with specimens in the Museum collection.

Twenty five species of termites were collected in southern Tsavo East during the present study. Three more species have been collected close to Voi and must be included in the list bringing the total number of termite species known from the study area to 28. These 28 species are listed in section 3.2.

3.2 SPECIES OF TERMITES COLLECTED IN SOUTHERN TSAVO EAST AND THE VOI AREA

ORDER: ISOPTERA

FAMILY: KALOTERMITIDAE Enderlein 1909

- *Epicalotermes* Silvestri 1918
  - *Epicalotermes kempae* (Wilkinson) 1954
- *Neotermes* Holmgren 1911
  - *Neotermes meruensis* (Sjostedt) 1907
- *Cryptotermes* Banks 1906
  - *Cryptotermes havilandi* (Sjostedt) 1900
  - *Cryptotermes* sp.I
- *Bifiditermes* Krishna 1961
  - *Bifiditermes azaniae* Williams 1976 (M.S.)
- Unidentified genus

FAMILY: RHINOTERMITIDAE Light 1921

SUB-FAMILY: COPTOTERMITINAE Holmgren 1910

- *Coptotermes* Wasmann 1896
  - *Coptotermes amanii* (Sjostedt) 1911

FAMILY: TERMITIDAE Westwood 1940

SUB-FAMILY: TERMITINAE Sjostedt 1926

- *Cubitermes* (Haviland) 1898
  - *Cubitermes glebae* (Sjostedt) 1913
  - *Cubitermes umbratus* Williams 1954
- *Promirotermes* Silvestri 1914
  - *Promirotermes bellicosi* Schmitz 1917
  - *Promirotermes massaicus* (Sjostedt) 1907
- *Microcerotermes* Silvestri 1901
  - *Microcerotermes parvus* (Haviland) 1898

Amitermes Silvestri 1901

Amitermes lonnbergianus (Sjostedt) 1911

Amitermes unidentatus (Wasmann) 1897

Amitermes sciangallorum Ghidini 1941

Amitermes messinae Fuller 1922

Amitermes somaliensis Sjostedt 1927

SUB-FAMILY: NASUTITERMITINAE Hare 1937

Trinervitermes Holmgren 1912

Trinervitermes gratiosus (Sjostedt) 1924

Trinervitermes dispar (Sjostedt) 1920

Trinervitermes bettonianus (Sjostedt) 1905

SUB-FAMILY: MACROTERMITINAE Kemner 1934

Macrotermes Holmgren 1909

Macrotermes subhyalinus (Rambur) 1842

Odontotermes Holmgren 1912

Odontotermes badius (Haviland) 1898

Odontotermes zambesiensis (Sjostedt) 1914

Odontotermes mediocris (Sjostedt) 1911

Microtermes Wasmann 1902

Microtermes allaudanus Sjostedt 1926

Microtermes vadschaggae Holmgren 1912

Microtermes sp.I

Synacanthotermes Holmgren 1910

Synacanthotermes zanzibarensis (Sjostedt) 1915

3.3 NOTES ON THE NATURAL HISTORY OF THE TERMITES OF TSAVO

Kemp (1955) studied the distribution of termites in North Eastern Tanzania. She recognised six habitat zones ranging from mountain rain forest to dry bushland very similar to much of Tsavo. Many of the termite species she recorded from dry bushland (habitat zones 2 and 3) were also found in Tsavo East during the present study, but there are differences between the two faunas.

I am most grateful to Josephine Pemberton for permission to reproduce the plates which she drew of the individual termite species. Usually only the soldier caste has been depicted because these are much more valuable for specific identification than the worker caste.

KALOTERMITIDAE

All the Kalotermitidae live enclosed in the dead wood on which they feed. This usually takes the form of dead branches and twigs still attached to the parent tree and usually well above ground level. Some members of the family also attack building timbers and furniture. There is one soldier caste and the front of the soldier's head is often very dark and sometimes sculptured. The workers are usually quite colourless; they are really larvae in a state of suspended development called pseudergates. Only one species, Epicalotermes kempae, was common in the study area, attacking dead branches on living and dead trees. Neotermes meruensis was also widely distributed, but was not as common as E. kempae. These two species appear to have very similar habitat requirements and were occasionally found in the same dead branch. Their soldiers are shown in Plate 1.

Crypotermes sp.I is designated the "East Africa coast sp." in the B.M.N.H. collection. It was only found once in a dead branch on a tree near Tsavo East National Park H.Q. Its soldier is figured in Plate 1.

Cryptotermes havilandi was not encountered during the present study, but has been recorded in the Voi area. Bifiditermes azaniae was found by R.M.C. Williams and M.J. Pearce (pers. comm.) in dead snags of Commiphora spp. trees just outside the south western boundary of the study area. One other species of kalotermitid was collected only once, from a dead branch on a living Delonix elata at Tsavo East H.Q. The soldier is depicted in Plate 1, but it has so far resisted attempts at identification. Cryptotermes sp.I, and the unnamed specimen were only collected from living trees; they may not be able to tolerate the high temperatures to which E. kempae and N. meruensis are probably exposed in the tops of dead trees.

The Kalotermitidae are dependent on mature, senescent and dead trees to provide nest sites. The destruction of woodland habitat in Tsavo probably produced an initial increase, especially of E. kempae and N. meruensis populations living on the dead trees. Regenerating woodlands will not provide suitable nest sites until the trees start to produce dead branches. Kalotermitidae are not especially important in the environment, but do assist the disintegration of dead trees.

RHINOTERMITIDAE

Coptotermes amanii was the only rhinotermitid collected in Tsavo. The soldier's head is yellow and pear shaped with a characteristic large pore just behind the mandibles (Plate 2). Nests are built underground and in the bases of dead trees, and the species forage inside tree trunks and large logs. The space left inside the wood is filled with a scaffolding of grey carton composed of organic faecal matter. Distribution was restricted to the Voi river valley and hill slopes near Voi town where rainfall is higher than on the open plains. This species contributes very little to the turnover of material in Tsavo as a whole.

TERMITIDAE: TERMITINAE

Cubitermes spp. are soil feeding termites which, in Tsavo, build small conical or hemispherical nest mounds up to 30 cm high. Many abandoned mounds were found, particularly on deep red soils, throughout the study area but occupied mounds were only found underneath large shrubs in the western part of the area. Occupied mounds are soft and moist inside and to survive in the arid conditions of Tsavo they probably need to be heavily shaded. The association with bushes may also be due to concentration of the soil organic matter the termites feed on and to accidents of swarming. The two species C. umbratus and C. glebae are shown in Plate 2. Both have one worker and one soldier caste, the workers being recognisable by their unusually large soft abdomens containing clearly visible pink viscera and grey gut contents. The two species appear to differ little in their requirements; they are common in the woodlands outside the park near Voi and changes in the habitat in the park have probably caused severe reductions in the populations and distribution of both species. Very little is known about the role of soil feeding termites in decomposition and nutrient cycling processes, but in the dry environment of Tsavo they are probably insignificant.

Promirotermes spp. are also soil feeders, but nest underground. They appear to be more widely distributed than Cubitermes and were found after rain feeding beneath wet pieces of wood, probably on fungi and bacteria growing on the wood surface. P. bellicosi was the only species encountered during the present study, and it is figured in Plate 2. P. massaicus has also been recorded near Voi. The soldier of this species is about twice the size of the P. bellicosi soldier but its head is not as strongly rectangular.

Microcerotermes is a genus in which many of the described species are hard to distinguish. The specimens collected during the present study are

thought to be M. parvus, a species which had previously been recorded in the area. There are two workers and one soldier caste, the latter being depicted in Plate 3. This termite is widely distributed and is abundant in places with many dead Commiphora spp. trees, where it is probably a locally important consumer of dead wood as well as helping to fragment dead trees making them available to more soil bound species. It attacks the wood internally, but constructs characteristic narrow covered runways, made from a soil-carton mixture and lined with grey faecal matter wherever it crosses exposed surfaces. The nest is in the ground. Elephant damage to woodland must have provided ideal conditions for this species which then declined as the bulk of the dead wood disappeared. It will be many years before regenerating woodlands again provide the large logs and dead trees this species prefers.

Of the five species of Amitermes recorded, A. lonnbergianus is the most widespread and abundant. It consumes dead wood, apparently preferring large logs and dead trees to small scattered fragments. It builds soil foraging covers similar to those of Odontotermes spp., but distinguished by their black faecal lining. A. unidentatus and A. messinae are also fairly widespread in the western part of the study area, tending to prefer moister situations. A. sciangallorum was only found in the wettest areas in the west of the study area. It occurred in several habitats including an area of black bottomland clay, liable to waterlogging, where few other termites occurred. It was found feeding on buffalo and elephant dung as well as dead wood. A. somaliensis was found once on the bank of the Tsavo river under a stone. It was apparently foraging for dead grasses. All these species nest underground but A. unidentatus and A. messinae have also been found nesting in abandoned Trinervitermes gratiosus mounds. The species of this genus may be more important as subterranean feeders than as consumers of surface litter. The soldier caste of each species is depicted in Plate 3.

NASUTITERMITINAE

Trinervitermes gratiosus is widespread in Tsavo especially on red soils. Its hard mounds up to 70 cm high are a conspicuous feature of the landscape especially in the long dry season when little standing grass remains. Neither T. bettonianus nor T. dispar build conspicuous mounds, the nests being at the base of grass tussocks and underground respectively. In some species of Trinervitermes several mounds may belong to the same colony (Sands, 1965b), but the indications are that in Tsavo, T. gratiosus normally only builds one mound per colony. Instead of the large mandibles of most soldier termites the soldiers of Trinervitermes use a jet of sticky fluid to immobilise their enemies. The fluid is squirted from a prominent snout on the front of the head (Plate 4) and sets rapidly on exposure to air. The workers are darker coloured than most other worker termites, probably reflecting the open air foraging habits of the genus which may be found in the open during daylight. Grasses are the normal diet of all three species, but in September 1976, T. gratiosus was found eating dead wood in a place where no grass was left. T. dispar was only found on a few occasions, always on the western side of the study area under logs and stones. T. bettonianus was never located on the ground although abandoned nest structures were found in grassland areas with alluvial soil in drainage lines. These are the favourite haunts of the Aardwolf, Proteles cristatus (sparrman) which was found to feed principally on T. bettonianus in the Serengeti (Kruuk and Sands, 1972). A specimen of P. cristatus found dead on the Nairobi-Mombasa road near Voi was dissected. The stomach contents consisted almost entirely of T. bettonianus workers and soldiers. Alates of this species were also collected at lights after rain in November 1975. Populations of Trinervitermes spp. are not large enough to compete seriously with large mammals for grasses and they are probably not important in the overall turnover of material. As the predominant food supply for the Aardwolf, T. bettonianus is however important to mammal conservation.

Fortunately it seems to live in the small areas of permanent grassland which are virtually unaffected by current changes in the habitat.

MACROTERMITINAE

Members of the subfamily Macrotermitinae are distinguished from all other termites by having a symbiotic relationship with fungi. These fungi, of the genus Termitomyces, grow in combs of partly digested vegetable material in the nests of the termites. The fungus breaks down the complex chemical bonds in the lignified material which forms the bulk of the diet of most Macrotermitinae, releasing nutrients which the termites can themselves digest. The combs have a number of subsidiary functions from providing a concentrated protein source in their fruiting bodies to maintaining the constant temperature and humidity in the very complex mounds of Macrotermes spp. (Sands, 1969).

Because the termites have to provide food for the metabolic activities of the fungus combs as well as for themselves the Macrotermitinae have higher weight specific food requirements than other termites (Wood, 1978). In collecting this additional food they are exposed to a high predation pressure from ants (Longhurst, 1978). The advantage conferred by the fungus combs is greatest in dry places where the available food is largely undecomposed, and termites which feed on rotten material or soil humus are at a disadvantage. The numbers of species and abundance of non-Macrotermitinae increases in wetter habitats, as microbial decomposition increases, at the expense of Macrotermitinae which normally only feed on undecomposed material (Wood, 1976). Tsavo being a very dry environment the termite fauna may be expected to be dominated by Macrotermitinae and this is indeed the case.

Macrotermes subhyalinus builds large earth mounds which are a prominent feature of the landscape in most of Tsavo East, although in many areas most of the mounds are abandoned. The structure of mounds built by

M. subhyalinus varies enormously depending on soil and climatic conditions (Harris, 1956). In Tsavo they range from low widespread collections of chimneys emerging from nearly level ground to 70 cm height, to tall pointed mounds 4 or 5 metres tall with few chimneys. The usual mound in the southern part of the Park is about 2 m high with a central dome of chimneys on top of a cone of eroded material, many mounds being built around a tree or shrub. Internally the chimneys descend up to one metre below ground level and are interconnected. Between the chimneys are the fungus combs in chambers 10-15 cm in diameter. The centre of the mound is occupied by a column of finely constructed galleries some of which contain larvae. The royal chamber is in this central part about 20 cm below ground level. It has a thicker wall and is bigger than the other galleries. M. subhyalinus has four adult neuter castes, major and minor workers and major and minor soldiers (Plate 5). Foraging parties were usually composed mainly of minor workers and minor soldiers, with a few major workers. They feed on any dead organic matter except very hard wood. Grasses are probably the most important item of diet, but elephant dung was removed rapidly and the species was encountered foraging to the tops of dead trees under heavy soil sheeting. Unprotected foraging for grasses was not observed. The population of M. subhyalinus mounds and the distribution of occupied and abandoned mounds will be discussed in detail in Section 8.

Odontotermes badius has only been recorded from the alluvial flood plain of the seasonal Voi river in the vicinity of Tsavo East Headquarters. It has two worker castes and one soldier (Plate 6). The nest is a low mound with many small chimneys. The species was seen feeding on grasses and elephant dung. Changes in the pattern of water flow from the Taita hills are causing rapid erosion of the rich alluvial deposits of the Voi river valley, and the habitat of this species is likely to disappear completely.

Odontotermes zambesiensis and O. mediocris are almost ubiquitous in southern Tsavo East and are the most abundant termites. Both species have two workers and one soldier caste (Plate 6). They nest in diffuse groups of subterranean chambers connected by narrow galleries. Some of the chambers contain fungus comb and brood. Both species are important consumers of dead wood and elephant dung, and probably also of dead grasses. O. mediocris was seen foraging on green grass and hair and decaying horn from animal carcasses. Both species construct mud sheet foraging covers over the surface of their food and can be found foraging throughout the day, though as with most termites activity is greatest at night. O. mediocris in particular searches the ground surface very widely for food, and often does not stay at any one food source for very long. O. mediocris swarms were common occurring during heavy rain at any time during either rainy season. It is difficult to predict how changes in the habitat affect such catholic feeders. Work reported in Section 4 shows that activity and probably populations were linked with the amount of food available. This is affected partly by fluctuations in grass production from year to year and partly by dead wood availability. Both are likely to decline in regenerating woodlands as the ground becomes more shaded and the trees are too young to shed branches. There is no evidence that the distribution of the two species has been affected by habitat changes.

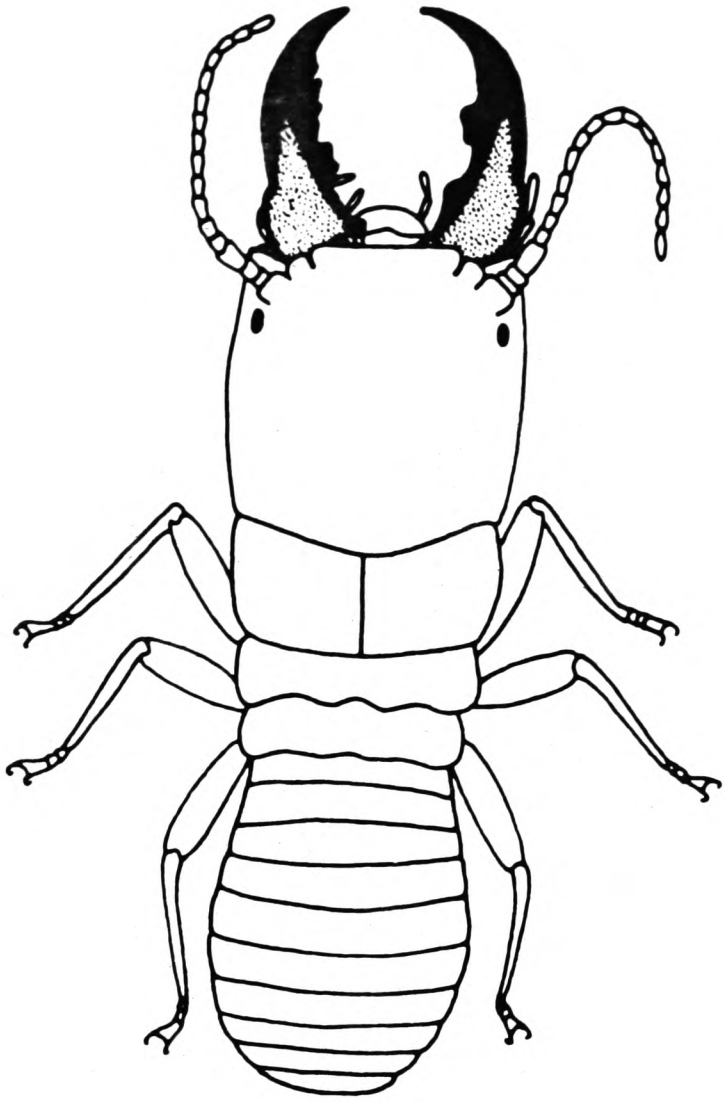
Three species of Microtermes were found in the study area. M. allaudanus was widespread in the dry open country of Tsavo East, but seems to prefer to forage in shaded places under shrubs or trees. M. vadschaggae was restricted to the wetter wooded areas in the west of the study area. Microtermes sp.I was recorded only once near Mukwaju in the centre of the area; it appears to belong to the same species as a specimen collected by Wilkinson at Hola on the Tana river 200 km to the north east. Specimens of another species were collected at Mtito Andei by Wilkinson. All these species have two worker castes and one soldier

(Plate 7). The nest is usually a diffuse series of chambers underground, but M. allaudanus was found sharing a Cubitermes glebae mound with the original occupants, and a fungus comb was discovered inside a large log. Feeding internally on logs and twigs and also elephant dung, Microtermes spp. make large chambers, packing the unused parts with soil. In savannas in other parts of Africa, Microtermes spp. have been found to play a dominant role in dead wood removal (Collins, 1977b). In Tsavo they are important consumers in the woodlands (Section 4.6) but much less important elsewhere. They are likely to increase when the regenerating woodlands approach maturity.

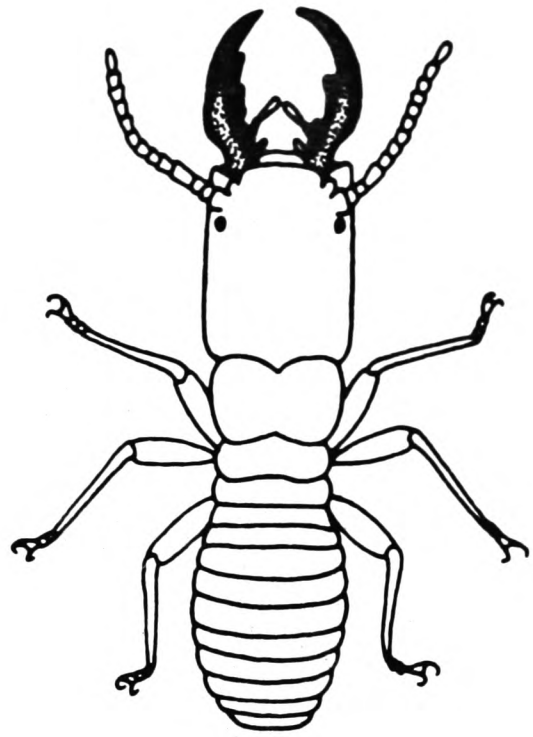
Synacanthotermes zanzibarensis was widespread but rarely encountered, being most abundant in the west of the study area. It is a small species with two worker castes and one soldier (Plate 7). It feeds on dead wood and elephant dung and its requirements are similar to Odontotermes mediocris, probably responding in the same way to changes in the habitat.

Plate 1

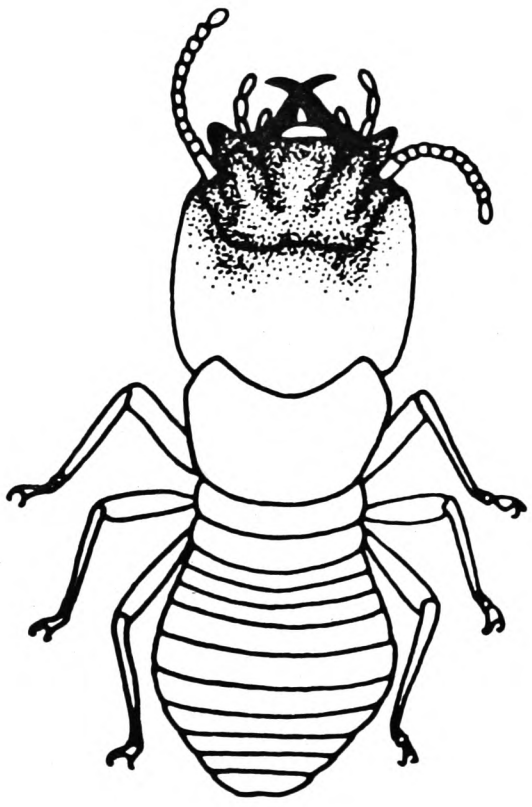
Soldiers of Kalotermitidae



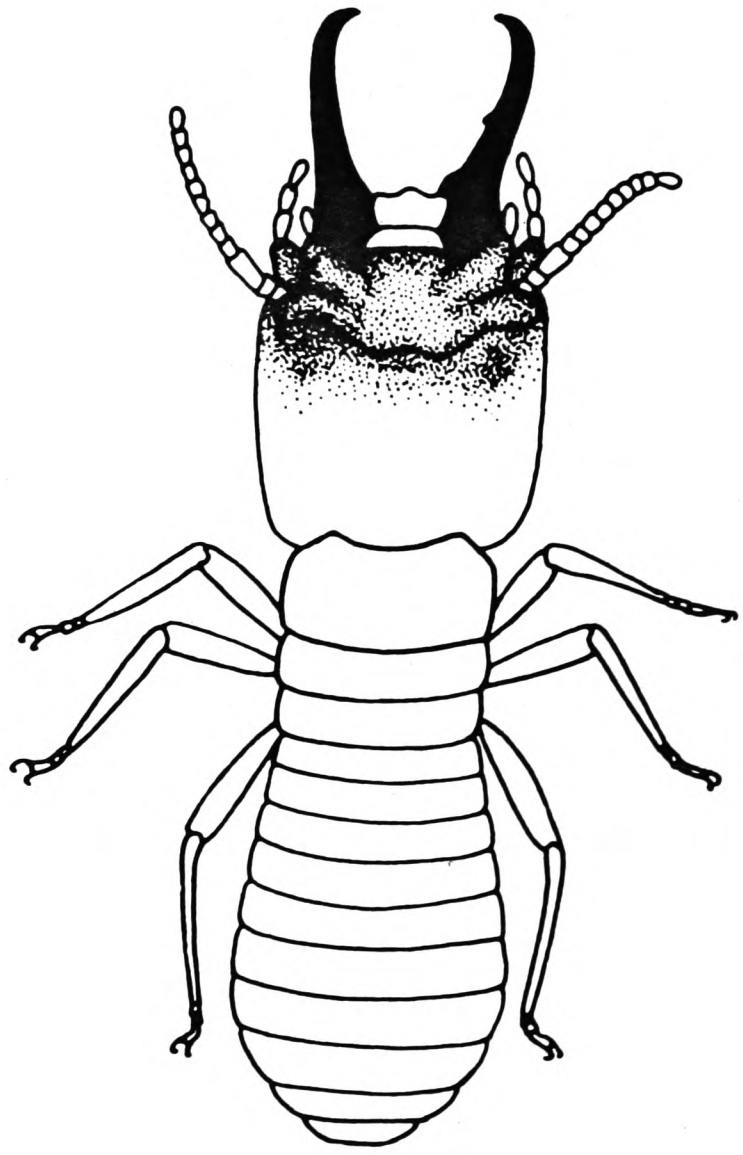
Neotermes neruensis x 10



Epicalotermes kerpae x 10



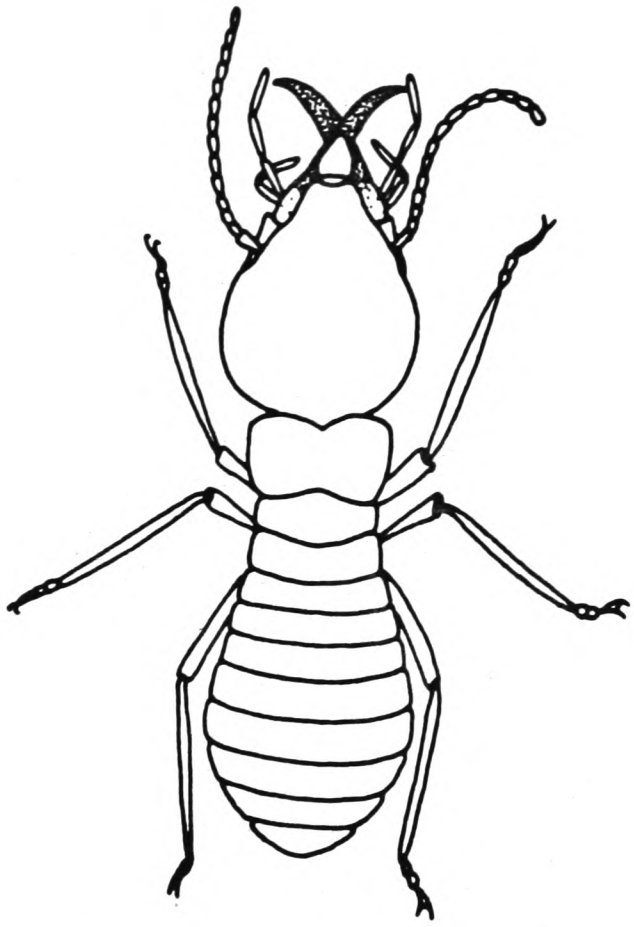
Cryptotermes sp.I x 20



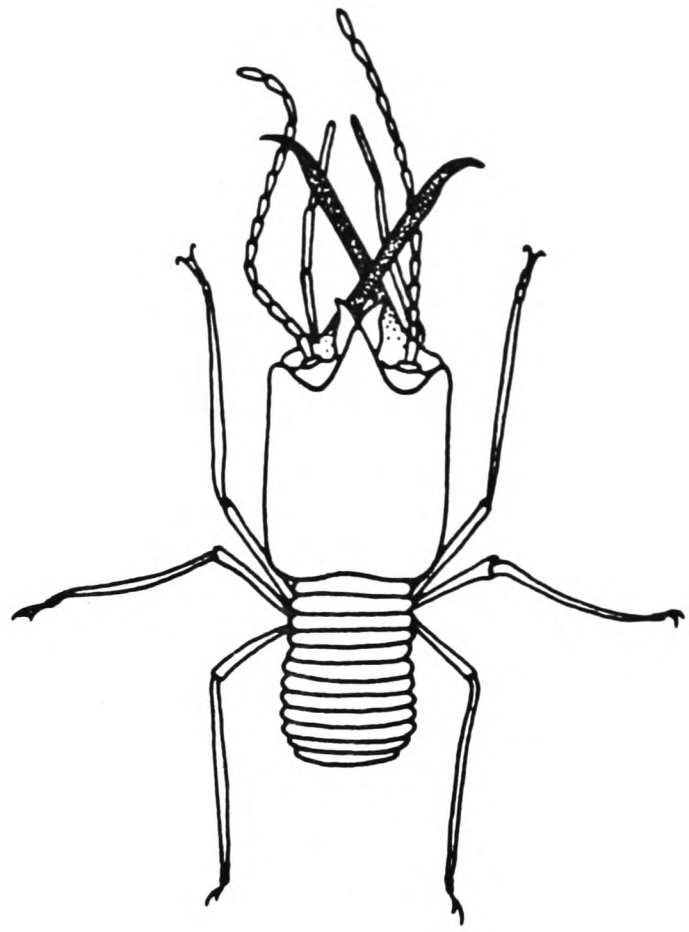
Unidentified sp. x 20

Plate 2

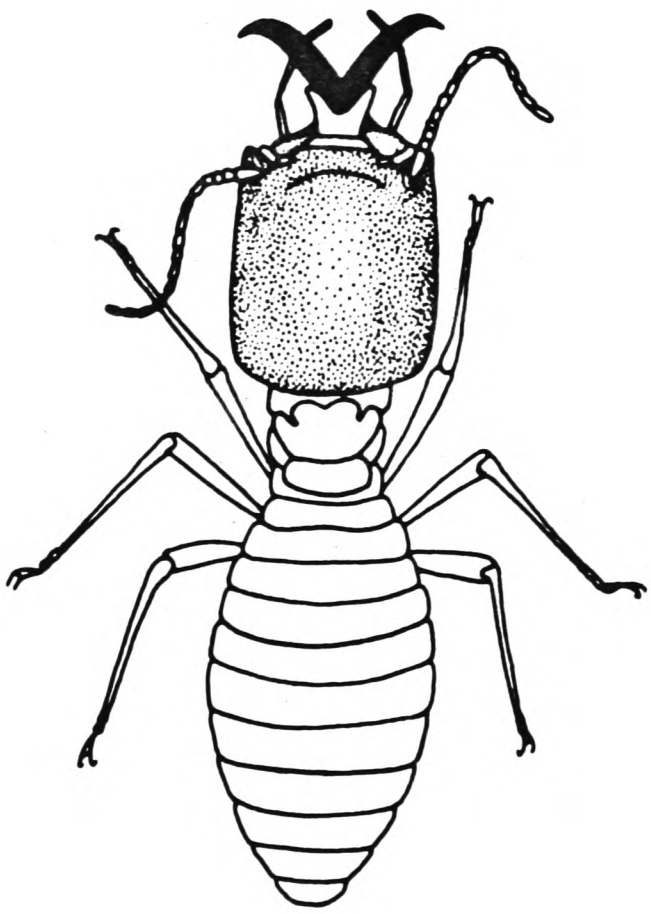
Soldiers of Rhinotermitidae and Termitidae



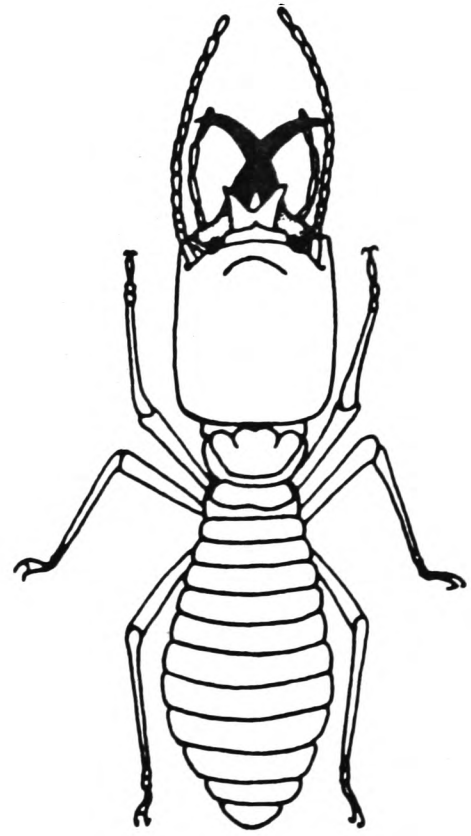
Coptotermes amanii x 10



Promirotermes bellicosi x 20



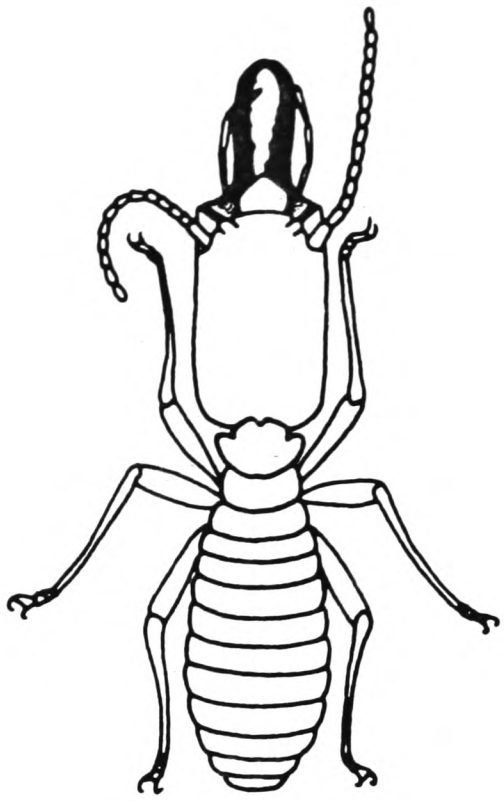
Cubitermes umbratus x 10



Cubitermes glebae x 10

Plate 3

Soldiers of Micrccerotermes and Amitermes

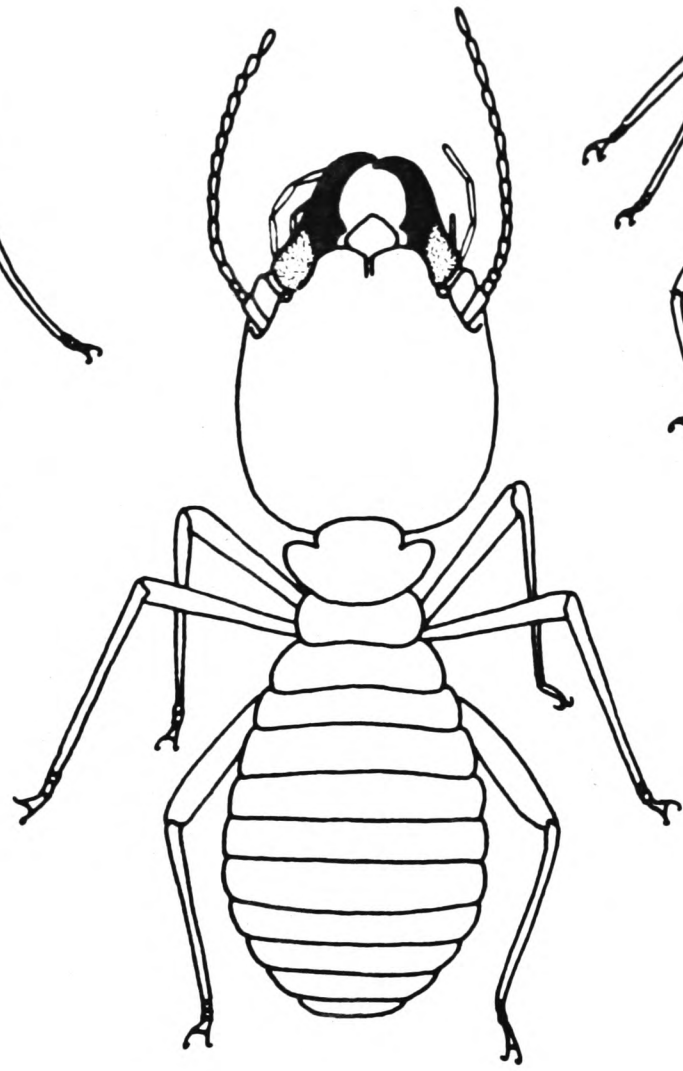


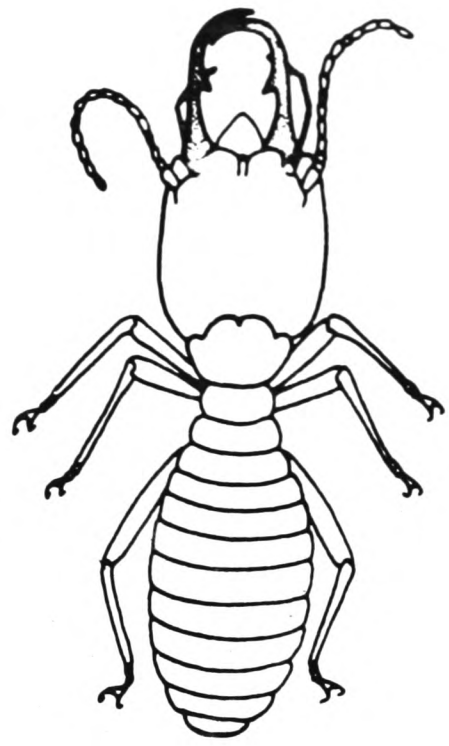
Microcerotermes

sp.I x 20

Amitermes

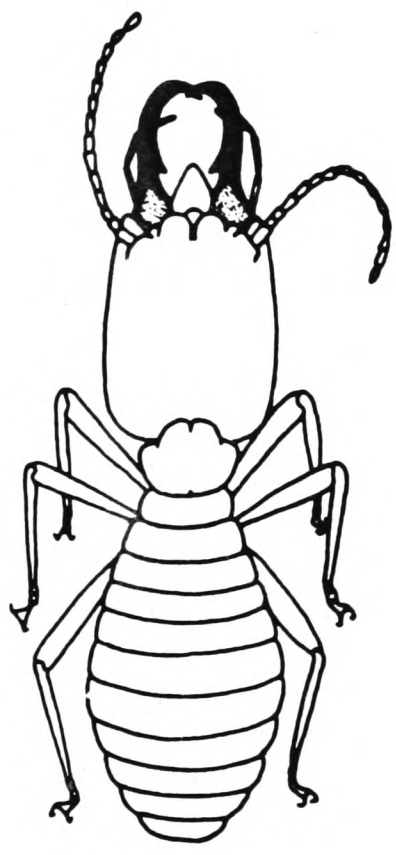
lonnbergianus x 10





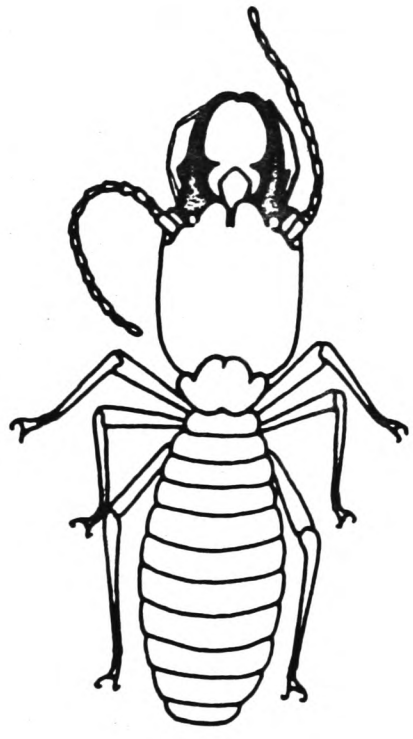
Amitermes

messinae x 20



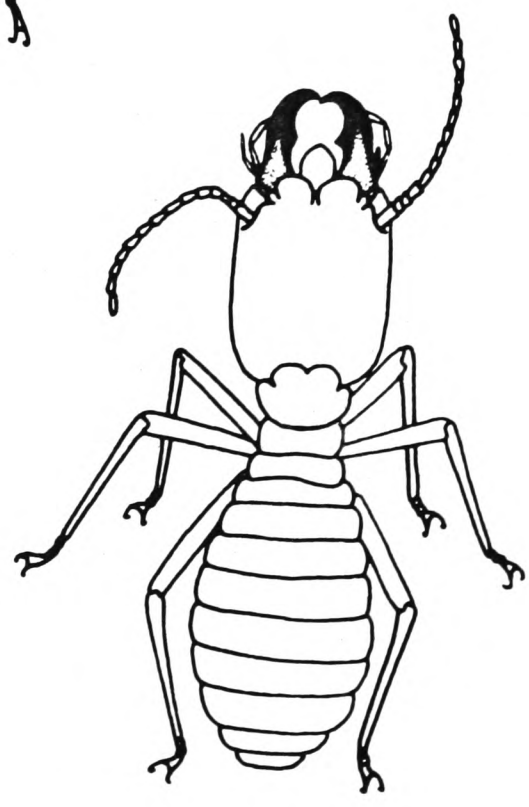
Amitermes

unidentatus x 20



Amitermes

sciangallorum x 20

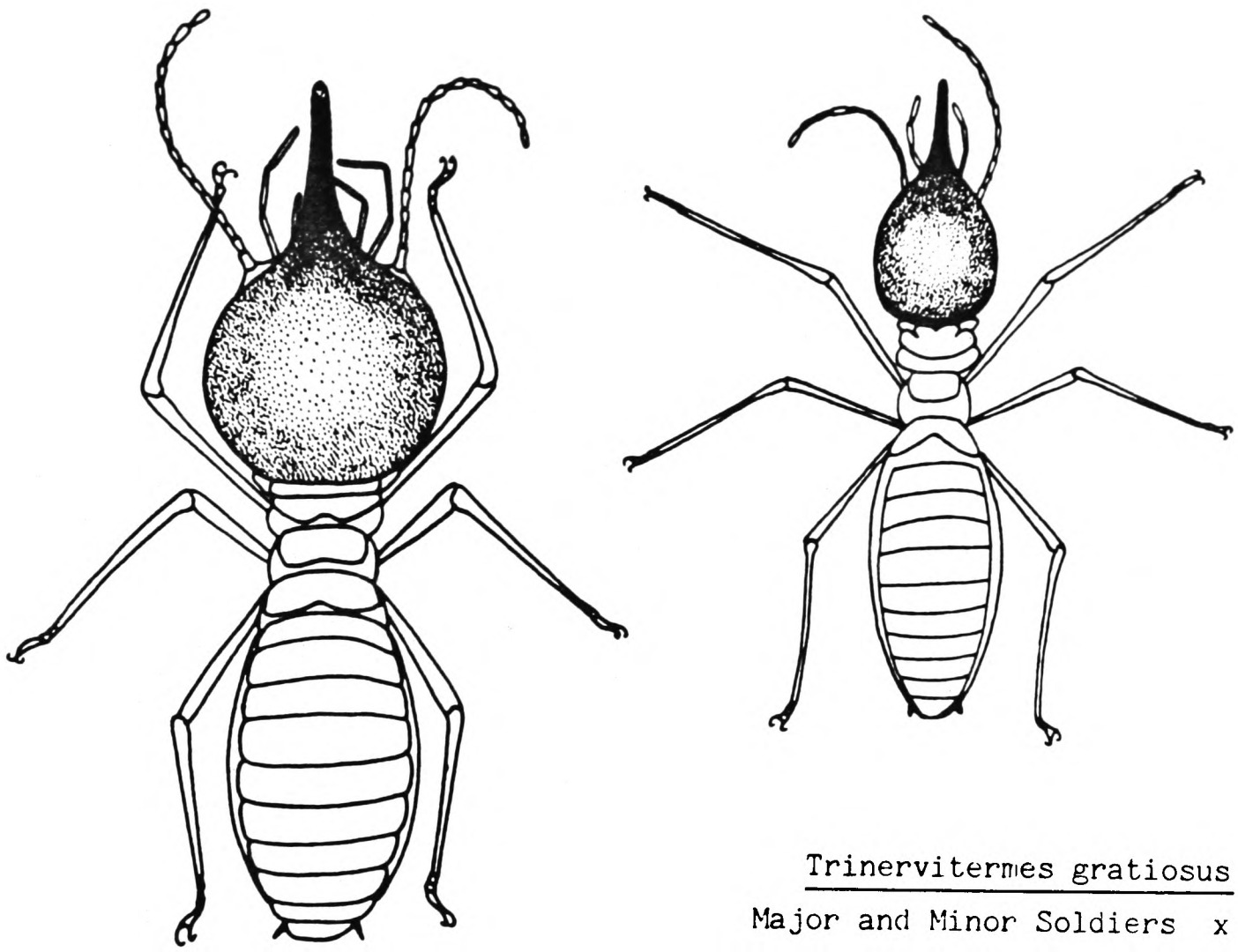


Amitermes

somaliensis x 20

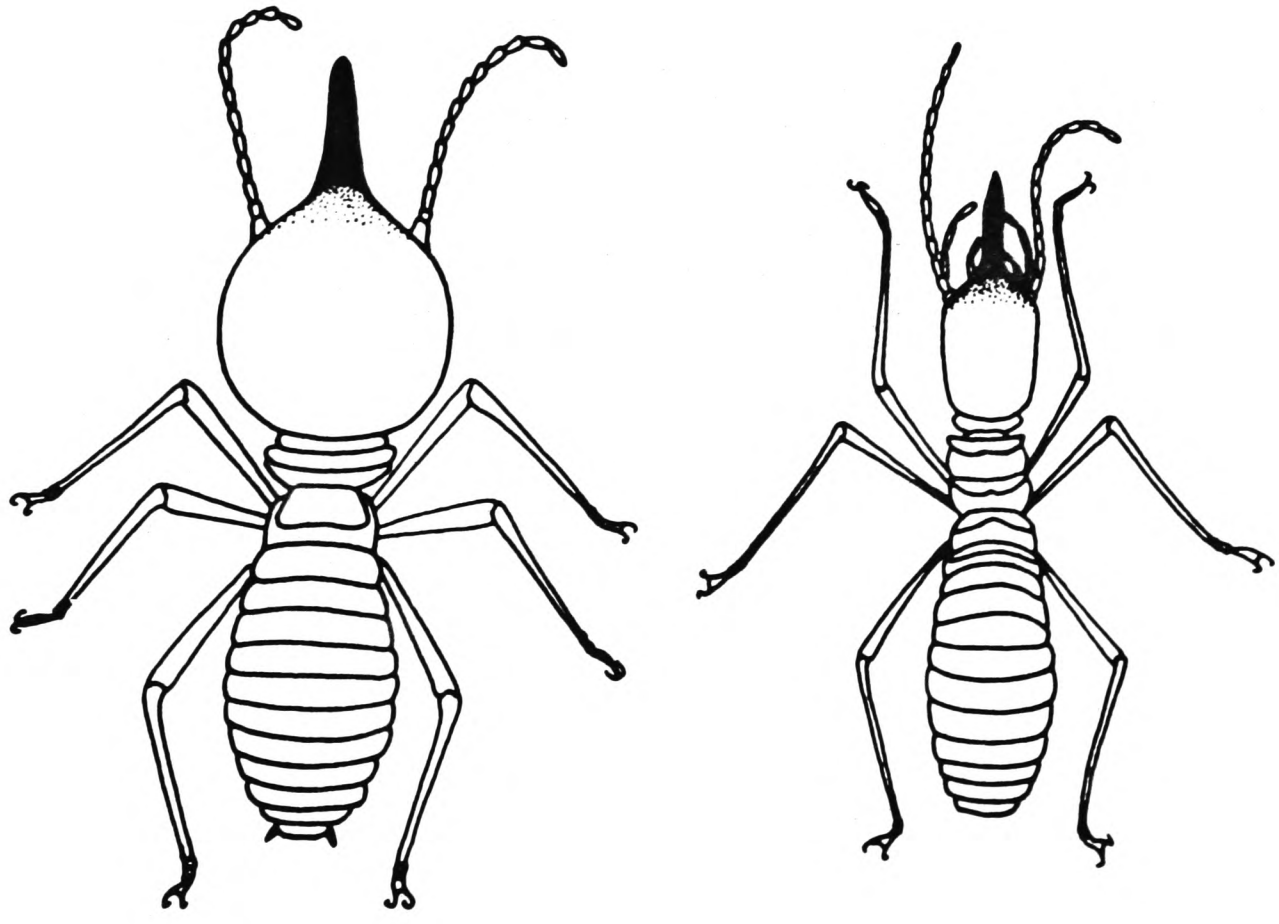
Plate 4

Soldiers of Nasutitermitinae



Trinervitermes gratiosus

Major and Minor Soldiers x 20



Trinervitermes dispar Major and Minor Soldiers x 20

Plate 5

Macrotermes subhyalinus Soldiers and Workers x 10

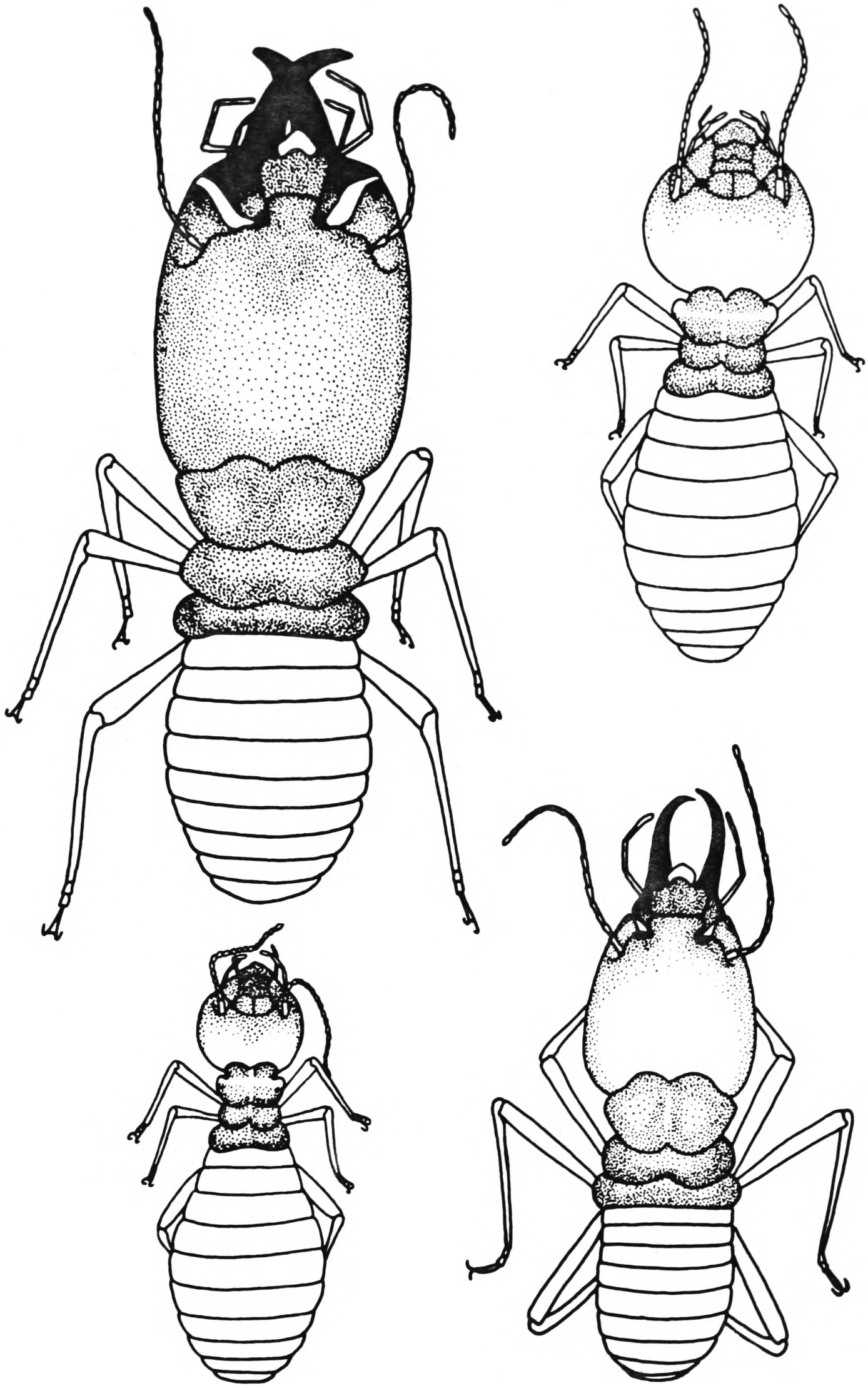
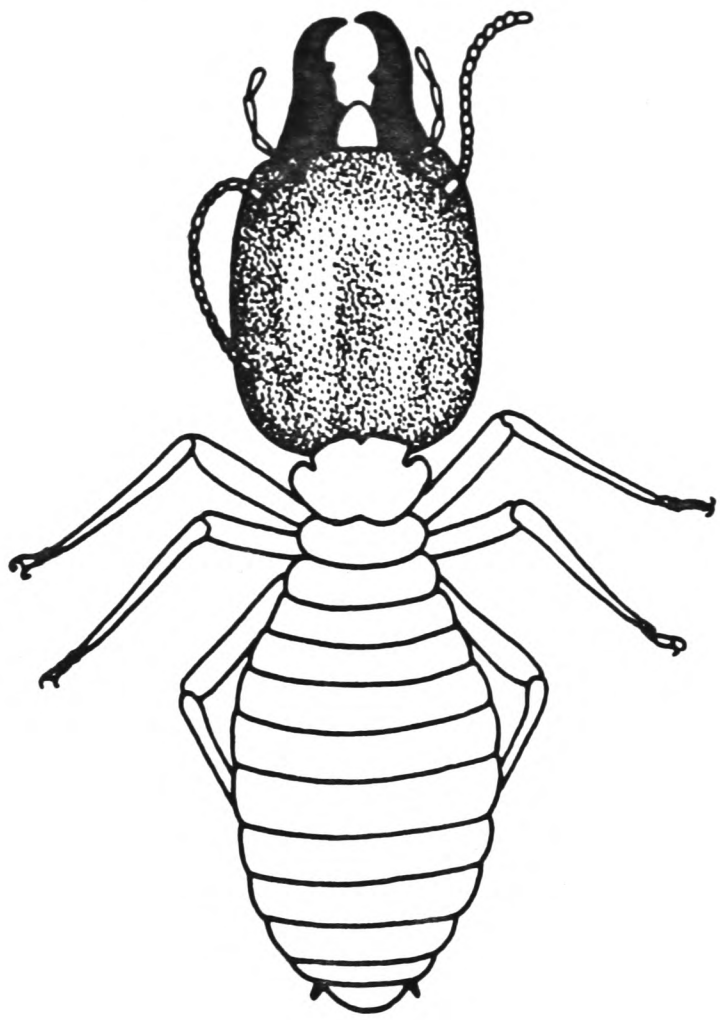
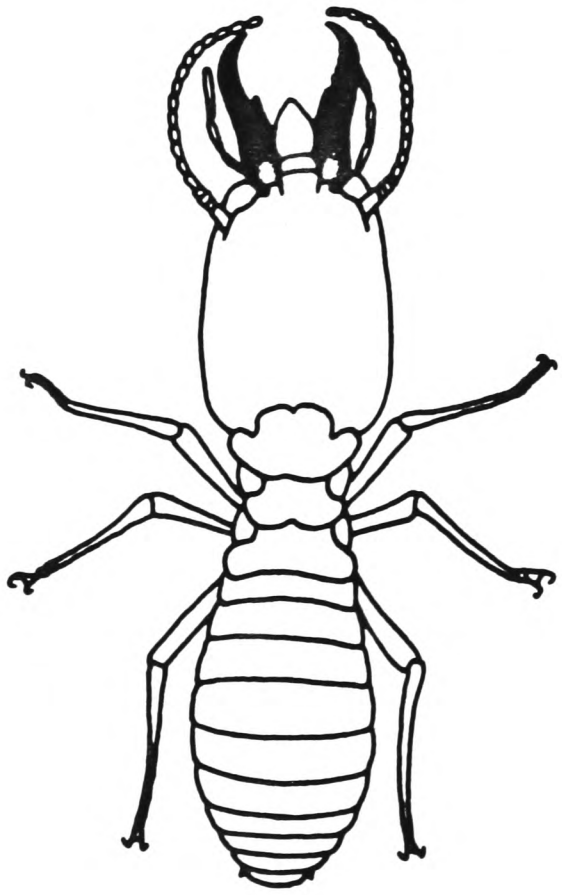


Plate 6

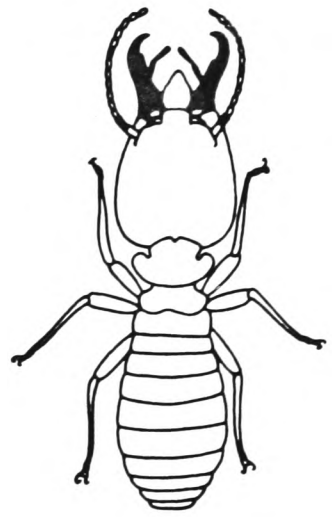
Soldiers of Odontotermes



Odontotermes badius x 10



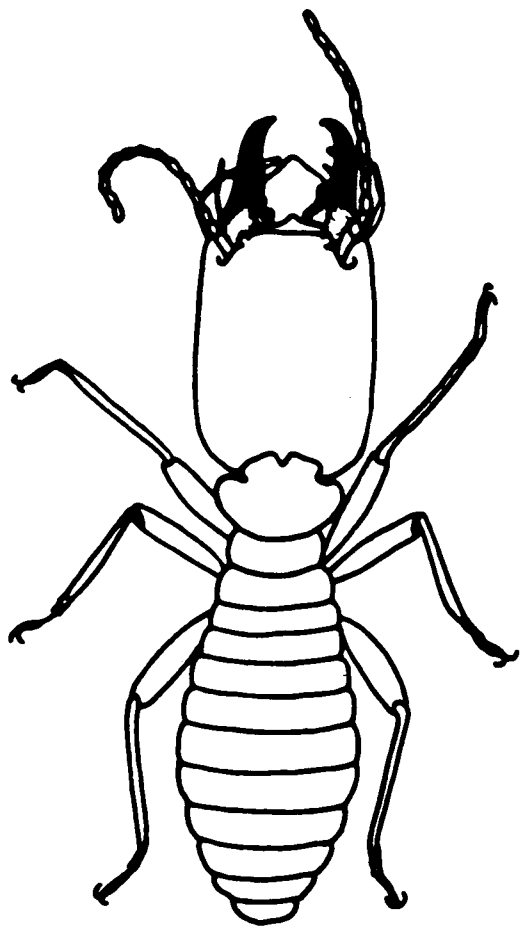
Odontotermes zambesiensis x 10



Odontotermes mediocris x 10

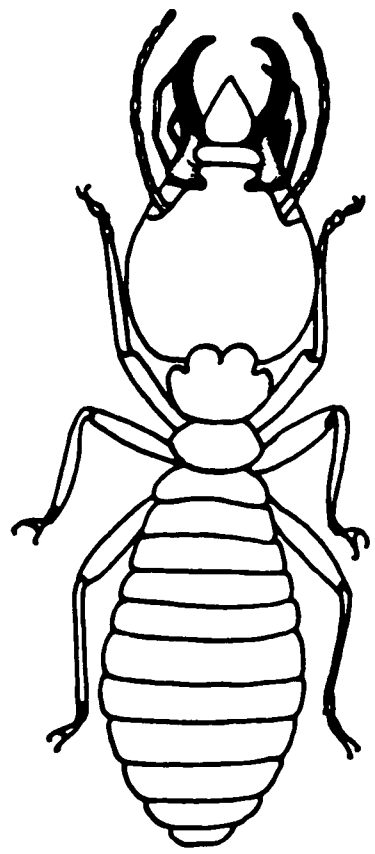
Plate 7

Soldiers of Macrotermitinae

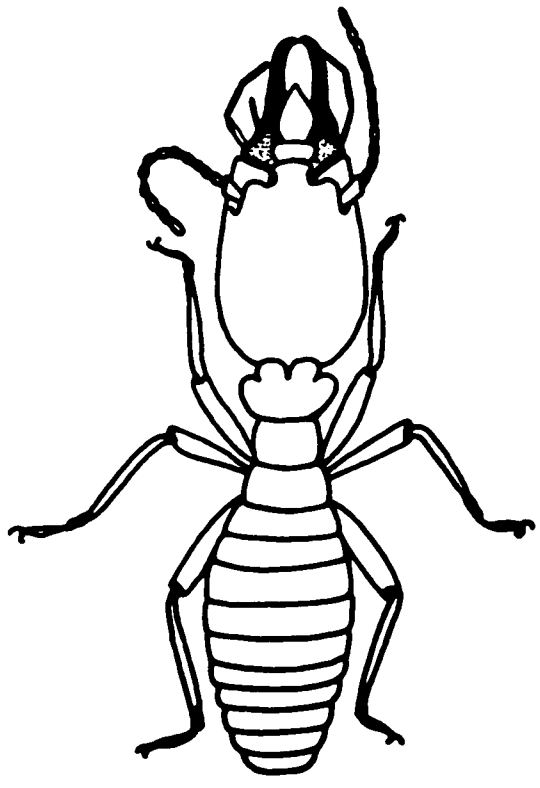


Synacanthotermes zanzibarensis

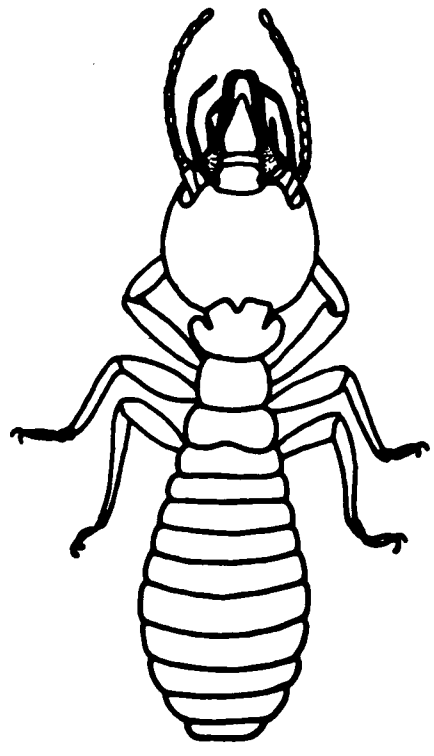
x 20



Microtermes sp.I x 20



Microtermes allaudanus x 20



Microtermes vadschaggae x 20

SECTION 4

THE PRODUCTION AND FATE OF DEAD WOOD IN TSAVO EAST

4.1 INTRODUCTION

Dead wood is an extremely diverse material and its decomposition is and equally varied process. Different tree species produce wood of widely different hardness and chemical composition both of which affect its palalability to termites (Haverty and Nutting, 1975a; Snyder, 1948). The dead wood may be part of a standing tree, living or dead, a fallen tree or dispersed fragments. The accessibility of wood in different situations varies between the different species of termites (Lepage, 1974). Buried wood is consumed faster than wood lying on the ground surface (Usher and Ocloo, 1974). Fragmentation increases the surface area available for attack and the diameter of a log affects the time taken for it to disappear (Collins, 1977b). Fungal and microbial attack also affect palalability (Sands, 1969).

The emphasis of the research described in this section was on the measurement of the rate of recruitment of dead wood to the soil surface and the rate at which it subsequently disappeared.

4.1.1 CHOICE AND DESCRIPTION OF EXPERIMENTAL SITES

Tsavo East south of the Galana River has an area of 4,100 km^2 and shows considerable variation in soils, vegetation and rainfall (Section 2). It was important to select experimental sites which would take these variations into account, but logistical considerations such as travelling time and petrol costs restricted the actual choice of sites and the frequency with which they could be visited. Nine sites were eventually chosen in consultation with W. van Wijngaarden who was engaged in mapping

the soils and vegetation of Tsavo East. One site was chosen for intensive study. It was representative of the predominant soil type (rhodic ferralsols) and rainfall regime (300-400 mm yr^{-1}). The other eight sites were widely scattered, encompassing the known main variations in the habitat. The positions of the experimental sites are indicated in Figure 2.1 and the main features of rainfall, soil and vegetation for each site are summarised in Table 4.4.1.

4.2 STUDIES AT THE MAIN EXPERIMENTAL SITE

The main experimental site was used for intensive studies of a) the rate of recruitment of dead wood to the soil surface, b) the standing crop of dead wood on the soil surface and c) the rate of disappearance of dead wood from the soil surface.

4.2.1 DIRECT MEASUREMENT OF THE RATE OF RECRUITMENT OF DEAD WOOD TO THE SOIL SURFACE

4.2.1.1 METHODS

Dead wood litter fall was measured on eleven 5 x 5 m quadrats which were located at random numbers of paces along two transects in the main study area (site M). These quadrats will be referred to as the M_R quadrats.

The quadrats were initially set up with large white painted stones marking each corner. These had two disadvantages; they did not mark the corners very precisely and they got moved about by elephants. These problems were largely overcome by forcing a 30 cm length of wire into the soil under each stone, with the end of the wire turned over flat on the surface of the ground. When a quadrat was being sampled the four wires were raised slightly and a tape measure stretched round them to mark the boundary.

Table 4.1.1

Brief Description of the Habitat at each Site used for Experimental Work in Southern Tsavo East. (See notes on next page).

Site	Rainfall during study. April 76-April 77	5 year Mean Rainfall 1972-1976	Vegetation Structure	Vegetation floristic association (see Appendix A)	Soil Type (from van Wijngaarden, pers. comm.)
M	375	352(1)	Open bushed grassland	1d	Erosional plain. Well drained very deep dusky red friable sandy clay over gravel. Rhodic ferralsol.
A	668	458	Thick wooded bushland	1d	As site M
B	264	327	Very open bushed grass-land	10	Erosional plain. Well drained very shallow yellowish brown stony sandy loam over limestone. Calcic cambisol.
C	-	496(2)	Open wood-land (c.20% canopy)	Commiphora spp.	As site M
D	401	265	Open bushed grassland	5a/b	Sedimentary plain. Moderately well drained, very deep brown friable sandy clay. Chromic-ferric luvisol.
E	236	213	Bushed grassland	1c	As site M
F	181	236	Very open bushed grassland	7	Alluvial fan deposit. Imperfectly drained, very deep, dark brown firm sandy clay-clay subsoil saline. Orthic luvisol, saline phase 1 (Solonetz).
G	377	426	Thick low bushed grassland	1b	As site M
L	388	320(1)	Bushed grassland	5a	As site D

(1) Found by interpolation between rainfall at the research station (TRP) and Aruba using the formula:

TRP - ((TRP - Aruba) x Distance TRP to site/Dist. TRP to Aruba).

(2) Mean 1970-74.

The quadrats were initially cleared of all dead wood in January 1976. At intervals ranging from three to six months all the wood which had fallen onto each quadrat was collected, brushed free of soil with a scrubbing brush and placed in a basket. This was weighed on a 10 Kg beam balance sheltered from the wind inside a vehicle. Large logs were weighed separately. The wood was thrown away where it would not interfere with the experiments.

The quadrats were sampled between 07.00 and 11.00 local time as the soil usually became too hot to touch after this time. Table 4.2.1 shows that the percentage moisture content of dead wood can fall almost twofold during the sampling period presumably in response to increasing temperature and the water holding capacity of the air. This effect was particularly marked after rain. To allow for this field weighed samples of dead wood from each quadrat were taken to the lab., cleaned thoroughly and dried at $105^{o}C$ for 48 hours. This gave a dry weight correction factor for each quadrat. The moisture content of the weighing baskets also changed with time, so the empty weights of these were obtained every time they were used.

4.2.1.2 RESULTS

Table 4.2.2 shows the weight of wood removed from each of the eleven randomly placed (M_R) quadrats at the end of each of three periods, (I) January to April 1976, (II) April to October 1976 and (III) October 1976 to April 1977. Periods I and III included the rainy seasons while period II was entirely in the long dry season.

Comparison, by student's t-test, of the data from the M_R quadrats of the two transects did not reveal any significant differences between transects within periods. The data within each period were therefore pooled. Analysis of the pooled data by student's t-test showed that wood

Table 4.2.1

An Example of the Change in Moisture Content

of Quadrat Wood Samples during the Day

Data from 8 May 1976. 7.5 mm rain recorded at TRP over the previous 24 hours:

Time (local)	% moisture in wood litter sample
07.30	21.9
08.30	19.7
09.00	23.0
10.30	16.8
12.00	13.4

Table 4.2.2

Weight of Dead Wood Removed from each M_R Quadrat at each Collection. g 25 m^{-2}

Transect & Quadrat		Period I 7.1.76-27.4.76		Period II 27.4.76-25.10.76		Period III 25.10.76-4.4.77		Combined Periods	
		Wet weight	Estimated dry weight	Wet	Est. dry	Wet	Est. dry	Wet	Est. dry
I	1	175	155.6	270	237.9	48	40	493	433.5
	2	697	619.6	190	167.4	55	46.9	942	833.9
	3	1395	1240.2	805	709.2	172	143.1	2372	2092.5
	4	25	22.2	70	61.7	0	0	95	83.9
	5	3330	2960.4	350	308.3	220	177	3900	3445.7
	6	219	194.7	215	189.4	87	75.1	521	459.2
II	1	120	100.9	27	23.7	0	0	147	124.6
	2	740	544.6	145	126.7	65	57.4	950	728.7
	3	1110	840.3	600	526.8	170	142.9	1880	1510
	4	0	0	675	587.2	75	59	750	646.2
	5	120	106.7	140	121.8	37	32	297	260.5
I	Mean	973.5	865.4	316.7	279.0	97	80.3	1387.2	1224.8
	S.E.	513.6	456.6	104.7	92.3	33.9	27.4	597.3	527.6
No.of days		111	111	181	181	161	161	453	453
	N	6	6	6	6	6	6	6	6
II	Mean	418	318.5	317.4	277.2	69.4	58.3	804.8	654
	S.E.	216.2	160.8	132.9	116.1	28.3	23.7	305.8	242.2
	Days	111	111	183	183	169	169	463	463
	N	5	5	5	5	5	5	5	5
I + II	Mean	721	616.8	317	278.2	84.5	70.3	1122.5	965.3
	S.E.	296.8	262.6	78.8	69.1	21.9	17.9	350.3	307.7
Mean Days		111	111	182	182	164.6	164.6	457.5	457.5
	N	11	11	11	11	11	11	11	11

fall was significantly less during period III than either period I ($p < .05$) or period II ($p < .01$). This suggests that variations in wood fall in Tsavo are not predominantly seasonal with respect to rainfall.

Because the wood fall varied with time, but not according to season, the longest run of available data should give a better picture of the overall recruitment of dead wood to the soil surface than any single shorter period. The results of the three periods were therefore combined and are given in Table 4.2.2. Using these data, mean daily and annual rates of dead wood litter fall were calculated using the expressions:

$$\text{Mean daily wood fall } (g\ m^{-2}) = \frac{\text{Mean fall over combined periods (g)}}{\text{Length of exposure (days)} \times 25}$$

$$\text{Mean annual wood fall } (g\ m^{-2}) = \text{Mean daily wood fall} \times 365$$

The results are given in Table 4.2.3.

4.2.1.3 DISCUSSION

Collins (1977b), working in Nigeria used a similar method for measuring dead wood litter fall. He cleared his quadrats weekly to prevent errors due to consumption of the wood by termites and other decomposers. In the present study, quadrats were left for up to six months between clearings and some consumption of the wood almost certainly occurred. This is not thought to be a serious source of error when compared with the overall variation in the results. Another source of error, tending to counteract the first, was the movement of pieces of wood from outside the quadrats to inside them as a result of large mammal activities.

The non-seasonality of litter fall in Tsavo East agrees with the findings of John (1973) who, working in Ghana, also found that wood litter fall was unrelated to season. Collins (1977b) observed slight peaks of wood fall associated with fire and heavy storms both of which are seasonal in Nigeria. There were no fires in Tsavo during the period of this study

Table 4.2.3

Mean Daily and Mean Annual Rates of Dead Wood Litter Fall Estimated from Eleven Randomly Located (M_R) Quadrats.

N	g m^{-2} day^{-1} $\pm$ 1 SE		g m^{-2} $year^{-1}$ $\pm$ 1 SE	
	wet weight	dry weight	wet weight	dry weight
11	0.10 $\pm$ 0.03	0.08 $\pm$ 0.02	35.82 $\pm$ 11.25	30.81 $\pm$ 9.78

and the most likely agent causing wood fall other than elephants was the wind. Both of these factors operate more or less continuously although the distribution of elephants does change seasonally (Cobb, 1976).

An explanation of the significantly lower wood fall in the last period (period III) should probably be sought in the long term fluctuations in the climate of Tsavo. Lepage (1974) recorded a massive increase in the production of dead wood in Senegal during the 1972 Sahelian drought. 1974 and 1975 were both dry years in Tsavo (Section 2.5) and this may have stimulated production of dead wood continuing into 1976. A long series of data would be needed to establish such a relationship between rainfall and wood fall.

4.2.2 AN INDEX FOR INDIRECT ESTIMATION OF DEAD WOOD FALL

4.2.2.1 INTRODUCTION

The fall of dead wood litter onto a particular area can only be measured directly when the area can be cleared periodically, or when all the wood present at a particular moment can be marked. It was however important to be able to make estimates of the fall of dead wood onto sample plots which could not be cleared or the wood marked. If a variable of the habitat could be found which could be used to predict wood fall the desired estimate could be made for each plot. The most suitable habitat variable seemed to be the density of live woody vegetation as this is the source of all the dead wood. The actual mass of woody vegetation could not be measured directly, so simple linear measurements of each plant were taken and used to calculate indices of the density of trees and shrubs.

4.2.2.2 METHODS

The randomly located M_R quadrats (Section 4.2.1) provide one estimate of dead wood litter fall but in order to relate wood fall to the density of woody vegetation a larger sample was needed. This did not need to be randomly distributed. Fifteen quadrats were therefore selected at the main study site enclosing a wide range of densities and species of woody vegetation. These were designated M_S quadrats and were used to supplement the sample already available from the M_R quadrats.

The height and greatest diameter of the crown of each of the woody plants on each of the M_R and M_S quadrats was measured. Two indices were calculated from these measurements:

$$\text{Index 1} = \sum_{i=1}^{N} (\text{Height} \times \text{Greatest Diameter})$$

$$\text{Index 2} = \sum_{i=1}^{N} \left(\text{Height} \times \left(\frac{\text{Greatest Diameter}}{2}\right)^2 \times \pi\right)$$

where N is the number of woody plants in the quadrat. Index 2 gives a crude estimate of the volume of the woody plants, whereas Index 1 is a purely notional parameter which is easy to calculate.

The wood fall on each quadrat was related to the index values by least squares linear regression.

4.2.2.3 RESULTS

The data for wood fall on each of the selected M_S quadrats are given in Table 4.2.4. The results show the same trends between periods as the randomly sited M_R quadrats, and the differences between periods carry the same significance as for the M_R quadrats (Section 4.2.1.2).

The values of the two indices calculated for each of the M_R and M_S quadrats are given in Table 4.2.5. Using the indices as the independent variables, linear regressions were calculated for wood fall (data from

Tables 4.2.2 and 4.2.4) against each index. In all cases index 1 gave regressions with a higher variance ratio (F) than index 2. For example the regression equations obtained using the data for wet weight of wood falling over all three periods combined were:

wood fall = $623.02 + 4.95 \times 10^{-2}$ Index 1; F = 89.82

wood fall = $858.17 + 3.53 \times 10^{-4}$ Index 2; F = 33.45

Index 1 was therefore used in all further analyses.

Total dry wood litter fall on each quadrat has been plotted against Index 1 in Figure 4.2.1. Three points fell considerably outside the range of the others and have not been plotted. These points were from M_S quadrats 10, 14 and 15 all of which had trees on them; a 5 m high Platycelyphium voense on 10, a 1 m Boscia coriacea and a Salvadora persica thicket on 14 and a 10 m high Melia volkensii on 15. It looks from these few points as if trees can not be treated in the same way as shrubs, so these quadrats were excluded from further analyses. The data from three other quadrats were incomplete and these have also been excluded.

The regression equations for wet and dry wood fall (g 25 m^{-2}) on index 1 (= I) are given below for each period with an estimate of the standard error (S.E.) of the regression coefficient (b) and the value of Student's t statistic calculated as b/S.E. All regression coefficients are significantly different from zero, for period I $p < .01$, for all the rest $p < .001$.

Period			S.E.	t
I	wet:	wood fall = 320.4 + 0.021 I	± .0059	3.56
	dry:	wood fall = 268.7 + 0.019 I	± .0051	3.73
II	wet:	wood fall = 258.5 + 0.023 I	± .0043	5.35
	dry:	wood fall = 226.9 + 0.020 I	± .0038	5.26
III	wet:	wood fall = 41.9 + 0.0056 I	± 0.00056	10
	dry:	wood fall = 35.1 + 0.0050 I	± 0.00050	10
Com-bined	wet:	wood fall = 623.0 + 0.049 I	± 0.0052	9.48
	dry:	wood fall = 532.2 + 0.044 I	± 0.0045	9.68

Table 4.2.4

Weight of Dead Wood Removed from each M_S Quadrat at each Collection. g 25 m^{-2}. L = Lost, N.C. = not calculated

Quadrat	Period I		Period II		Period III		Combined Periods	
	Wet	Est. dry	Wet	Est. dry	Wet	Est. dry	Wet	Est. dry
1	492	437.4	125	110.1	44	38.8	661	586.3
2	940	835.7	2670	2352.3	424	383.3	4034	3571.2
3	745	662.3	L	L	263	233.5	N.C.	N.C.
4	190	168.9	505	444.9	60	51.4	755	665.2
5	520	462.3	525	462.5	105	91.7	1150	1016.5
6	562	499.6	705	621.1	61	51.8	1328	1172.5
7	435	386.7	1380	1215.8	195	173.7	2010	1776.2
8	280	248.9	465	409.7	82	69	827	727.6
9	Destroyed							
10	3175	2822.6	3500	3083.5	1185	1080.7	7860	6987
11	1275	1133.5	1600	1409.6	522	452.6	3397	2995.6
12	1125	1000.1	1360	1198.2	261	233.1	2746	2431.4
13	2880	2560.3	3015	2656.2	L	L	N.C.	N.C.
14	3010	2675.9	2770	2440.4	662	590.5	6442	5706.8
15	1180	1049	1390	1224.6	915	814.3	3485	3088.0
Mean	1200.6	1067.4	1539.2	1356.0	367.6	328.0	2891.2	2560.4
S.E.	278.4	247.5	308.5	271.8	100.6	91.0	670.2	595.3
Days	125	125	165	165	157	157	447	447
N	14	14	13	13	13	13	12	12

Table 4.2.5

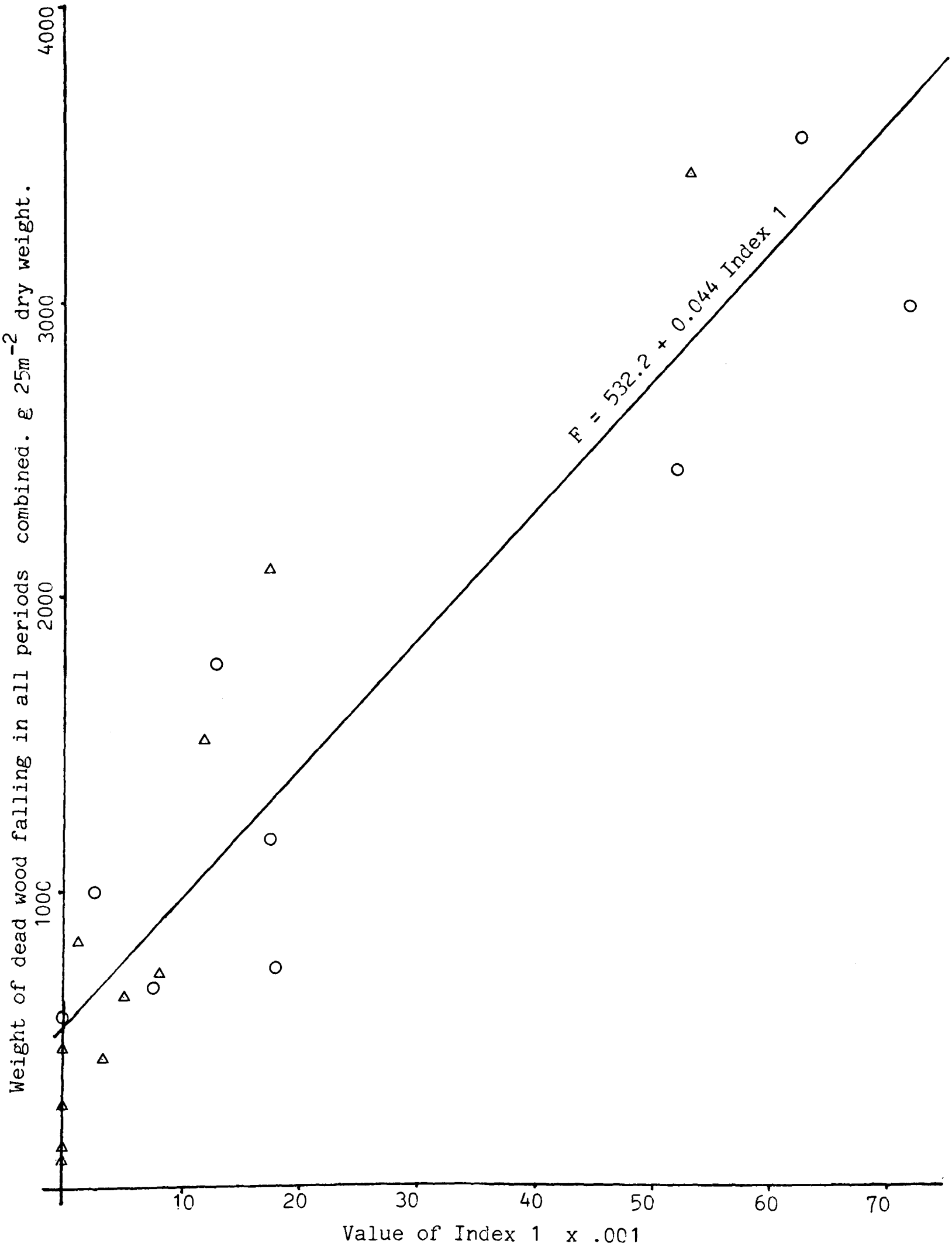
Index Values of the Density of Woody Vegetation on Each M_R and M_S quadrat

Quadrat		Index 1	Index 2
M_R	I 1	3400	45553
	2	1000	39270
	3	17200	1108982
	4	0	0
	5	50300	5222107
	6	0	0
	II 1	0	0
	2	8000	502655
	3	11800	526217
	4	4950	213825
	5	0	0
M_S	1	0	0
	2	62600	5544915
	3	26500	1361094
	4	7500	388772
	5	2500	98175
	6	17400	1176529
	7	12600	848230
	8	17700	1750653
	9	destroyed	
	10	167000	42827731
	11	71700	7319125
	12	50400	9500180
	13	107100	30718540
	14	41700	4771293
	15	2068600	2421600000

Figure 4.2.1

Relationship between an index of bush density and the fall of dry dead wood litter on $25m^2$ quadrats, in all periods combined.

O = M_s quatdats Δ = M_r quadrats



4.2.2.4 DISCUSSION

In order to use general regressions based on an index to predict actual events on small sample plots, the regression must be reasonably accurate. All the regression coefficients are significantly different from zero, but the value of t increased steadily from period I (t = 3.73 for dry weight regression) to period III (t = 10) implying that the later regressions give a better prediction than the earlier one. The combined period regressions give predictions almost as good as the regressions for period III. In Section 4.2.1.3 it was suggested that wood fall over the earlier periods may have been stimulated by the drought in 1974-1975. The increasingly close relationship between shrub density and wood fall during this study indicates that when rainfall is roughly normal for the region wood fall is closely related to gross woody vegetation standing crop, but when rainfall is very low other factors such as the drought tolerance of individual species of trees and shrubs affect the production of dead wood.

4.2.3 THE STANDING CROP AND DISAPPEARANCE OF DEAD WOOD LITTER

4.2.3.1 METHODS

Forty 5 x 5 m quadrats were set up along four transects at randomly paced intervals at the main experimental site (M). These quadrats, designated the M_C quadrats, were sampled periodically in exactly the same way as the wood recruitment (M_R) quadrats (Section 4.2.1) except that after weighing all the wood was returned to its quadrat. Samples for determining the dry weight correction were taken from outside the quadrat.

The height and greatest diameter of each bush on each M_C quadrat was measured and index 1 (Σ(heigh x greatest diameter)) was calculated for each quadrat as explained in Section 4.2.2.

An estimate of the dead wood fall onto each M_C quadrat in each period was made using the calculated index values and the regressions in Section 4.2.2.3.

Disappearance of dead wood from each M_C quadrat in each period was calculated by subtracting the change in the standing crop on the quadrat during the period from the estimated fall of wood onto the quadrat.

4.2.3.2 RESULTS

The data from the forty M_C quadrats are given in Table 4.2.6a-d. The mean standing crops for each of the four lines of these quadrats, and the mean for all the 38 surviving quadrats combined are also given. To convert the various instantaneous standing crop measurements to an estimate of the mean standing crop during each of the periods I to III the mean was taken of the values at the beginning and end of each period. The value for all three periods combined was taken to be the mean of all the four instantaneous values. The results are given in Table 4.2.7.

Haverty and Nutting (1975c) found that dead wood litter had an aggregated distribution in their Sonoran Desert study area. They used the formula:

$$\frac{\chi^2}{(N-1)} = \frac{S^2}{\bar{x}}$$

to test for non-random distribution where S^2 represents the variance, $\bar{x}$ the mean and N the sample size. High values of χ^2 imply that the samples were aggregated (Southwood, 1966). Using the data from all 38 viable M_C quadrats for all three periods combined gave the values:

	$\bar{x}$	S^2	$S^2/\bar{x}$
wet weights	8820	6.35×10^7	7199.5
dry weights	7985	5.05×10^7	6324.4

indicating that dead wood had a highly aggregated distribution in Tsavo.

Nye (1961) used estimates of litter standing crop and litter fall to estimate turnover time for the litter using the relationship:

$$\text{Annual litter fall} = \text{litter standing crop} \times \text{Decomposition Constant (DC)}$$

The inverse of the decomposition constant gives the mean time, in years, for the material being considered to disappear completely. Using the figures for wood fall (Table 4.2.3) and standing crop (Table 4.2.7) it can be seen from Table 4.2.8 that the decomposition constant was .0997 using the wet weight figures and .0973 using the dry weight figures. The mean disappearance times were 10.03 and 10.28 years respectively.

The values for the changes in standing crop of dead wood on each M_C quadrat in each period and over all three periods combined are given in Table 4.2.9a-d. Also given in this table are the values for the index of woody vegetation on each quadrat (Σ(height x greatest diameter) of all shrubs) used to obtain the estimates of dead wood fall in each period. The disappearance of dead wood from each quadrat in each period was calculated by subtracting the change in the standing crop from the estimate of wood fall and these results are also given in Table 4.2.9.

The results for each line of quadrats are summarised in Table 4.2.10 as the mean weight of wood which disappeared in each period. Quadrats 1,7 and 2,2 were omitted from these calculations as the data from them were incomplete. The results have also been combined to give the mean disappearance of wood over the whole sample of 38 quadrats in each period.

To test whether disappearance rates varied between periods the disappearance was calculated for each quadrat in g m^{-2} day^{-1} from the expression:

$$\text{Disappearance from quadrat i (g } m^{-2} \text{ day}^{-1}\text{)} = \frac{\text{est. disappearance on quadrat i in period j}}{\text{duration of period j in days} \times 25}$$

The mean daily disappearance for each period taken over all 38 quadrats is given in Table 4.2.11. There is a significant difference between

disappearance rates estimated on a wet weight basis between periods I and III ($p < .05$) but the dry weights do not show any significant differences. As there is no indication of a difference related to seasons the best estimate of disappearance which can be made from these data should be given by combining the data from all three periods, as with the estimate of dead wood fall (Section 4.2.1.2). The annual disappearance of dead wood was estimated from all 38 quadrats over all periods as

wet weight disappearance: 35.0 g $m^{-2}yr.^{-1}$ S.E. 8.59

dry weight disappearance: 28.1 g $m^{-2}yr.^{-1}$ S.E. 5.71

A second estimate of dead wood turnover time can be made from these figures:

$$\text{Turnover time} = \frac{\text{Mean standing crop}}{\text{annual disappearance}}$$

$$= \frac{359.4}{35.0} = 10.27 \text{ years wet, DC} = 0.0974$$

$$\frac{316.7}{28.1} = 11.27 \text{ years dry, DC} = 0.0887$$

The percentage of the dead wood which disappeared annually was calculated for each quadrat. The results are given in Table 4.2.12. Annual disappearance was estimated from Tables 4.2.9 and 4.2.10 as:

$$\frac{\text{Total disappearance on quadrat} \times 365}{\text{Length of exposure in days}}$$

The arcsin transformation was used to estimate the mean and standard error of the percentage disappearance. Quadrats 4.8 and 4.9 were omitted from these calculations and are bracketed in Table 4.2.12; their disappearance estimates were close to 100% of the mean standing crop, a great deal higher than any other quadrat, probably due to interference by large mammals. The mean percentage disappearance was:

	% disappearance $yr.^{-1}$	S.E.	Turnover time (yrs)	Decomposition Constant
wet weight	12.69	2.35	7.88	.1269
dry weight	9.83	1.73	10.17	.0983

The sample size was 36. There is reasonably good agreement between the three estimates of turnover time of 10.03, 10.27 and 7.88 years from wet weights and 10.28, 11.27 and 10.17 years from dry weights.

Table 4.2.6a

Transect 1. Standing Crop of Dead Wood on each M_C Quadrat on each of Four Sampling Dates
(g 25 m^{-2})

Quadrat No.	8.1.76		28.4.76		28.10.76		15.4.77	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	4650	4134	5810	4886	5415	4744	5172	4650
2	34170	30377	35960	30242	35220	30007	35204	30240
3	20810	18500	23315	17160	21430	18730	19888	16964
4	9045	8041	9465	6891	16190	13681	15480	13468
5	2335	2076	2830	2142	2590	2274	2505	2172
6	2870	2551	3890	2777	3060	2662	2822	2472
7	destroyed							
8	16930	15051	16672	14821	16350	14224	16037	14260
9	7570	6730	8675	7712	9015	7843	8658	7697
10	8730	7761	8150	7245	8195	7130	7538	6701
Mean	11901.1	10580.1	12751.9	10430.7	13051.7	11255	12589.3	10957.9
S.E. N = 9	3462.5	3078.1	3612.0	2993.4	3515.5	2999.4	3492.1	2988.0

Table 4.2.6b

Transect 2

Quadrat No.	2.1.76		26.4.76		6.10.76		30.3.77	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	3740	3254	4295	3818	4600	4053	3782	3506
2	1190	1035	destroyed					
3	3900	3393	3790	3369	4260	3753	3882	3599
4	5680	4942	5180	4605	5340	4704	5195	4816
5	7970	6934	2195	1951	2530	2229	2308	2139
6	8530	7421	7590	6747	8105	7140	7231	6703
7	2850	2479	3390	3014	3670	3233	3702	3276
8	3310	2880	3883	3452	4880	4299	4345	3867
9	990	861	1425	1267	1530	1348	1418	1293
10	10320	8978	10590	9414	8995	7925	9253	8494
Mean	5254.5	4571.4	4704.2	4182.0	4878.9	4298.3	4568.4	4188.2
S.E. N = 9	1026.2	892.8	940.2	835.9	801.2	705.9	802.4	741.5

Table 4.2.6c

Transect 3

Quadrat No.	3.1.76		26.4.76		9.10.76		30.3.77	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	9760	8491	10245	9108	11890	10475	9281	8501
2	8960	7795	7410	6587	7670	6757	7346	6677
3	2220	1931	4330	3849	4445	3916	4138	3670
4	14660	12754	15260	13566	15300	13479	12261	11366
5	1230	1070	1540	1369	1745	1537	1448	1342
6	2090	1818	2307	2051	2535	2233	1970	1826
7	4310	3750	5517	4905	5725	5044	5548	5143
8	18840	16391	19974	17757	20250	17840	18801	17428
9	2670	2321	3055	2716	3210	2828	3110	2883
10	1980	1723	3005	2671	3060	2696	2892	2681
Mean	6672	5804.6	7060.3	6458	7583	6680.6	6679.5	6151.9
S.E. N = 10	1945.6	1692.7	1985.9	1726.0	1974.9	1739.8	1731.0	1605.2

Table 4.2.6d

Transect 4 and Overall Means

Quadrat No.	5.1.76		27.4.76		25.10.76		4.4.77	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	7070	6151	7025	6245	7605	6700	7258	6728
2	3210	2793	4335	3854	4555	4049	4104	3804
3	5620	4889	5332	4740	5285	4013	4745	4399
4	30580	26605	32435	28835	31115	27412	29679	27512
5	6520	5672	17160	15255	16850	14845	16758	15535
6	12240	10649	11910	10588	12550	11057	11820	10957
7	14770	12850	14230	12650	14145	12462	14058	13032
8	380	331	510	453	580	511	473	438
9	4390	3819	4435	3943	4305	3793	3993	3701
10	21410	18627	22135	19678	21720	19135	21040	19504
Mean S.E. N = 10	10619 2958.3	9238.5 2573.8	11950.7 3107.5	10624.1 2762.6	11871 2976.9	10397.7 2638.2	11392.8 2890.5	10561.1 2679.5
Overall Mean S.E. N = 38	8613.4 1291.2	7547.2 1136.2	9137.2 1371.3	7956.2 1170.8	9366.2 1328.8	8178.0 1154.8	8819.5 1292.4	7985.4 1153.2

Table 4.2.7

Mean Standing Crop (S) of Dead Wood at the

Main Experimental Site (M) Taken over 38 Quadrats

Period	Mean wet wt. S. g $25m^{-2}$	Mean dry wt. S. g $25m^{-2}$	Wet wt. S g m^{-2}	dry wt. S g m^{-2}
I	8875.3	7751.7	355.0	310.1
II	9251.7	8067.1	370.1	322.7
III	9092.8	8081.7	363.7	323.3
Combined	8984.1	7916.7	359.4	316.7

Table 4.2.8

Calculation of the Decomposition Constant from the

Estimates of Wood Litter Fall and Standing Crop

	wet	dry
Wood litter fall (g m^{-2} $yr.^{-1}$) (F)	35.82	30.81
Dead wood standing crop (g m^{-2}) (S)	359.4	316.7
Decomposition constant (F/S)	.0997	.0973
Time to decompose completely (yrs.)	10.03	10.28

Table 4.2.9a

Transect 1. Changes in the Standing Crop (CS) of Dead Wood and Wood Fall (F) on the M_C Quadrats in each Period. Wood Disappearance (D) Calculated from D = F - CS. F Estimated from Index 1 Regression, Section 4.2.2. (g $25m^{-2}$).

	Period I		Period II		Period III		Combined Periods		Index I
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry	
1 CS	+ 1160	+ 752.2	- 395	- 142	- 243	- 94.4	+ 522	+ 515.8	
1 F	430.9	367.9	375.9	330.4	71.3	60.9	880.6	761.0	5200
1 D	- 729.1	- 384.3	770.9	472.4	314.3	155.3	358.6	245.2	
2 CS	+ 1790	+ 135.1	- 740	- 234.6	- 16	+ 232.6	+ 1034	+ 133.1	
2 F	637.0	553.1	594.8	523.4	126.1	109.1	1361.1	1187.8	14900
2 D	- 1153	418	1334.8	758	142.1	- 123.5	327.1	1054.7	
3 CS	+ 2505	- 1340.1	- 1885	+ 1570	- 1542	- 1765.5	- 922	- 1535.6	
3 F	507.4	436.7	457.1	402.0	91.6	78.8	1058.9	919.4	8800
3 D	- 1997.6	1776.8	2342.1	- 1168	1633.6	1844.3	1980.9	2455	
4 CS	+ 420	- 1150	+ 6725	+ 701	- 710	- 213	+ 6435	- 662	
4 F	524.4	451.9	475.2	417.9	96.2	82.8	1098.6	954.6	9600
4 D	104.4	1601.9	- 6249.8	- 283.1	806.2	295.2	- 5336.4	1616.6	
5 CS	+ 495	+ 66.2	- 240	+ 132	- 85	- 102.2	+ 170	+ 96	
5 F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
5 D	- 174.6	202.5	498.5	94.9	126.9	137.3	453	436.2	
6 CS	+ 1020	+ 225.6	- 830	- 115	- 238	- 189.9	- 48	- 79.3	
6 F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
6 D	- 699.6	43.1	1088.5	341.9	279.9	225	671	611.5	

..../cont'

7	CS F D	-	-	-	-	-	-	- 689 2277.5 3170.5	- 3532 2001.7 5533.7	33400
8	CS F D	- 258 320.4 578.4	- 229.8 268.7 498.5	- 322 258.5 580.5	- 597 226.9 823.9	- 313 41.9 354.9	+ 32.9 35.1 2.2	- 893 623.0 1516	- 793.9 532.2 1326.1	0
9	CS F D	+ 1105 1914.0 809	+ 982.4 1700.5 718.1	+ 340 1951.1 1611.1	+ 130.9 1719.1 1588.2	- 357 465.8 822.8	- 146 407.5 553.5	+ 1088 4338.1 3250.1	967.3 3832.0 2864.7	75000
10	CS F D	- 580 320.4 900.4	- 515.7 268.7 784.4	+ 45 258.5 213.5	- 115.3 226.9 342.2	- 657 41.9 698.9	- 428.7 35.1 463.8	- 1192 623.0 1815	- 1059.7 532.2 1591.9	0

Table 4.2.9b

Transect 2

	Period I		Period II		Period III		Combined Periods		Index 1
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry	
1 CS	+ 555	+ 564.5	+ 305	+ 234.3	- 818	- 546.7	+ 42	+ 252.1	9500
F	522.2	450	472.9	415.9	95.6	82.3	1093.6	950.2	
D	- 32.8	- 114.5	167.9	181.6	913.6	629	1051.6	698.1	
2 CS	destroyed								
F									
D									
3 CS	- 110	- 23.7	+ 470	+ 383.8	- 378	- 154.5	- 18	+ 205.6	3000
F	384.1	325.9	326.2	286.6	58.8	50.0	771.6	664.2	
D	494.1	349.6	- 143.8	- 97.2	436.8	204.5	789.6	458.6	
4 CS	- 500	- 336.6	+ 160	+ 99.5	- 145	+ 111.3	- 485	- 125.8	6800
F	464.9	398.5	412.0	362.2	80.3	68.9	959.9	831.4	
D	964.9	735.1	252	262.7	225.3	- 42.4	1444.9	957.2	
5 CS	+ 65	+ 98.3	+ 335	+ 277.5	- 222	- 89.4	+ 178	+ 286.4	2700
F	377.7	320.2	319.4	280.6	57.2	48.5	756.8	651	
D	312.7	221.9	- 15.6	3.1	279.2	137.9	578.8	364.6	
6 CS	- 940	- 673.6	+ 515	+ 393	- 874	- 437.4	- 1299	- 718	0
F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	
D	1260.4	942.3	- 256.5	- 166.1	915.9	472.5	1922	1250.2	

..../cont'd

7	CS	+ 540	+ 534.2	+ 280	+ 219.6	+ 32	+ 43	+ 852	+ 796.8	4300
	F	411.7	350.7	355.6	312.5	66.2	56.5	836	721.4	
	D	- 128.3	- 183.5	75.6	92.9	34.2	13.5	- 16	- 75.4	
8	CS	+ 523	+ 572.3	+ 997	+ 847.3	- 535	- 432.3	+ 985	+ 987.3	9300
	F	518.0	446.2	468.4	412	94.5	81.3	1083.7	941.4	
	D	- 5	- 126.1	- 528.6	- 435.3	629.5	513.6	98.7	- 45.9	
9	CS	+ 435	+ 405.5	+ 105	+ 81.1	- 112	- 54.7	+ 428	+ 431.9	0
	F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	
	D	- 114.6	- 136.8	153.5	145.8	153.9	89.8	195	100.3	
10	CS	+ 270	+ 436.1	- 1595	- 1489.9	+ 258	+ 569.7	- 1067	- 484.1	0
	F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	
	D	50.4	- 167.4	1853.5	1716.8	- 216.1	- 534.6	1690	1016.3	

Table 4.2.9c

Transect 3

	Period I		Period II		Period III		Combined Periods		Index 1
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry	
1 CS	+ 485	+ 616.6	+ 1645	+ 1367.3	- 2609	- 1973.7	- 480	+ 10.2	6200
F	452.1	387.0	398.4	350.3	76.9	65.9	930.1	805.0	
D	- 32.9	- 229.6	- 1246.6	- 1017	2685.9	2039.6	1410.1	794.8	
2 CS	- 1550	- 1207.7	+ 260	+ 169.6	- 324	- 79.8	- 1614	- 1117.9	7700
F	484.0	415.7	432.3	380.1	85.4	73.3	1004.4	871	
D	2034	1623.5	172.3	210.5	409.4	153.1	2618.4	1988.9	
3 CS	+ 70	+ 104.4	+ 115	+ 66.6	- 307	- 245.6	- 122	- 74.6	0
F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	
D	250.4	164.3	143.5	160.3	348.9	280.7	745	606.8	
4 CS	+ 600	+ 811.9	+ 40	- 86.8	- 3039	- 2113.4	- 2399	- 1388.3	5800
F	443.6	379.4	389.4	342.3	74.7	63.9	910.3	787.4	
D	- 156.4	- 432.5	349.4	429.1	3113.7	2177.3	3309.3	2175.7	
5 CS	+ 310	+ 299	+ 205	+ 168.2	- 297	- 195	+ 218	+ 272.2	6600
F	460.6	394.7	407.5	358.2	79.2	67.9	949.9	822.6	
D	150.6	95.7	202.2	190	376.2	262.9	731.9	550.4	
6 CS	+ 217	+ 232.6	+ 228	+ 182.4	- 565	- 407.1	- 120	+ 7.9	1300
F	348.0	293.5	287.9	252.8	49.2	41.6	687.4	589.4	
D	131	60.9	59.9	70.4	614.2	448.7	807.4	581.5	

..../cont'd

CS	+ 1207	+ 1154.9	+ 208	+ 139.1	- 177	+ 99.3	+ 1238	+ 1393.3	
7 F	545.6	471.0	497.7	437.8	101.8	87.7	1148.1	998.6	10600
D	- 661.4	- 683.9	289.7	298.7	278.8	- 11.6	- 89.9	- 394.7	
CS	+ 1134	+ 1366.1	+ 276	+ 83.3	- 1449	- 411.7	- 39	+ 1037.7	
8 F	626.3	543.6	583.5	513.4	123.3	106.6	1336.3	1165.8	14400
D	- 507.7	- 822.5	307.5	430.1	1572.3	518.3	1375.3	128.1	
CS	+ 385	+ 393	+ 155	+ 104.1	- 100	+ 63	+ 440	+ 560.1	
9 F	362.9	306.8	303.6	266.7	53.2	45.0	722.1	620.2	2000
D	- 22.1	- 86.2	148.6	162.6	153.2	- 18	282.1	60.1	
CS	+ 1025	+ 948.8	+ 55	+ 24.5	- 168	- 15	+ 912	958.3	
10 F	409.6	348.8	353.3	310.5	65.6	56.0	831.1	717	4200
D	- 615.4	- 600	298.3	286	233.6	41	- 80.9	- 241.3	

Table 4.2.9d

Transect 4

	Period I		Period II		Period III		Combined Periods		Index 1
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry	
CS	- 45	+ 94.3	+ 580	- 454.8	- 347	+ 28.2	+ 188	- 332.3	
1 F	420.2	358.4	364.6	320.4	68.5	58.5	855.8	739	4700
D	465.2	264.1	- 215.4	775.2	415.5	30.3	667.8	1071.3	
CS	+ 1125	+ 1061.1	+ 220	+ 195.6	- 450	- 245	+ 895	+ 1011.7	
2 F	388.4	329.7	330.7	290.6	60.0	51	781.5	673	3200
D	- 736.6	- 731.4	110.7	95	510	296	- 113.5	- 338.7	
CS	- 288	- 149.3	- 47	- 727.1	- 540	+ 385.6	- 875	- 490.8	
3 F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
D	608.4	418	305.5	954	581.9	- 350.5	1498	1023	
CS	+ 1855	+ 2230.1	- 1320	- 1422.4	- 1436	+ 100.1	- 901	+ 907.8	
4 F	328.9	276.3	267.5	234.9	44.2	37.1	642.8	549.8	400
D	- 1526.1	- 1953.8	1587.5	1657.3	1480.2	- 63	1543.8	- 358	
CS	+ 355	+ 439.5	- 310	- 410	- 92	+ 689.7	- 47	+ 719.2	
5 F	1323.3	1169.8	1323.7	1166	308.7	269.4	2961.0	2608.85	47200
D	968.3	730.3	1633.7	1576	400.7	- 420.3	3008	1889.65	
CS	- 330	- 60.8	+ 640	+ 468.6	- 730	- 99.5	- 420	+ 308.3	
6 F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
D	650.4	329.5	- 381.5	- 241.7	771.9	134.6	1043	223.9	

..../cont'd

	CS	- 540	- 199.9	- 85	- 188.3	- 87	+ 570.1	- 712	+ 181.9	
7	F	339.5	285.8	278.8	244.8	47.0	39.6	667.6	571.8	900
	D	879.5	485.7	363.8	433.1	134	- 530.5	1379.6	389.9	
	CS	+ 130	+ 122.8	+ 70	+ 57.6	- 107	- 72.5	+ 93	+ 107.9	
8	F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
	D	190.4	145.9	188.5	169.3	148.9	107.6	530	424.3	
	CS	+ 45	+ 123.4	- 130	- 150	- 312	- 91.2	- 397	- 117.8	
9	F	2481.3	2210.2	2553.7	2250.4	616.8	540.0	5660.7	5006.7	101700
	D	2436.3	2086.8	2683.7	2400.4	928.8	631.2	6057.7	5124.5	
	CS	+ 725	+ 1051.3	- 415	- 542.7	- 680	+ 368.8	- 370	+ 877.4	
10	F	320.4	268.7	258.5	226.9	41.9	35.1	623.0	532.2	0
	D	- 404.6	- 782.6	673.5	769.6	721.9	- 333.7	993	- 345.2	

Table 4.2.10

Mean Disappearance of Dead Wood on each Transect of M_C Quadrats and on all 38 Quadrats Combined

D = disappearance S.E. = standard error Days = number of days exposure

Transect		Period I		Period II		Period III		Combined Periods		N
		wet	dry	wet	dry	wet	dry	wet	dry	
1	Mean D	- 262.4	628.8	243.3	330	575.5	421.3	559.5	1355.8	9
	S.E.	324.1	233.0	840.0	255.7	160	187.1	804.8	296.6	
	Days	121	121	173	173	139	139	433	433	
2	Mean D	311.3	169.0	173.1	189.4	374.7	164.9	861.6	524.9	9
	S.E.	167.6	142.0	225.2	203.5	128.9	117.5	237.7	161.6	
	Days	115	115	163	163	145	145	423	423	
3	Mean D	57.0	- 91.0	72.5	122.1	978.6	589.2	1110.9	625.0	10
	S.E.	242.8	219.7	149.4	131.8	345.9	259.8	352.5	272.0	
	Days	114	114	166	166	172	172	452	452	
4	Mean D	353.1	99.2	695.0	858.8	609.4	- 49.8	1660.7	910.5	10
	S.E.	341.3	339.4	305.2	258.3	126.0	114.9	552.8	521.5	
	Days	113	113	181	181	161	161	455	455	
Combined	Mean D	119.5	191.1	300.6	381.1	642.9	280.8	1065.9	849.5	38
	S.E.	140.1	127	218.5	114.9	110.2	96.6	260.8	175.2	
	Mean Days	115.6	115.6	170.9	170.9	169.1	169.1	455.6	455.6	

Table 4.2.11

Mean Daily Disappearance of Dead Wood in each Period g m^{-2} day^{-1} (N = 38)

	Period I		Period II		Period III		Combined	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
Mean	.0433	.064	.0684	.0868	.1634	.0705	.0958	.077
S.E.	.0484	.044	.0504	.0263	.0265	.0244	.0235	.0157

Table 4.2.12

Calculation of Annual Percentage Disappearance of Dead Wood on each M_C Quadrat from all Periods Combined. S = standing crop; D = disappearance.

Quadrat		Transect 1		Transect 2		Transect 3		Transect 4	
		wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	Mean S Annual D % D	5262 302.3 5.74	4603 206.7 4.49	4104 907.4 22.11	3658 602.4 16.47	10294 1138.7 11.06	9144 641.8 7.02	7239 535.7 7.40	6456 859.4 13.31
2	Mean S Annual D % D	35138 275.7 0.78	30216 889.1 2.94			7846 2114.4 26.95	6954 1606.1 23.10	4051 -91.0 -2.25	3625 -271.7 -7.49
3	Mean S Annual D % D	21360 1669.8 7.82	17838 2069.5 11.60	3958 681.3 17.21	3528 395.7 11.22	3783 601.6 15.90	3341 490.0 14.67	5245 1201.7 22.91	4510 820.6 18.20
4	Mean S Annual D % D	12545 -4498.4 -35.86	10520 1362.7 12.95	5349 1246.8 23.31	4767 826.0 17.33	14370 2672.3 18.60	12791 1756.9 13.74	30952 1238.4 40.01	28133 -287.2 -1.02
5	Mean S Annual D % D	2565 381.9 14.89	2166 367.7 16.98	3751 499.4 13.31	3313 314.6 9.50	1491 591.0 39.64	1329 444.5 33.45	14322 2413.0 16.85	12827 1515.9 11.82
6	Mean S Annual D % D	3160 565.6 17.90	2615 515.6 19.72	7864 1658.5 21.09	7003 1078.8 15.40	2225 652.0 29.30	1982 469.6 23.69	12130 836.7 6.90	10813 179.6 1.66

..../contd

7	Mean S Annual D % D			3403 -13.8 -0.41	3000 -65.06 -2.17	5275 -72.6 -1.38	4710 -318.7 -6.77	14301 1106.7 7.74	12748 312.8 2.45
8	Mean S Annual D % D	16497 1277.9 7.75	14589 1117.8 7.66	3854 85.2 2.21	3624 -39.6 -1.09	19466 1110.6 5.71	17354 103.4 0.60	486 (425.2) (87.49)	433 (340.4) (78.61)
9	Mean S Annual D % D	8479 2739.7 32.31	7495 2414.8 32.22	1341 168.3 12.55	1192 85.6 7.18	3011 227.8 7.57	2687 48.5 1.80	4281 (4859.5) (113.51)	3814 (4110.9) (107.78)
10	Mean S Annual D % D	8153 1530 18.77	7209 1341.9 18.61	9789 1758.3 17.96	8703 876.9 10.08	2734 -65.3 -2.39	2443 -194.9 -7.98	21576 796.6 3.69	19236 -276.9 -1.44

4.2.3.3 DISCUSSION

Examination of Table 4.2.9 shows that sometimes the estimates of wet and dry weight standing crops changed in opposite directions on a particular quadrat in a particular period. This apparent paradox occurs because the changes in the standing crop were almost always very small compared with the total standing crop. The dry weight correction factors varied from one weighing to the next so that an increase in the total wet weight could become a decrease in the estimated dry weight and vice versa. For example on quadrat 4, line 2:

	6 October 1976	30 March 1977	Change
Standing crop (S) wet (g)	5340	5195	-145
Correction factor	.881	.927	
Estimated S dry (g)	4704.5	4815.8	+111.3

Table 4.2.9 also gives some negative estimates of disappearance which need to be explained. They occurred when the actual fall of dead wood onto a quadrat was greater than the sum of the estimated fall and the actual disappearance. Although the negative disappearance figures can not have been real events, they are a result of the real variation in sample measurements of standing crop and of wood litter fall used to estimate disappearance and they remain valid as part of the sample used to estimate the mean disappearance in each period.

The results have been given in terms of both wet and estimated dry weights all the way through this analysis. The reason for this was the frequent disparity between wet and dry estimates of the changes in standing crop and wood disappearance on individual quadrats. The final estimates of mean disappearance using all the data are roughly in the ratio predicted from sample measurements of water content, despite the differences in the individual samples. This implies that the sample size was large enough to give a good estimate of mean disappearance despite the high variability of

the single quadrat estimates.

The estimate of dead wood disappearance of 35 g m^{-2} $yr.^{-1}$ wet weight, 28.1 g m^{-2} $yr.^{-1}$ dry weight compares remarkably well with the general estimate of wood litter fall of 35.8 g m^{-2} $yr.^{-1}$ wet weight, 30.8 g m^{-2} $yr.^{-1}$ dry weight. As a direct result of the close agreement of these figures the decomposition constant estimated from the disappearance of dead wood, .0974 wet and .0887 dry, agrees well with the same constant estimated from wood fall, .0996 wet and .0973 dry. The same standing crop figures were used in estimating both pairs of constants. A third estimate of the same quantity using estimates of the annual percentage disappearance of dead wood on each quadrat gave the decomposition constants 0.1269 wet and 0.0983 dry, again close to the former estimates. Dead wood in Tsavo East takes on average between eight and eleven years to disappear completely.

Collins (1977b), working in Southern Guinea Savanna in Nigeria (rainfall 1175 mm $yr.^{-1}$) found disappearance times for dead wood of 0.488 years for twigs (< 2 cm diameter) and 3.629 years for logs (> 2 cm diameter) with a mean time for all wood of 2.028 years (decomposition constant = 0.4931). John (1973) estimated times of 1.2 years for twigs, 1.3 years for small wood and 9.2 years for medium sized logs at Kade, Ghana (rainfall 1630 mm $yr.^{-1}$) and Hopkins (1966), using blocks of a wood highly palatable to termites, estimated 1-2 years for disappearance in southern Nigerian forests (rainfall 2072 mm $yr.^{-1}$). Haverty and Nutting (1975c) gave figures for the mean standing crop, 212.7 g m^{-2}, and wood litter fall, 45 g m^{-2} $yr.^{-1}$, giving a mean disappearance time for dead wood in Arizona of 4.73 years (rainfall 330 mm $yr.^{-1}$). Compared with these estimates dead wood disappears very slowly in Tsavo as would be expected from its low rainfall relative to the West African sites. This effect of low rainfall may have been exaggerated by the drought in 1974-75 which probably stimulated wood fall and depressed termite activity leading to an abnormally high standing crop of dead wood. The study in Arizona included an exceptionally cold winter when wood fall was stimulated

by heavy snow and frost damage to trees, so this estimate of decomposition time was probably depressed.

To separate the disappearance of dead wood into an estimate of consumption by termites and an estimate of other causes would have required a measurement of the rate of disappearance of the wood when termites were prevented from reaching it. For instance Collins (1977b) suspended samples of wood above the ground and recorded their rate of weight loss. Aerial dead wood is hardly attacked in Tsavo, except by kalotermitids and cerambycid larvae, neither of which operate at ground level where the only signs of fungal and bacterial decomposition were seen, so a suspended control would not have given the data required. No other adequate control could be devised. Nevertheless for several reasons it is believed that almost all the wood which disappeared from the ground surface was consumed by termites, and that the estimate of dead wood disappearance is a good approximation to termite consumption. There are many standing dead trees in Tsavo which show no external signs of decomposition, other than the loss of the bark, after five or more years. Their upper parts are attacked internally by termites, mainly Epicalotermes kempae and Microcerotermes sp.I and by the larvae of cerambycid beetles and by xylocopid bees, which eventually cause fragmentation of the dead wood and its precipitation to the ground. Beetle larvae and bees were never found in dead wood on the ground, the province of this study. Some logs were left on the surface of the ground for a year. Many of these were virtually unattacked by termites and these lost a mean of 0.45% dry weight, again indicating very low levels of activity by organisms other than termites. Discs of wood cut from Commiphora trees were used extensively for experiments on termite activity (Sections 4,3 and 4.6). After heavy rain some fungal growth was noticed on discs in contact with soil, but stopped when the discs dried out a few days later. Anderson and Coe (1974) studied the decomposition of elephant dung in Tsavo by

measuring the evolution of carbon dioxide from fresh dung over a period of 14 days. By the end of this period the dung had nearly dried out and the evolution of CO_2 was equivalent to a weight loss of .01% per day, 3.65% per year. Kingston (1977) found that once elephant dung has dried out completely termites are the only invertebrates which attack it until it is rewetted by rain. Elephant dung often has a higher concentration of nutrients than the vegetation originally eaten by the elephant. It may therefore be expected to be a relatively attractive material for both micro- and macro-decomposers compared with nutrient deficient dead wood. For the rest of this section estimates of wood disappearance will be treated as estimates of consumption by termites. The limits on the estimates of disappearance are so broad that they almost certainly encompass the true value for consumption by termites.

4.2.4 INDIRECT ESTIMATION OF DEAD WOOD LITTER FALL

4.2.4.1 INTRODUCTION

In Section 4.2.1 the mean rate of recruitment of dead wood to the ground surface was estimated from wood fall onto 11 random M_R quadrats. This was a small sample and the result can now be checked using the much larger sample of random quadrats given by combining the quadrats from the M_R series with the M_C quadrats used to estimate wood disappearance in Section 4.2.3.

In Section 4.2.2 regressions were calculated between an index of the density of bushes and the fall of dead wood on 25 m^2 M_C quadrats. These regressions were used in Section 4.2.3 to estimate the fall of dead wood onto quadrats where this could not be measured directly but the index could be measured accurately and it was pointed out in discussion (Section 4.2.2.4) that to use general regressions, based on an index, to predict actual events on small sample plots the regressions must be reasonably accurate.

The regressions can also be used to estimate the mean wood fall over wider areas, but in this case the index value for the area must be sampled and the distribution of the index must also be known accurately.

4.2.4.2 RESULTS

Using the values for Index 1 (height x greatest diameter of shrubs) for the 50 randomly sited (11 M_R, 39 M_C) quadrats (Tables 4.2.5 and 4.2.9) the distribution of the index was examined and plotted in Figure 4.2.2. 16 (32%) of the quadrats were bare while 34 had index values ranging from 400 to 101,700. The high proportion of bare quadrats clearly reflects habitat heterogeneity and made it necessary to separate the calculation of overall wood fall into two parts, the fall on bare quadrats and the fall on those with bushes. Mean wood fall on the bare quadrats was estimated from the five bare M_R and M_S quadrats (Tables 4.2.2 and 4.2.4) and the results are given in Table 4.2.13.

The frequency distribution of the index is clearly not normal even after the bare quadrats have been removed (Figure 2.2.2). Log_{10} of the index is however normally distributed (Figure 2.2.3) with mean 3.840, standard error 0.0914 giving a 95% confidence interval from 3.661 to 4.020. Taking the antilog of these figures to transform them back to the original index gives the mean value of 6925 with 95% confidence interval 4585 to 10461. The mean wood fall for each period was calculated using these values of the index, from the regression equations. The results are given in Table 4.2.13.

To combine the estimates of wood fall onto the bare quadrats with the estimates from the bushed quadrats the daily wood fall estimates for each were multiplied by the respective frequencies of their quadrat type in the habitat (.32 for bare quadrats; .68 for bushed quadrats). The resulting figures were added together to give an aggregated mean daily dead wood fall for the habitat at the main study site (Table 4.2.13). The wood fall

Figure 4.2.2

Frequency distribution of Index 1, bush density, on 50 quadrats.

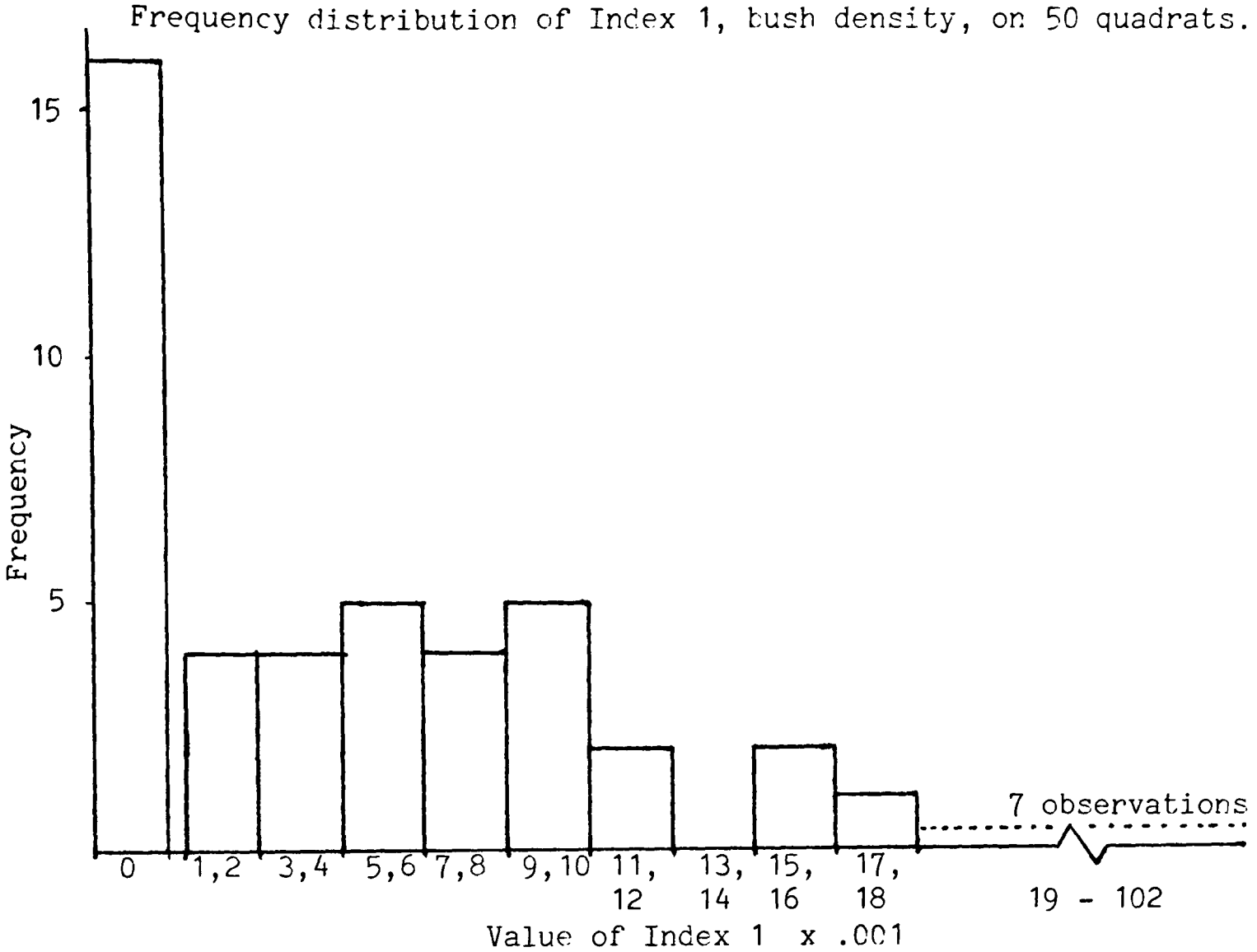
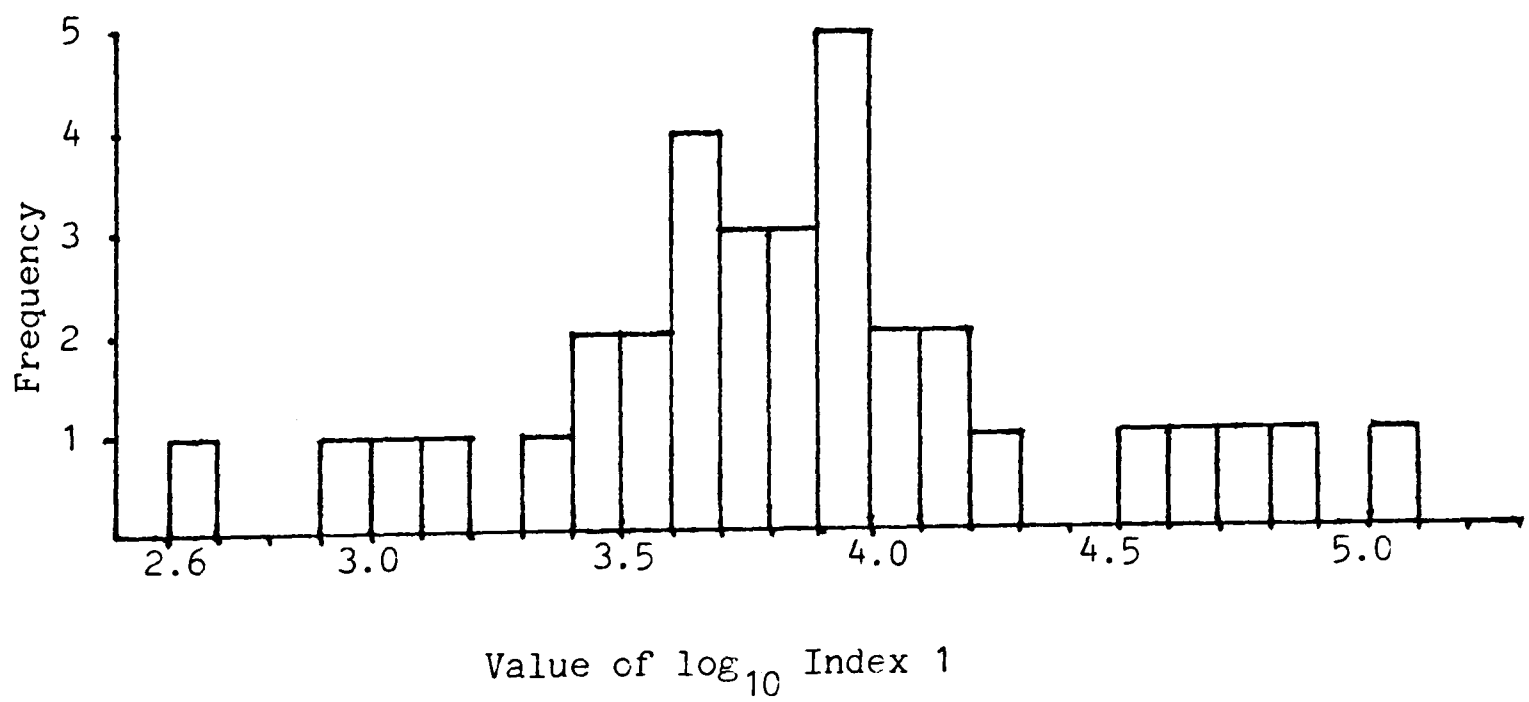


Figure 4.2.3

Frequency of $\log_{10}$ Index 1 on 34 quadrats with bushes.



estimated for all periods combined was:

wet weight	20.3 g m^{-2} $yr.^{-1}$	95% confidence limits 15.1 - 26.4
dry weight	17.6 g m^{-2} $yr.^{-1}$	95% confidence limits 13.0 - 23.1

4.2.4.3 DISCUSSION

Two methods have been used to estimate dead wood litter fall and they gave rather different results. The direct measurement of fall on 11 M_R quadrats (Section 4.2.1) gave an estimate of 35.8 ($\pm$ 25.1) g m^{-2} $yr.^{-1}$ wet weight, 30.81 ($\pm$ 21.8) g m^{-2} $yr.^{-1}$ dry weight. The indirect method used in the present section gave 20.3 (15.1 - 26.4) g m^{-2} $yr.^{-1}$ wet weight and 17.6 (13.0 - 23.1) g m^{-2} $yr.^{-1}$ dry weight. All limits are 95% confidence intervals.

It has been suggested (Section 4.2.1.3) that the fall of dead wood litter is stimulated by drought conditions. Termite activity is depressed by dry conditions seasonally (Section 5) and also in drought years (Lepage, 1974). Reduction in termite activity and increased wood fall may be expected to lead to an increase in the standing crop of dead wood. On the other hand the indirect estimate of dead wood fall (17.6 g m^{-2} $yr.^{-1}$ dry weight) is less than the disappearance of dead wood (28.1 g m^{-2} $yr.^{-1}$ dry weight) and if this represented the real situation during the period of this study the standing crop of dead wood would have declined. The mean dry weight standing crop on the 38 viable M_C quadrats increased from January 1976 (7547.2 g 25 m^{-2}, SE $\pm$ 1136.2) to April 1977 (7985.4 g 25 m^{-2}, SE $\pm$ 1153.2) (Table 4.2.6). The probability that the means are different is just 0.1, sufficient to reject the one tailed nul hypothesis that the actual standing crop declined during the study period. Despite the wide confidence limits the direct estimate of wood fall (35.8 g m^{-2} $yr.^{-1}$ wet weight, 30.81 g m^{-2} $yr.^{-1}$ dry weight) has therefore been adopted as the better estimate.

Table 4.2.13

Estimation of Wood Litter Fall using the Index Regressions

		Period I 111 days		Period II 183 days		Period III 169 days		Combined 463 days		
		wet	dry	wet	dry	wet	dry	wet	dry	
Mean wood fall on plots without bushes	g $25m^{-2}$ S.E. g $25m^{-2}$ day^{-1}) S.E.	195.2 80.3 .0664 .0253	172.4 71.7 .0586 .0226	115.4 33.0 .0260 .0071	101.3 28.2 .0228 .0063	33.6 16.2 .0083 .0040	29.2 14.0 .0072 .0035	344.2 108.4 .0304 .0097	302.9 96.5 .0267 .0087	N=5
Mean wood fall on bushed plots	g $25m^{-2}$ 95% limit g m^{-2} day^{-1} 95% limit	467.5 417.8-542.6 .1685 .1506-.1955	400.9 356.2-468.4 .1445 .1284-.1688	414.8 362.0-494.6 .0907 .0791-.1081	364.7 318.1-435.1 .0797 .0695-.0951	81.0 67.8-101.0 .0192 .016 -.0239	69.5 57.9-87.1 .0164 .0137-.0206	778.7 685.3-919.9 .0673 .0592-.0795	674.6 591.6-800 .0583 .0511-.0691	N=34
No bushes	g m^{-2}) day^{-1} x .32) 95% limit	.0212 0-.0437	.0187 0-.0388	.0083 .0020-.0146	.0073 .0017-.0129	.0027 0-.0062	.0023 0-.0054	.0097 .0011-.0183	.0085 .0008-.0163	
Bushed	g m^{-2}) day^{-1} x .68) 95% limit	.1146 .1024-.1329	.0983 .0873-.1148	.0617 .0538-.0735	.0542 .0473-.0647	.0131 .0109-.0163	.0112 .0093-.0140	.0458 .0403-.0541	.0396 .0347-.0470	
Mean wood fall whole habitat	g m^{-2} day^{-1} 95% limit	.1358 .1024-.1766	.117 .0873-.1536	.07 .0558-.0881	.0615 .049-.0776	.0158 .0109-.0225	.0135 .0093-.0194	.0555 .0414-.0724	.0481 .0355-.0633	

Collins (1977a) reviewed the available information on litter fall in Africa and concluded that the total dry weight of litter (g m^{-2}) falling in a year (LF) is strongly related to rainfall (AP) (mm yr^{-1}) ($p < .01$) by the expression

$$LF = 0.59\ AP - 111.73$$

He also found that leaf litter made up a fairly constant proportion of the total litter fall ranging from 0.632 (Collins, 1977a) to 0.767 (John, 1973) the mean being 0.683.

The five year mean rainfall calculated for the main experimental site (M) was 352 mm (Section 4.1.2). Applying this figure to Collins's regression gives an estimate of total litter fall of 95.95 g m^{-2} yr^{-1} dry weight of which 65.53 g is leaf litter and 30.42 g other material including fruits and flowers but mainly wood. The only noticeable fruits falling on the study area were from trees such as Delonix elata which produces large woody pods which were included with the dead wood in my experiments and Melia volkensii which produces plum sized fleshy fruits but not on any of the plots used in these analyses. Almost all the 30.42 g was therefore dead wood. This is almost identical to the direct estimate of mean dry dead wood fall, 30.81 g m^{-2} yr^{-1}, and lends further support to this figure rather than the indirect estimate. The estimated rainfall at the main experimental site in 1976 was 316 mm, giving a total dry weight litter fall from Collins' regression of 74.71 g m^{-2} yr^{-1} of which 51.03 g is leaf litter and 23.68 g wood etc. This is considerably less than the mean measured fall of 30.81 g. The five year mean rainfall therefore appears to be a better predictor of wood fall than the short term rainfall.

4.3 STUDIES AT SUBSIDIARY EXPERIMENTAL SITES; EXTENSION OF DEAD WOOD DISAPPEARANCE ESTIMATES TO OTHER HABITAT TYPES IN TSAVO

4.3.1 INTRODUCTION

In Section 4.2 the production of wood litter and its disappearance were described for a single site. Tsavo is a very varied place, and to make the study more generally applicable the effects of environmental variation on dead wood disappearance needed to be taken into account. The direct measurements at site M were used as a basis for extending the disappearance estimates to other habitats by using a simple index of termite activity at other selected sites.

In Section 4.1.2 descriptions were given of each of the sites used to extend the estimates of consumption at the main site (M). When these sites were chosen W. van Wijngaarden had just begun his detailed survey of the soils and vegetation of Southern Tsavo East, and he gave me invaluable advice on the choice of sites. However the experiments do not cover all combinations of the main variables soil, vegetation and rainfall. The north of the study area including the dissected erosional plains (Figure 2.1) and the region of very low mean rainfall (Figure 2.4) are particularly underrepresented.

4.3.2 METHODS

At seven of the eight sites chosen for the extensive experiments thirty discs of wood were laid out at 5 m intervals along a transect. An identical transect was laid at the main site (M). At the eighth site (L) ten quadrats were set up in exactly the same way as the 40 M_C quadrats of the main experiment. They were established at random numbers of paces along one transect. The wood from each quadrat was collected, weighed and returned to the quadrat at roughly the same time intervals as at the main

plot. The regressions of wood fall on the bush index (Section 4.2.2) were used to estimate dead wood fall onto each quadrat.

Commiphora wood was chosen for the disc experiments as it is soft and therefore easy to saw compared with most other local trees. Dead Commiphora trees were abundant near Voi and most of the main wood feeding species present in Tsavo had been observed eating it. The majority of discs used were between 10 and 20 cm in diameter, 1-4 cm thick and weighed between 100 and 400 g, but as the wood was sawn by hand some of the discs were outside this range. Before being used the discs were dried in a ventilated drying oven at 105^{o}C for 48 hours and weighed hot as they absorbed moisture very rapidly as they cooled.

Once a month each transect was visited and each disc was examined for signs of termite attack. If termites were present the disc was labelled, using a waterproof marking pen, with its transect and position and taken back to the laboratory in a polythene bag to prevent loss of the termites. Often there were signs that a disc had been attacked but no termites were present. In this case the disc was examined for the characteristic signs left by different species of termites and the species most likely to have left the signs present was recorded as the attacker. If the disc had been noticeably consumed it was labelled and returned to the laboratory, a new disc being substituted on the transect. A noticeable consumption assessed subjectively proved to be equivalent to a consumption by termites of about 1 g. Discs which had not been attacked, or noticeably consumed if there were signs of attack, were put back on the ground beside the point they were taken from to avoid confusion of signs from one month with signs from the next.

In the laboratory the termites were separated from the disc and soil adhering to it and counted (Section 5.2). The discs were scrubbed in water to remove all remaining soil, oven dried for 48 hours at 105^{o}C and weighed.

The experiment was set up in May 1976, first sampled in June 1976 and last sampled in April 1977. Indices of termite activity can be calculated from the data in various ways. The purpose of the index being to estimate annual consumption at each site the total weight of discs consumed by termites over all eleven months was used. Annual consumption at each site was estimated from the expression:

$$\text{Annual Consumption at site i} = \frac{\text{Consumption on transect i}}{\text{Consumption on transect M}} \times \text{Disappearance at site M}$$

where annual disappearance at site M is given in Section 4.2.3.

4.3.3 RESULTS

4.3.3.1 WEIGHT LOST BY UNATTACKED DISCS

Some of the discs on the transects were not attacked by termites. Most of these were only collected at the end of the experiment and used as controls to estimate weight loss due to agencies other than termites. The data from these discs are given in Table 4.3.1. The data were examined for relationships between weight lost and initial weight of the discs, weight lost and exposure time and percentage weight lost and exposure time. No relationships which could be used predictively were found. There were no significant differences between mean weights lost on the different transects, nor between the discs collected from transect D in December and those collected in April. Transect C was extensively disturbed by people between March and April 1977, so none of the discs collected were known to be unattacked, and could not be used as controls.

Unattacked discs lost a mean weight of 3.1 g (S.E. .403, N = 68) regardless of exposure time. The discs were only weighed to the nearest gram so three grams will be used as the weight lost from attacked discs not attributable to termites. Most of this loss probably occurred in the laboratory during cleaning and drying.

4.3.3.2 WEIGHT LOST BY DISCS ATTACKED BY TERMITES

The data for the weight lost by each disc attacked by termites is given in Appendix B. A summary of the weight of disc wood eaten by termites in each month is given in Table 4.3.2. Subtraction of the control loss (3 g) from the total weight lost sometimes gave a negative estimate of consumption in a month, these figures could have been converted to zeros but preserving the notional negative estimates maintains the correct control loss in the total losses from each transect. The estimated consumption at each of the sites is given in Table 4.3.7.

4.3.3.3 WOOD CONSUMPTION ON QUADRATS AT SITE L

The standing crop of dead wood on each quadrat at site L is given in Table 4.3.3 for each weighing. The changes in standing crop in each period are given in Table 4.3.4 with the estimated wood fall on each quadrat in each period and consumption, estimated by subtraction of the change in standing crop from the estimated fall. These figures are summarised in Table 4.3.5 where the mean and standard error of the consumption estimates in each period are presented, and converted to daily values in Table 4.3.6. The annual consumption was estimated to be 28.3 g m^{-2} wet weight (S.E. 15.6), 22.0 g m^{-2} dry weight (S.E. 13.2). These figures all have very large standard errors, and the annual consumption is not significantly different from the annual consumption estimated at the main experimental site (M).

Table 4.3.1

Weight Lost by Control Discs from the Transects. Discs were Collected in two Months, April, 1977 (A) and December, 1976 (D).

	Transect	Initial wt. g	Final wt.g	loss g.	% loss	Month set	Month coll.	Time Months
A	1	188	186	2	1.06	Feb	A	2
	4	172	171	1	0.58	Feb	A	2
	19	378	364	14	3.70	Jan	A	3
	20	246	246	0	0.00	March	A	1
B	4	172	162	10	5.81	Feb	A	2
	6	282	276	6	2.13	Sept	A	7
	10	211	210	1	.47	Feb	A	2
	11	224	221	3	1.34	March	A	1
	12	188	185	3	1.60	Feb	A	2
	15	209	206	3	1.43	March	A	1
	21	356	340	16	4.49	May	A	11
	26	149	149	0	0.00	March	A	1
	28	327	322	5	1.53	Dec	A	4
D	7	313	310	3	0.96	May	D	7
	15	347	344	3	0.86	Sept	D	3
	21	336	335	1	0.30	July	D	5
	24	176	176	0	0.00	May	D	7
	25	209	208	1	0.48	May	D	7
	1	316	315	1	0.32	March	A	1
	2	250	245	5	2.0	March	A	1
	5	125	123	2	1.6	Dec	A	4
	6	149	144	5	3.36	Jan	A	3
	8	251	251	0	0.00	Dec	A	4
	9	160	157	3	1.87	Dec	A	4
	10	167	166	1	0.60	Dec	A	4
	13	222	220	2	0.9	Dec	A	4
	14	229	227	2	0.87	Dec	A	4
	20	130	126	4	3.08	Dec	A	4
	22	376	379	-3	-0.8	Feb	A	2
	23	116	114	2	1.72	Dec	A	4
	25	430	427	3	0.7	March	A	1

	Transect	Initial wt. g.	Final wt.g.	loss g.	% loss	Month set	Month coll.	Time Months
D cont.	26	187	183	4	2.14	Jan	A	3
	28	119	118	1	0.84	Feb	A	2
	29	101	100	1	0.99	Dec	A	4
E	1	238	236	2	0.84	June	A	10
	4	125	123	2	1.6	March	A	1
	8	135	131	4	2.96	Nov	A	5
	9	169	167	2	1.18	May	A	11
	10	152	152	0	0.0	Feb	A	2
	11	170	169	1	0.59	March	A	1
	15	269	270	-1	-0.37	Jan	A	3
	16	249	250	-1	-0.4	March	A	1
	17	364	354	10	2.75	Feb	A	2
	24	131	127	4	3.05	Feb	A	2
	29	129	122	7	5.43	May	A	11
	30	106	101	5	4.72	Feb	A	2
F	2	411	410	1	0.24	March	A	1
	3	382	375	7	1.83	Jan	A	3
	24	247	245	2	0.81	March	A	1
	25	238	236	2	0.84	March	A	1
	26	319	316	3	0.94	March	A	1
G	5	137	136	1	0.73	March	A	1
	13	102	101	1	0.98	March	A	1
	18	147	147	0	0.0	March	A	1
	20	148	144	4	2.7	Jan	A	3
	21	143	143	0	0.0	Jan	A	3
	23	149	142	7	4.7	May	A	11
	24	247	244	3	1.21	March	A	1
	26	117	116	1	0.85	Jan	A	3
H	2	500	495	5	1.0	Jan	A	3
	3	255	252	3	1.18	Jan	A	3
	6	219	218	1	0.46	Feb	A	2
	7	482	471	11	2.28	Feb	A	2
	13	102	100	2	1.96	Feb	A	2
	14	316	311	5	1.58	March	A	1
	17	309	305	4	1.29	Dec	A	4
	20	227	223	4	1.76	Jan	A	3
	26	282	278	4	1.42	Feb	A	2

Table 4.3.2

Consumption of Transect Discs by Termites in each of Eleven months (g).

Month	Transects							
	A	B	C	D	E	F	G	M
June	76	5	55	-4	57	9	37	-6
July	45	26	66	9	123	52	27	19
August	86	-2	35	0	71	15	16	-1
Sept	21	0	0	3	5	50	15	31
Oct	27	-1	11	1	26	20	0	1
Nov	6	9	40	1	19	6	24	18
Dec	15	3	11	0	27	0	0	16
Jan	82	4	122	-5	69	41	98	11
Feb	19	47	70	20	92	14	-2	30
March	0	22	28	21	45	8	38	1
April	9	14	23	3	28	32	17	13
Total	386	127	461	49	562	247	270	133

Table 4.3.3

Standing Crop of Dead Wood on Quadrats at Site L at each Weighing (g).

Quadrat No.	8.2.76		24.5.76		1.11.76		16.4.77	
	wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry
1	7742	6813	7870	6996	7569	6527	7452	6437
2	4540	3995	4881	4339	5122	4417	5617	4948
3	10771	9478	12219	10863	13005	11214	12325	11050
4	662	583	1145	1018	1175	1013	1083	968
5	10278	9045	10280	9139	9735	8394	9738	8760
6	890	783	930	827	865	746	920	836
7	2327	2048	2890	2569	2720	2345	4995	4414
8	3485	3067	4110	3654	3480	3001	3361	3065
9	8843	7782	9050	8045	9345	8058	6731	6135
10	2375	2090	2505	2227	2730	2354	2070	1896
Mean	5191.3	4568.4	5588	4967.7	5574.6	4806.9	5429.2	4850.9
S.E.	1226.3	1079.1	1265.3	1124.8	1304.2	1124.6	1187.5	1060.4

Table 4.3.4

Calculation of Consumption on Quadrats at Site L in each Period (g).

CS = Change in standing crop; F = estimated fall; C = consumption

Quadrat		Period I		Period II		Period III		Combined Periods		Index 1
		wet	est. dry	wet	est. dry	wet	est. dry	wet	est. dry	
1	CS	+127.5	+183	-301	-469.8	-116.5	- 89.9	-290	-376.7	5250
	F	431.9	368.9	377.0	331.4	71.6	61.2	883.1	763.2	
	C	304.4	185.9	678	801.2	188.1	151.1	1173.1	1139.9	
2	CS	+341	+344.2	+241	+ 77.6	+494	+531.0	+1077	+952.8	3500
	F	394.7	335.5	337.5	296.6	61.8	52.5	796.4	686.2	
	C	53.7	- 8.7	96.5	219	-432.2	-478.5	-280.6	-266.6	
3	CS	+1448	+1384.2	+786	+351.3	-680	-164	+1554	+1571.5	18750
	F	718.8	626.6	681.7	600.0	147.9	128.2	1551.8	1357.1	
	C	-792.2	-757.6	-104.3	248.7	827.9	292.2	- 2.2	-214.4	
4	CS	+483	+435.3	+30	- 4.7	-92	-45.1	+421	+385.5	2500
	F	373.5	316.4	314.9	276.7	56.0	47.5	746.9	642.2	
	C	-109.5	-118.9	284.9	281.4	145	92.6	325.9	256.7	
5	CS	+2	+94.3	-545	-744.6	+3	+366	-540	-284.3	15000
	F	639.1	555.0	597.0	525.4	126.7	109.6	1366.0	1192.2	
	C	637.1	460.7	1142	1270	123.7	-256.4	1906	1476.5	
6	CS	+40	+43.6	-65	-80.9	+55	+90.3	+30	+53	400
	F	328.9	276.3	267.5	234.9	44.2	37.1	642.8	549.8	
	C	288.9	232.7	332.5	315.8	-10.8	-53.2	612.8	496.8	

..../cont'd

7	CS F C	+563 586.0 23	+521.4 507.3 -14.1	-170 540.6 710.6	-223.8 475.6 699.4	+2275 112.5 -2162.5	+2068.2 97.2 -1971	+2668 1242.2 -1426	+2365.8 1082.2 -1283.6	12500
8	CS F C	+625 373.5 -251.5	+587.0 316.4 -270.6	-630 314.9 944.9	-653.1 276.7 929.8	-119 56.0 175	+64.2 47.5 -16.7	-124 746.9 870.9	-1.9 642.2 644.1	2500
9	CS F C	+207 896.2 689.2	+263.6 786 522.4	+295 870.1 575.1	+12.5 766.1 753.6	-2614 195.1 2809.1	-1923.4 169.7 2093.1	-2112 1965.4 4077.4	-1647.3 1724.5 3371.8	27100
10	CS F C	+130 403.2 273.2	+136.9 343.1 206.2	+225 346.5 121.5	+127.1 304.5 177.4	-660 63.9 723.9	-457.7 54.5 512.2	-305 816.2 1121.2	-193.7 703.8 897.5	3900

Table 4.3.5

Mean Consumption on Site L Quadrats (g $25m^{-2}$ $period^{-1}$)

with Standard Errors

Period	Days	wet	est. dry
I	106	117.9 ± 133.5	43.8 ± 118.3
II	160	478.2 ± 126.2	569.6 ± 117.9
III	167	239.0 ± 387.2	36.5 ± 315.0
Combined	433	837.8 ± 462.2	·651.9 ± 392.9

Table 4.3.6

Mean Consumption on Site L Quadrats (g m^{-2} day^{-1})

with Standard Errors

Period	wet	est. dry
I	.045 ± .050	.017 ± .045
II	.120 ± .032	.142 ± .029
III	.057 ± .093	.008 ± .075
Combined	.077 ± .043	.060 ± .036

Table 4.3.7

Site	C. wet g m^{-2} yr^{-1}	C. dry g m^{-2} yr^{-1}	5 year rainfall mean '72-'76 mm	Wood fall dry wt. from Collins (1977b)
A	102.1	82.0	458	50.24
B	33.4	26.8	327	25.74
C	121.3	97.4	496	57.35
D	11.6	9.3	265	14.14
E	147.9	118.7	213	4.42
F	65.0	52.2	236	8.72
G	71.1	57.0	426	44.26
M	35.0	28.1	352	30.42
L	28.3	22.0	320	24.43

Total dead wood consumption at 9 sites, measured directly at sites M (Section 4.2.3.2) and L (Section 4.3.3.3) and indirectly at other sites from weight lost by discs:

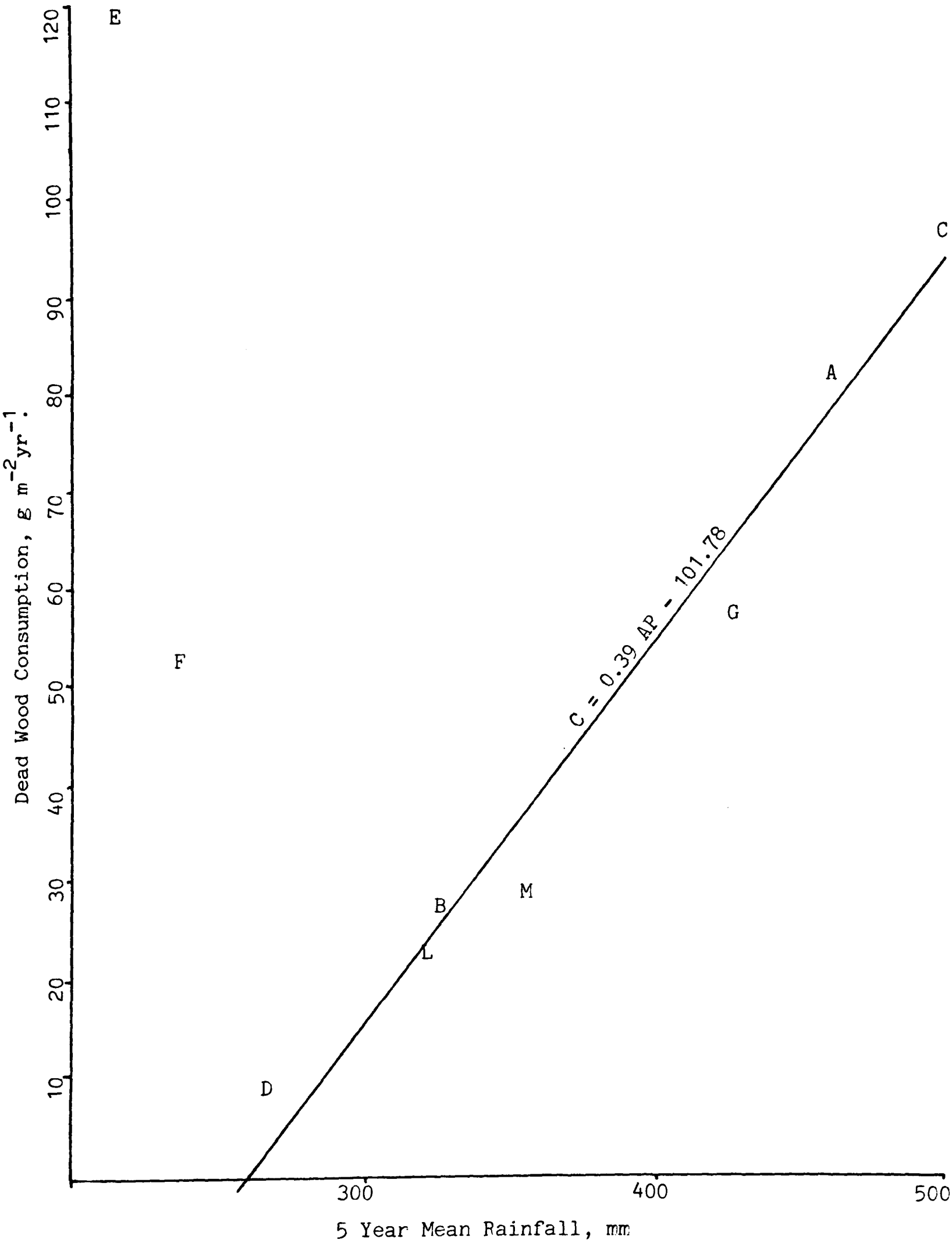
$$\text{Annual consumption site i} = \frac{\text{C Tsct i}}{\text{C tsct M}} \times \text{D at site M}$$

(where C = consumption and D = disappearance)

5 year mean rainfall and estimated dead wood fall.

Figure 4.3.1

The relationship between rainfall and dead wood consumption in Tsavo East. Points E and F are omitted from the regression.



4.3.4 DISCUSSION OF CONSUMPTION FIGURES FOR TSAVO

All the estimates of dead wood consumption at the various study sites are summarised in Table 4.3.7. The five year mean rainfall for each site, as calculated in Section 4.1.2 is also given in the table. Consumption is plotted against rainfall in Figure 4.3.1 and most of the points indicate a strong relationship between the two. The regression equation

$$C = 0.39\ AP - 101.78$$

($r = 0.98$, S.E. of b = 0.033) was obtained from the data omitting points E and F. It has to be borne in mind that these figures are not properly independent estimates of consumption, all except L being derived from a proportional relationship with M. L is also not independent of M because the fall of dead wood onto the quadrats at L was estimated from regressions obtained at site M. This does not invalidate the regression, but it implies that the regression constant in particular is very dependent on one point, M.

In order to accept a relationship between rainfall and consumption based on the points used and omitting points E and F the exaggerated consumption at these points must be explained. It is possible that the general relationship between consumption of wood and rainfall does increase below about 250 mm mean annual rainfall although it is hard to see why this should be so. Most of the soil living termites in Tsavo are opportunists, feeding on grass, dead wood and dung (Sections 3 and 6). Lepage (1974) found that most of the termites in the Sahel Savanna in Senegal were also opportunists, and that the availability of grass and wood were roughly complementary both seasonally, grass having a peak at the end of the rains, wood fall being greatest towards the end of the dry season, and between years, wood fall due to die back of trees being accentuated in drought years when very little grass was produced. So little rain had fallen in sites E and F in the period before my experiments (Table 2.2) that there was no standing grass or grass litter at site E and very little at F. Some grass grew at these sites during

the rains in December 1976, but this stayed green for most of the remaining four months of the experiment. There was dead grassy material available at all the other sites throughout the experiment, although it was often concentrated in small patches not evenly dispersed. Trinervitermes gratiosus was found eating dead wood at site E, the species is a specialised grass feeder and this observation supports the hypothesis that all termites switched to eating dead wood during the experiment. Lepage (1974) observed a similar phenomenon in Senegal.

In Table 4.3.7 estimates are given of dead wood fall at each site calculated from Collins' (1977a) regression of litter fall on annual rainfall (Section 4.2.4.3). There is quite good agreement between estimated wood fall and consumption at sites with rainfall between 250 and 350 mm yr^{-1}, but at higher rainfall consumption is considerably greater than estimated wood fall. It is possible that this actually happened especially if grass was in short supply, and wood fall may have been greater than usual. Alternatively, the index method may have overestimated wood consumption in wetter parts of Tsavo.

The analysis of consumption can be extended to examine differences between different soil and vegetation types. Neither of these qualitative variables is related to consumption of wood as closely as is rainfall. Some points can not be fitted to the rainfall regression, but their explanation should probably be sought in details of the pattern of rainfall, and the grass production dependent on it, not in static features of the habitat.

4.4 DISCUSSION OF CONSUMPTION IN TSAVO IN RELATION TO OTHER STUDIES OF CONSUMPTION BY TERMITES

Wood (1978) has reviewed the few available field estimates of food consumption by termites. Before the present investigation field consumption of dead wood by termites had only been estimated in five studies: Haverty and Nutting (1974, 1975b and c) in an Arizona desert; Lee and Wood (1971b) in South Australian sclerophyll forest; Collins (1977b) in Guinea Savanna in Nigeria; Williams (1973) and Usher and Ocloo (1974), Usher (1975) in Ghana. These estimates were made using a variety of methods which differ in their reliability. Haverty and Nutting (op.cit.) used a simulation method based on weekly field counts of foraging parties of termites on dead wood in 50 m^2 quadrats and lab estimates of activity and feeding rates in relation to temperature. They estimated that the species with the greatest number of foragers on dead wood at any instant, Heterotermes aureus, consumed 7.9 g m^{-2} yr^{-1} of dry dead wood. This was not the species with the greatest instantaneous mass of foragers on dead wood, Paraneotermes simplicicornis had a mean of 13,088 foraging termites ha^{-1} weighing 32.69 g whereas H.aureus had 64,918 foragers ha^{-1} weighing 24.15 g. One other scarce species also attacked dead wood. Consumption was only estimated for H.aureus. Dead wood standing crop was estimated from the weight of wood on each quadrat, mean 212.7 g m^{-2} and wood litter fall on the same quadrats after one year was 45 g m^{-2} yr^{-1}.

Lee and Wood (1971b) estimated consumption of dead wood by Nasutitermes exitiosus as 11.6 g m^{-2} yr^{-1}. They used a field estimate of population density and a laboratory estimate of weight specific consumption at one temperature. There were eight other species of termites in the area most of which attacked dead wood. Wood litter production was estimated at 70 g m^{-2} yr^{-1}.

Williams (1973) and Usher (1975) both used the graveyard method with wooden blocks set in the ground. They used wood from a tree known to be palatable to termites and they worked in the same place, Kumasi in Ghana. Their results are surprisingly different. Williams estimated a consumption of 540 to 1508 g m^{-2} yr^{-1} whereas Usher's estimate was 210 g m^{-2} yr^{-1}. Wood (1978) has pointed out several sources of error in using baiting techniques notably prebaiting to attract termites and encourage population buildup, and subjective assessment of attack rather than measured weight loss. Usher's experiment was run over nineteen weeks without prebaiting, so he probably avoided the problem of a population increase, and his figures show that the rate of consumption did not change during most of his experiment so that the population was probably stable. Usher's figure for consumption is therefore taken to be the most likely one for Kumasi.

Collins (1977b) made the only direct measurements of consumption of naturally occuring dead wood. He measured wood litter production on sixteen 10 x 10 m quadrats which were cleared weekly. Wood fall was estimated at 139.1 g m^{-2} yr^{-1} and standing crop at 282.1 g m^{-2}. A further sixteen 10 x 10 m quadrats were used to estimate consumption. Ten Kg of logs >2 cm diameter and 0.5 Kg <2 cm diameter were placed on each quadrat and weighed at intervals of six weeks. Control logs were suspended above the ground. Consumption of wood litter by termites was estimated as 83.5 g m^{-2} yr^{-1}.

These consumption estimates are summarised in table 4.4.1 together with the rainfall figures for the sites, taken from the Times Atlas when not available from the original work. Estimates of wood litter fall, calculated from Collins (1977a) regression (section 4.2.4.3) when otherwise unavailable, are also given and used to calculate the percentage of fall consumed. Figure 4.4.1 shows consumption (C) (g m^{-2} yr^{-1}) plotted against rainfall (AP) (mm yr^{-1}) and a regression calculated to fit the points has the equation

$$C = 0.14\ AP - 37.7$$

(S.E. of b = 0.031, r = 0.94, N = 5). The regression coefficient of this equation is not significantly different from the coefficient of the equation using only the Tsavo data (section 4.3.4). Both sets of data were combined, omitting E and F of the Tsavo set, giving the regression (figure 4.4.2)

$$C = 0.13\ AP - 12.94$$

(S.E. of b = 0.024, r = 0.91, N = 11). A regression of consumption against wood litter fall (F) (figure 4.4.3) gave the relationship

$$C = 0.93\ F - 30.48$$

(S.E. of b = 0.14, r = 0.97, N = 5). This indicates that the importance of termites as consumers of dead wood declines as total wood fall and rainfall increase.

Table 4.4.1

Independent Estimates of Wood Litter Consumption by Termites in Various Places

Number	Author	Place	Rainfall mm yr^{-1}	Wood fall (F) g $m^{-2}yr^{-1}$	Consumption (C) g m^{-2} yr^{-1}	100 x C/F
1	Haverty and Nutting (1975b)	Arizona	330	45	7.9	17.6
2	Lee and Wood (1971b)	South Australia	300 - 400	70	11.6	16.6
3	Usher (1975)	Ghana	1499	244.9*	210	85.7
4	Collins (1977b)	Nigeria	1175	139.1	83.5	60.0
5	Present Study	Kenya	352	30.8	28.1	91.2

* Calculated from Collins (1977a) regression (section 4.2.4.3)

Figure 4.4.1

Regression of dead wood consumption against rainfall using data from various sites in Africa detailed in table 4.4.1.

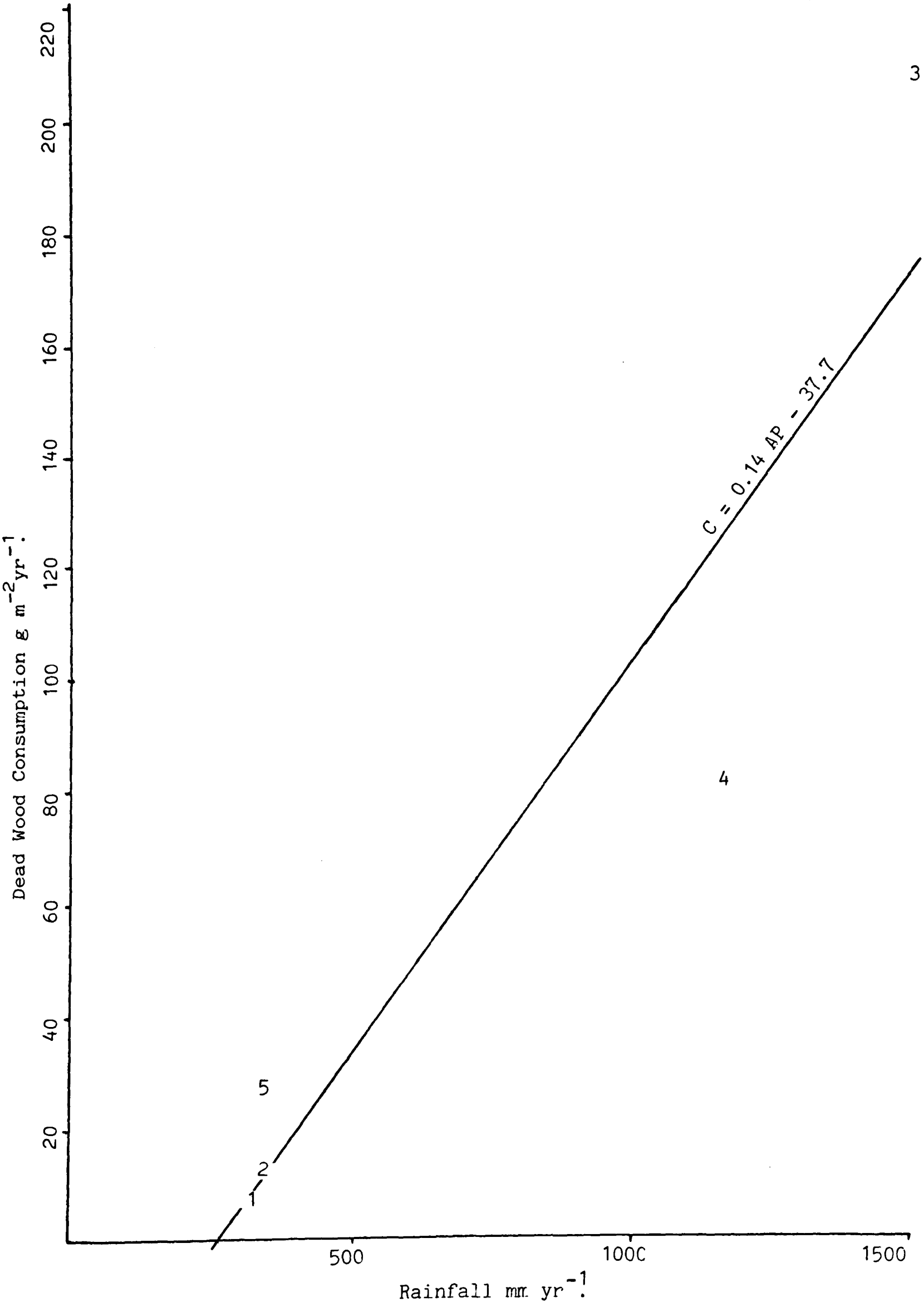


Figure 4.4.2

Regression of dead wood consumption against rainfall using data from the present study and other sites in Africa. Sites E & F omitted.

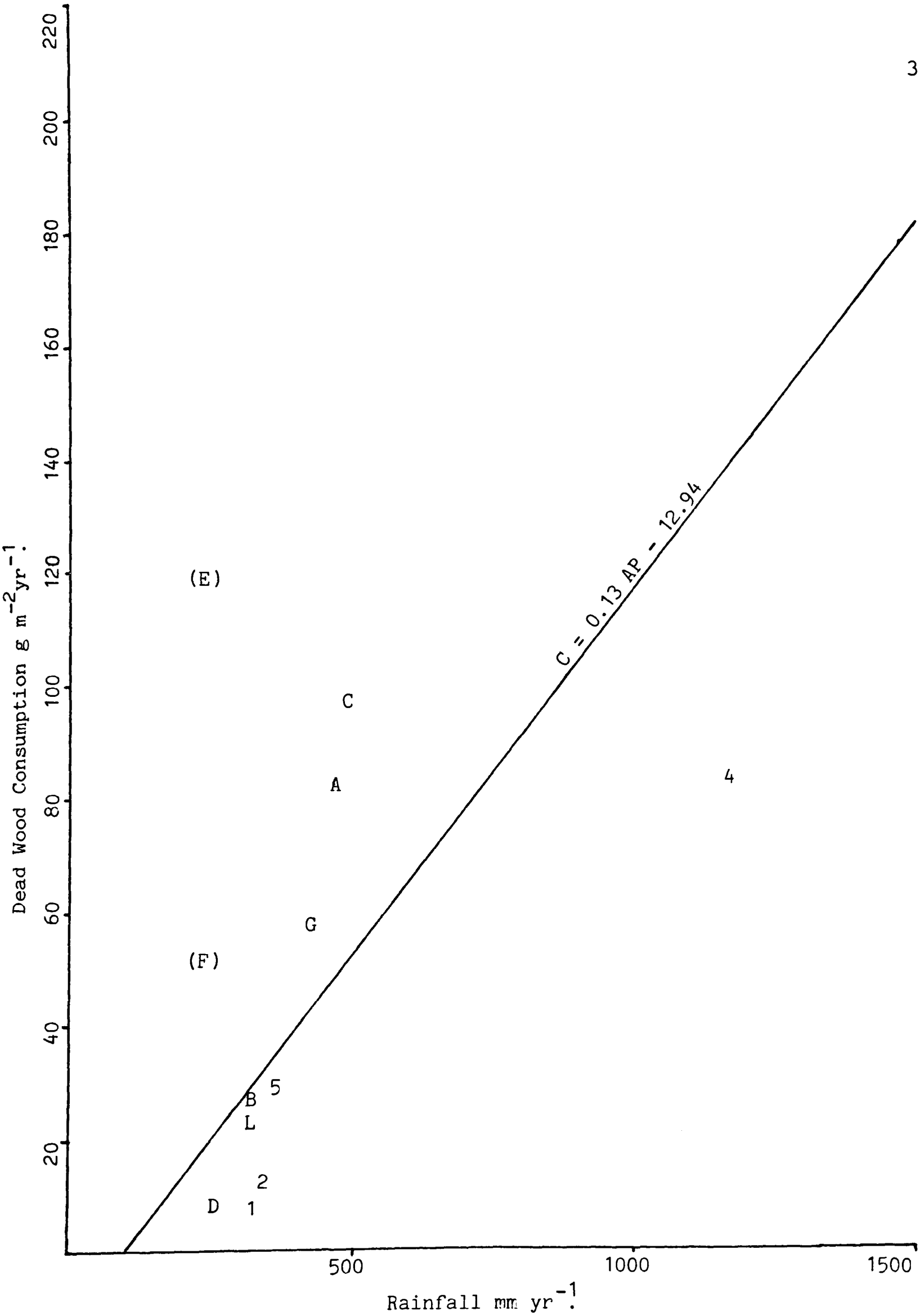
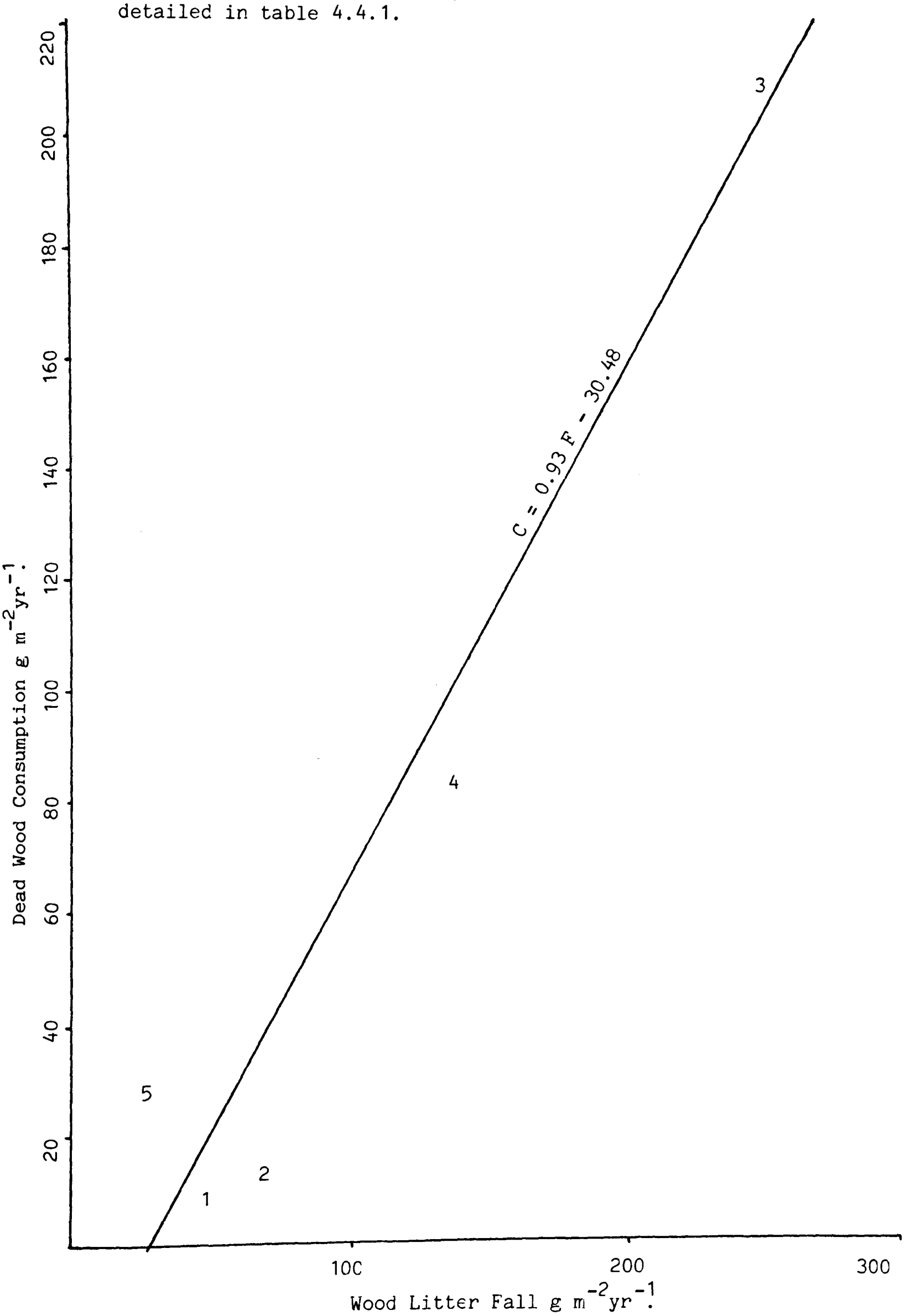


Figure 4.4.3

The relationship between dead wood litter fall and dead wood consumption by termites using data from various sites in Africa detailed in table 4.4.1.



4.5 THE IMPACT OF TERMITE CONSUMPTION ON PRIMARY PRODUCTION COMPARED WITH THE IMPACT OF LARGE HERBIVORES

Earlier in this thesis a predictive relationship between annual rainfall (AP) (mm $yr.^{-1}$) and dead wood consumption by termites (C) (g m^{-2} $yr.^{-1}$) was established (section 4.4)

$$C = 0.13\ AP - 12.94$$

Other workers have demonstrated relationships between rainfall and primary production (Walter, 1954; Whittaker, 1970) and rainfall and total litter fall (Collins, 1977a). Collins summarised the available information on litter fall from woody vegetation (g m^{-2} $yr.^{-1}$) (LF) in Africa and concluded that this was related to rainfall by the regression

$$LF = 0.59\ AP - 111.73$$

On average 68.3% of this production was leaf litter, most of the remaining 31.7% being dead wood. Rosenzweig (1968) instead of using rainfall regressed actual evapotranspiration (AE) (mm $yr.^{-1}$) against net annual above-ground primary production (NAAP) (g m^{-2} $yr.^{-1}$) and obtained the relationship

$$\log_{10} NAAP = 1.66\ (\pm 0.27)\ \log_{10} AE - 1.66\ (\pm 0.07)$$

but he stated that in arid areas where potential evapotranspiration is greater than actual precipitation AE is approximately equal to AP. Coe, Cumming and Phillipson (1976) used this relationship to calculate NAAP for a number of areas in Africa. They took AP = AE when AP $\leqslant$ 700 mm $yr.^{-1}$, and no additional water supplies,such as ground water, were available. They also found that total large herbivore biomass (LHB) (Kg Km^{-2}) was related to rainfall (AP) (mm $yr.^{-1}$) by the equation

$$\log_{10} LHB = 1.685\ (\pm 0.238)\ \log_{10} AP - 1.095\ (\pm 0.661)$$

Large herbivore production (LHP) (Kg Km^{-2} $Yr.^{-1}$) was related to rainfall by the equation

$$\log_{10} \text{LHP} = 1.649\ (\pm\ 0.486)\ \log_{10} \text{AP} - 1.72\ (\pm\ 0.903)$$

and large herbivore energy expenditure (LHE) (KJ h^{-1} Km^{-2}) was related to rainfall by the equation

$$\log_{10} \text{LHE} = 1.683\ (\pm\ 0.397)\ \log_{10} \text{AP} - 0.37\ (\pm\ 1.109)$$

These relationships provide a basis on which consumption by termites can be compared with consumption by large herbivores in dry tropical situations. To do this it was necessary to obtain an estimate of large herbivore consumption from the relationships given by Coe et al. (1976). Weigert and Evans (1967) estimated a production / consumption (P/C) efficiency of 1.5% for wild ungulates in Tanzania. This estimate was based on the energetic values of the plant matter consumed and animal tissues produced. Values for the energetic equivalents of these materials taken from Petrusewicz and Macfadyen (1970) were 4250 cal gm^{-1} for plant tissue and 5750 cal gm^{-1} for animal tissue. This gives a P/C ratio, for Tanzanian ungulates, of 1.1% calculated on the basis of the dry weight ratios of production and consumption. Phillipson (1973) employed a value of P/C of 0.64% based on the dry weight ratio (about 0.86% on an energetic equivalent basis). Using a variety of values for P/C, namely 0.5%, 1.0% and 2.0% the production to rainfall regression of Coe et al. (1976) was used to calculate large herbivore consumption (LHC) according to the equation

$$\text{LHC}\ (g\ m^{-2}\ yr.^{-1}) = \text{LHP} \times \frac{C}{P} \times \frac{1}{1000}$$

The range of values of P/C was used to explore the effect that different large herbivore P/C ratios would have on the relative relationships of consumption by large herbivores and termites.

The various equations used are summarised in table 4.5.1. Table 4.5.2 tabulates the estimates obtained for primary production (NAAP), total litter fall (LF), wood fall (F), large herbivore consumption (LHC) and consumption of dead wood by termites (C) under different mean annual

rainfall regimes. Figure 4.5.1 is a pictorial representation of these data when mean rainfall $\leqslant 800$ mm yr^{-1}. Above this value some of the curves, especially that for primary production, probably lose their approximation to reality (see Coe et al. (1976)).

The proportions of primary production and litter fall consumed by large herbivores and wood eating termites are given in table 4.5.3 and plotted in figure 4.5.2.

This partial model of production and consumption in dry tropical ecosystems has been presented because it provides an order of magnitude comparison between the estimates of dead wood consumption by termites, litter fall and consumption by large herbivores. More data are needed to check on and improve the regressions presented, particularly the regression of consumption by termites against rainfall. An important assumption affects the model, namely that evapotranspiration is equal to rainfall. This is approximately true up to 700 mm annual rainfall, but also depends on regularity of the rainfall, soil type and existing vegetation cover. Van Wijngaarden (in prep.) has found in Tsavo that grass and herb production on similar soils receiving the same amount of rain may vary by a factor of two under different circumstances. The model also assumes that water is not lost by run-off or direct evaporation.

Another problem with the model is that the data on which the separate regression lines were based were collected over different ranges of rainfall. Coe et al. (1976) used data covering the range 165 mm to 1150 mm to calculate their large herbivore regressions. Most of Collins's (1977a) figures were in the range 1175 to 2100 mm with only one less than 1000 mm at 435 mm. Extrapolation of his regression below 1000 mm is supported by the good fit of his lowest point to the regression and by my estimate of dead wood production which is close to that predicted from his regression. All but two of the data points for my regression of consumption of dead wood by termites are below 500 mm rainfall, and the regression does not

Table 4.5.1

Equations Relating Rainfall to Vegetation Production and to Large Herbivore and Termite Consumption

AP = Annual Precipitation; AE = Annual Evapotranspiration; TC = Termite Wood Consumption; LF = Total Litter Fall; F = Wood Fall; NAAP = Net Above-Ground Annual Primary Production; LHP = Large Herbivore Production; LHC = Large Herbivore Consumption; P = Production; C = Consumption.

Author	Regression	Units
Present study	$TC = 0.13\ AP - 12.94$	AP mm $yr.^{-1}$ mean TC g m^{-2} $yr.^{-1}$ dry weight
Collins (1977a)	$LF = 0.59\ AP - 111.73$ $F = 0.317\ LF$	LF and F g m^{-2} $yr.^{-1}$ dry weight
Rosenzweig (1968)	$\log_{10} NAAP = 1.66\ (\pm 0.27)\ \log_{10} AE - 1.66\ (\pm 0.07)$	AE mm $yr.^{-1}$ NAAP g m^{-2} $yr.^{-1}$ dry weight
Coe et al. (1976)	$\log_{10} LHP = 1.649\ (\pm 0.486)\ \log_{10} AP - 1.72\ (\pm 0.903)$	LHP Kg Km^{-2} $yr.^{-1}$ dry weight
	$LHC = LHP \times \frac{C}{P} \times \frac{1}{1000}$	LHC g m^{-2} $yr.^{-1}$ dry weight C/P dry weight ratio

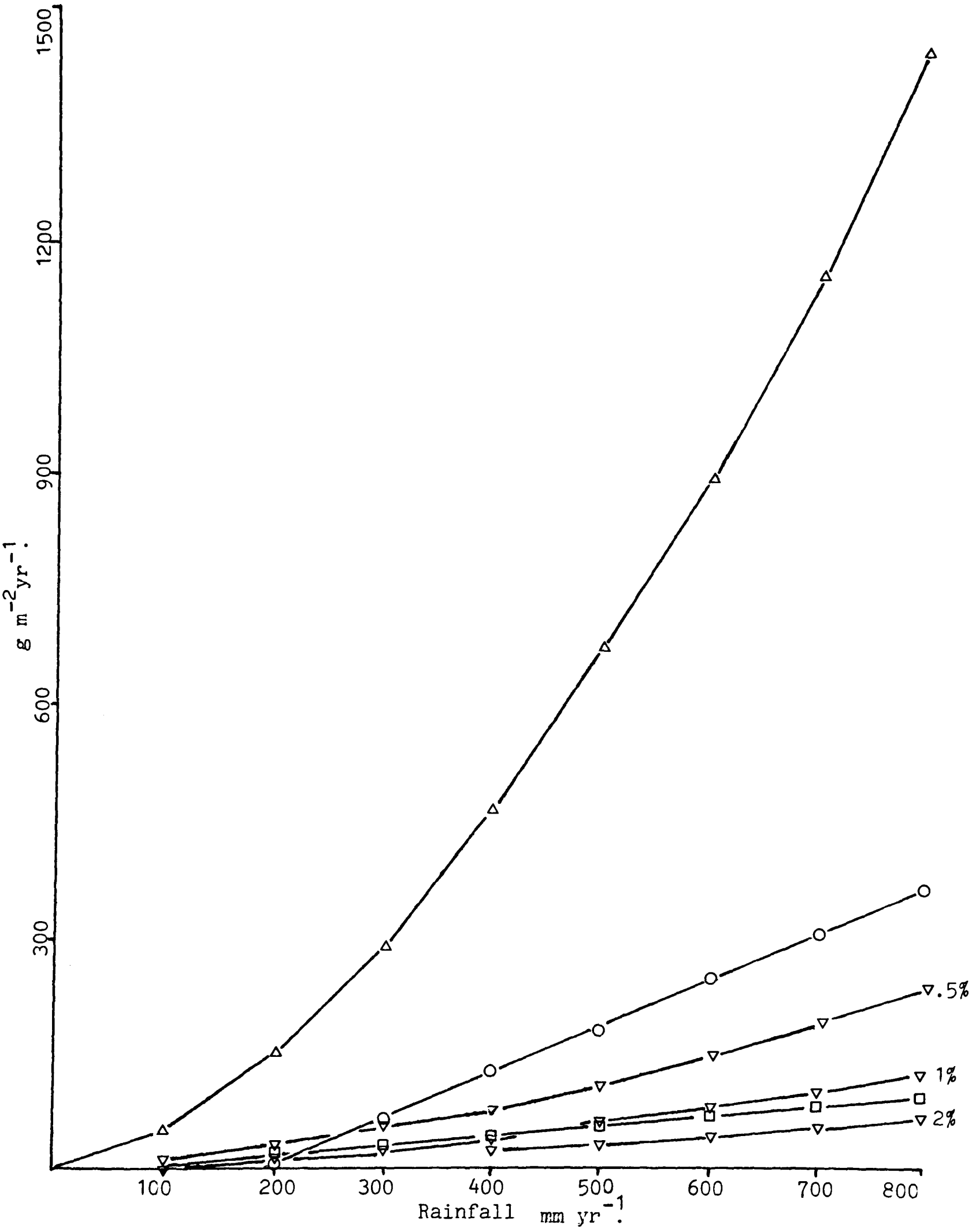
Table 4.5.2

Estimates of Primary Production (NAAP); Litter Fall (LF); Wood Fall (F); Large Herbivore Consumption (LHC) and Consumption of Dead Wood by Termites (C) in relation to Rainfall.

Rainfall mm yr^{-1}	NAAP	LF	F	LHC			C
				P/C .5 %	P/C 1 %	P/C 2 %	
100	45.7	-	-	7.6	3.8	1.9	-
200	144.4	6.3	2.0	23.7	11.9	5.9	13.1
300	283.1	65.3	20.7	46.3	23.2	11.6	26.1
400	456.5	124.3	30.4	74.4	37.2	18.6	39.1
500	661.1	183.3	58.1	107.6	53.8	26.9	52.1
600	894.8	242.3	76.8	145.3	72.6	36.3	65.1
700	1155.7	301.3	95.5	187.3	93.7	46.8	78.1
800	1442.5	360.3	114.2	233.5	116.7	58.4	91.1
1000	2089.3	478.3	151.6	337.3	168.7	84.3	117.1
1500	4095.5	773.3	245.1	658.3	329.1	164.6	182.1
2000	6602.5	1068.3	338.6	1057.9	528.9	264.5	247.1
2500	9562.7	1363.3	432.2	1528.4	764.2	382.1	312.1

Figure 4.5.1

Primary Production and consumption by large herbivores and termites in relation to rainfall.



△ = Primary Production Above Ground.

○ = Total Litter Fall.

□ = Dead Wood Consumption by Termites.

▽ = Consumption by Large Mammal Herbivores (.5, 1 and 2% P/C ratios)

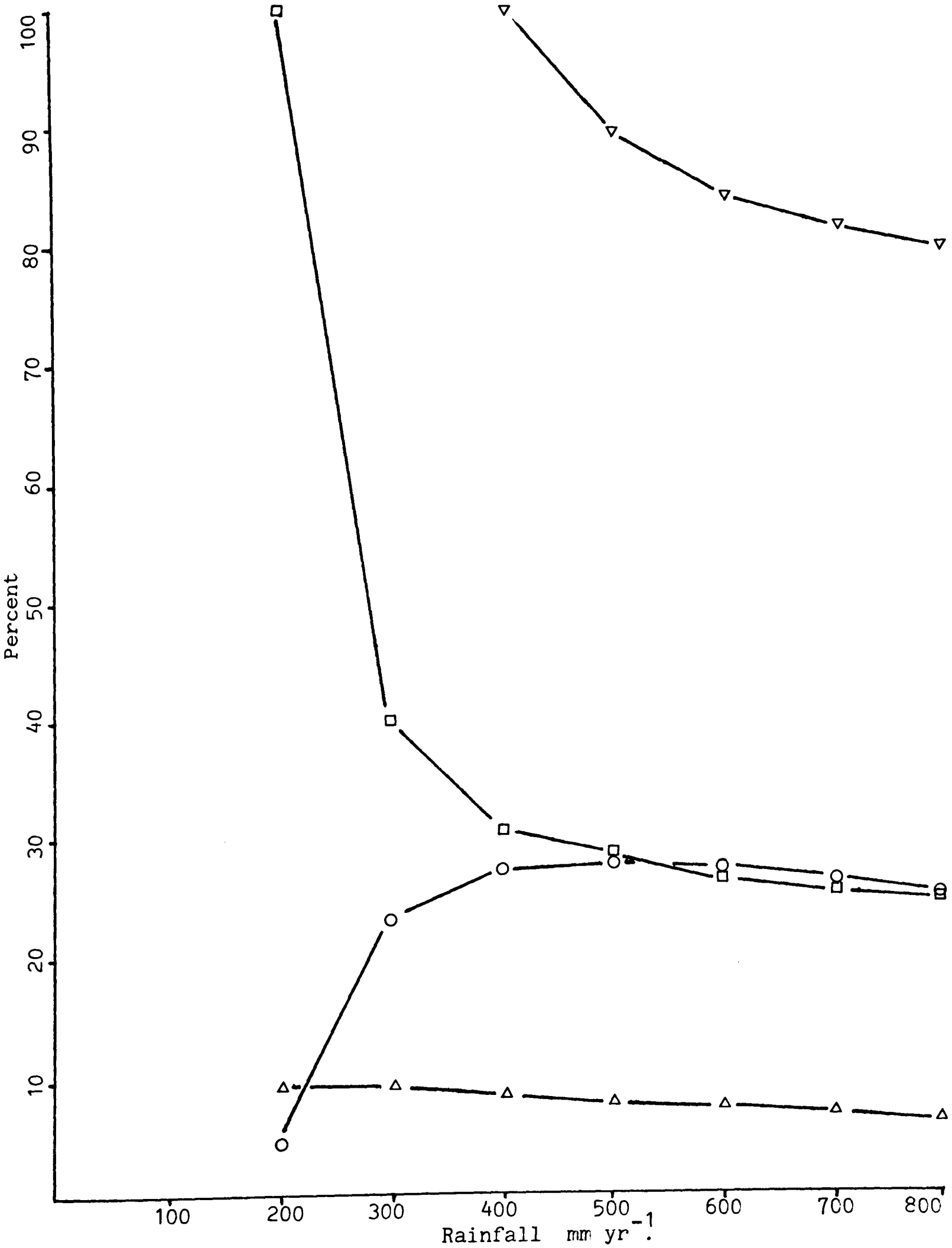
Table 4.5.3

Consumption Estimates as Percentages of Primary Production (NAAP), Total Litter Fall (LF) and Wood Litter Fall (F). LHC = Large Herbivore Consumption, C = Wood Consumption by Termites

Rainfall	$\frac{LF}{NAAP} \times 100$	$\frac{LHC(.5\%)}{NAAP} \times 100$	$\frac{LHC(1\%)}{NAAP} \times 100$	$\frac{LHC(2\%)}{NAAP} \times 100$	$\frac{C}{NAAP} \times 100$	$\frac{C}{LF} \times 100$	$\frac{C}{F} \times 100$
100	-	16.6	8.3	4.2	-	-	-
200	4.3	16.4	8.2	4.1	9.1	(100)	(100)
300	23.1	16.4	8.2	4.1	9.2	40.0	(100)
400	27.2	16.3	8.1	4.1	8.6	31.5	(100)
500	27.7	16.3	8.1	4.1	7.9	28.4	89.7
600	27.1	16.2	8.1	4.1	7.3	26.9	84.8
700	26.1	16.2	8.1	4.0	6.8	25.9	81.8
800	25.0	16.2	8.1	4.0	6.3	25.3	79.8
1000	22.9	16.1	8.1	4.0	5.6	24.5	77.2
1500	18.8	16.1	8.0	4.0	4.4	23.5	74.3
2000	16.2	16.0	8.0	4.0	3.7	23.1	73.0
2500	14.3	16.0	8.0	4.0	3.3	22.9	72.2

Figure 4.5.2

Proportion of total production and of litter fall consumed by wood eating termites.



△ = C / NAAP x 100

□ = C / LF x 100

▽ = C / F x 100

○ = LF / NAAP x 100

fit any of the points particularly well (figure 4.4.2). Some of these points are underestimates of dead wood consumption because only part of the dead wood eating termite fauna was investigated by Lee and Wood (1971a) and Haverty and Nutting (1975b). Total consumption of litter by termites is probably at least double the dead wood consumption in arid localities like Tsavo.

Two tentative conclusions can be drawn from the model. 1) In regions of very low rainfall (< 400 mm yr^{-1}) it predicts that termites are the only decomposers of dead wood, their importance declining as rainfall increases. 2) Consumption of dead wood by termites is similar to consumption of grass and browse by large herbivores over a wide range of rainfall values. When consumption of other materials by termites is also considered they are likely to remove considerably more than the large herbivores.

A large part of the estimated primary production remains unaccounted for by the model. It can be assumed that this is all degraded eventually in one way or another (Slobodkin, Smith and Hairston, 1967). Important herbivores other than large mammals are small mammals, seed eating birds and various invertebrates chiefly insects. Sinclair (1975) found that small mammals took 0.1 and 4.3% of primary production in different habitats in Serengeti, but only about 0.68% for the ecosystem as a whole, but Phillipson (1973) estimated 4.44% for the ecosystem. Seed production by grasses can be a considerable proportion of primary production in tropical ecosystems, most of this production is probably removed by seed eating birds, eg. Quelea quelea (Ward, 1965) and by harvesting ants (Golley and Gentry, 1964). Grasshoppers took 4.1 and 8.1 % of primary production in different habitats in Serengeti (Sinclair, 1975), 6% being the mean figure for the ecosystem as a whole. The remaining production either enters the decomposer system or is burned. Sinclair (1975) estimated that decomposers took 19.2 and 49.5 % of production in different habitats in Serengeti, 32.5% for the ecosystem as a whole, while fire accounted for 53.3 and 12.5 % of production

35.3% for the whole ecosystem. Phillipson (1973) ignored fire and estimated that 85.1% of Serengeti production was removed by invertebrates mainly as detritus. Collins (1977b) found that 31.8% of the wood and leaf litter fall was burned in Southern Guinea Savanna in Nigeria. These figures give a strong indication that the production not accounted for by herbivores or termites in the model presented here is either consumed by other invertebrates or burned, with a small proportion going to birds and small mammals. Much more work is needed on these aspects of tropical ecosystem energetics before they can be incorporated in a general model based on rainfall.

4.6 RELATIVE IMPORTANCE OF DIFFERENT WOOD FEEDING SPECIES OF TERMITES

4.6.1 INTRODUCTION

The importance of any organism in its ecosystem depends partly on its ability to use the energy available in the system for its own production (Wood and Sands, 1978). Different species of termites are adapted to foraging in different ways on different types of food. They have different micro-habitat requirements and different relationships with other organisms. These factors determine their relative efficiencies as energy converters in different habitats. The feeding habits of all the termite species found in Tsavo were discussed in Section 3. Out of the 24 species collected 16 fed regularly on dead wood. These ranged from the arboreal Kalotermitidae, each colony depending on a single dead branch, to the diffuse subterranean colonies of Odontotermes, catholic feeders with ranges covering the whole ground surface. Some species ate more of the wood on the ground surface than others. To measure the relative importance of different species a bait method similar to one described by Collins (1977b) was employed.

4.6.2 METHODS

At the main experimental site (M) a plot of 6000 m^2 was used for bait experiments to measure the relative importance of different species of termites, and to examine their foraging behaviour (Section 5). The plot (100 m x 60 m) was cleared of all moveable dead wood and 714 discs of Commiphora wood were laid out in a 3 x 3 m grid on the surface of the ground. The discs were similar to the ones used for the transect experiments (Section 4.6.2). The experiment was set up in mid April 1976 and all the discs were examined monthly for a year. All inspections were in the middle of the month. Discs with termites were placed in polythene bags, labelled with their grid position and returned to the laboratory for identification, separation and counting of

the termites, cleaning, drying and weighing of the discs. When no termites were found but a disc had been attacked it was examined for characteristic signs left by each termite species and attributed to the species most likely to have left the signs present. Discs showing noticeable signs of consumption were labelled and returned to the laboratory for cleaning, drying and weighing. Discs were replaced beside the old position to avoid confusion of signs made one month with signs made the next month. Occasionally more than one species of termite was recorded as having attacked a bait. The weight loss was then divided between the two species in the ratios of total weight losses of discs attacked by each species of termites singly during the month.

The experiment, designed to make a direct estimate of consumption by wood feeding termites, required that the site be cleared of all dead wood other than the discs. Wood (1978) has summarised the problems of using bait experiments in this way. There is evidence that populations of termites were affected by the experimental conditions, which is not surprising when it is considered that the original standing crop of dead wood of 316.7 g m^{-2} was replaced with 15.1 g m^{-2} of discs distributed completely regularly as opposed to the highly aggregated distribution of the original material (Section 4.4.2). There were indications that the monthly disturbance affected some species of termites. Grid points at which a disc had active termites on it one month were often completely unattacked in the next month. Disturbance may have affected the two species of Odontotermes much more than Microtermes allaudanus or Amitermes lonnbergianus as the latter were much more faithful to the grid points which they attacked. It is impossible with the present data to be certain whether consumption by particular species was seriously affected by disturbance. Termites removed from the discs were usually not very numerous, but estimates of several thousand Microtermes allaudanus on a single disc were frequent and on one occasion 30,000 were collected. This could well have affected the colony population and hence its consumption.

Data collected during the disc transect experiments (Section 4.6.3) also

provided estimates of the relative importance of the different species of termites, assessed directly from the measurements of weight lost by each disc (Appendix B).

4.6.3 RESULTS

The raw data for the bait grid experiment are extremely cumbersome and have not been included in this thesis.

In any one month most of the discs were not attacked and a sample of these was used as a control. The control baits lost a mean of 4.1 g (S.E. 0.277, N = 343) regardless of the length of time they were exposed for or the rainfall during that period. Most of this loss probably occurred during cleaning and drying.

Data for monthly consumption of the discs by each termite species are given in Table 4.6.1. The total consumption by each species over the whole year was divided by the total consumption by all species to give the proportion eaten by each species. The total consumption by all species in each month was divided by the annual consumption to give the proportion of total consumption eaten in each month. Table 4.6.1 shows that consumption fell sharply after the first month of the experiment and never regained a quarter of the April-May level even during the rains in December and January. Thirty six percent of the total consumption occurred in the first month of the experiment. This suggests that the termite population fell due either to a severe shortage of food or to disturbance. This is the inverse situation to most baiting experiments which have been equally invalid as a means of measuring consumption because excess highly palatable food was usually provided leading to an increase in the population (Wood, 1978).

Populations of different species may have been affected in different degrees by the probable food shortage. To examine this possibility it is useful to compare the grid figures with consumption on the disc transect at site M where other dead wood was not removed. Figures for total consumption

of disc wood at each disc transect by each species of termites are given in Table 4.6.2. Transect M was only about 50 m from the bait grid plot. Of the three species which attacked the transect discs, Odontotermes mediocris ate about the same proportion of the total consumption on grid and transect, both O. zambesiensis and Amitermes lonnbergianus ate a higher proportion on the transect. However three species of wood feeding termites were found on the grid but not on the transect, two of these, Synacanthotermes zanzibarensis and Microcerotermes sp.I ate insignificant quantites of wood, but Microtermes allaudanus removed 13% of the total grid consumption which accounts for some of the discrepancy between grid and transect.

Because of the difference between the first month and all others it is difficult to use the data from the grid experiment to estimate the total consumption by each species in each month. It was however considered valid to use the observed proportions of total consumption (table 4.6.1) in conjunction with the annual estimate of total termite consumption of dead wood (28.1 g m^{-2} yr^{-1} dry weight, Section 4.2.3) to estimate the total annual wood consumption by each species. The results are given in Table 4.6.3.

To examine the changes in consumption from month to month some correction must be applied to the April-May figures to make them comparable with the rest. This was a wet period and personal observations of termite activity suggest that the natural rate of consumption in April-May was approximately equal to the rate in December-January. Each of the April-May consumption estimates was therefore multiplied by 522/2199, retaining the original proportions consumed by each species. This is clearly not an ideal procedure and probably leads to an underestimate of consumption by A. lonnbergianus for the first month as consumption by this species only fell later in the year. Consumption of disc wood in each month is shown in the histograms of Figure 4.6.1. The numbers from Table 4.6.1 were used, employing the corrected estimates for the first month.

At the beginning of the grid baiting experiment the standing crop of disc wood was 90,600 g (15.1 g m^{-2}) and 6,076 g (1.01 g m^{-2}) were consumed by termites in the year. This gives a decomposition constant of 6.71% with the wood taking 14.91 years to disappear completely. This is considerably longer than the turnover time estimated from the quadrat experiments at the same site (Section 4.2.3.2) where the dry weight decomposition constant was about 10% per year, 10 years to disappearance for a standing crop of 316.7 g m^{-2}. This provides further evidence that the experimental conditions affected the termite populations to such an extent that consumption fell even more than the proportional decrease in the amount of food available.

The data for consumption of bait wood by different termite species on each of the disc transects (from experiments described in Section 4.3.2) is given in Appendix B. Consumption of the baits by each species of wood eating termite on each transect over the whole eleven months exposure is given in Table 4.6.2. The monthly data for consumption by each species are highly variable for each transect, some species only attacked the baits intermittently indicating that the sample size was too small to measure monthly variations in activity by individual species at the transect sites. At the main experimental site (M) the disc transect sampled only three of the six wood feeding termites present on the bait grid. Two of the additional species ate a negligible amount on the grid but the third, Microtermes allaudanus, was responsible for 13% of the total wood consumption on the grid and its absence from the transect is quite a serious source of error which may also have affected transects B, D, E, F and G.

The monthly consumption of bait wood by all species on the transects is given in Figure 4.6.2. It is important to remember that these results only represent the proportional consumption in each month of an eleven month run, not a whole year. The missing month, April to May, is wet and consumption would have been about 20% of the annual total.

Using the estimates of the total wood consumption at each disc transect site (Table 4.3.7) and the proportion eaten by each species of termite (Table 4.6.2) consumption by each species at each site was calculated. The results are given in Table 4.6.5.

Table 4.6.1

Weight of Bait Wood Consumed each Month by

each Species of Termite on the Grid Plot (6000 m^2) (g).

Month	O. mediocris	O. zambesiensis	M. allaudanus	S. zanzibarensis	A. lonnbergianus	Microcerot-ermes sp.I	Months consumption	Propn. of Total consump. in Month %
A-M	1602	371	146		35	45	2199	36.19
(A-M[1])	(380)	(88.1)	(34.7)		(8.3)	(10.7)	(522)	
M-J	109	156	41	4	23	6	339	5.58
J-J	220	79	58		60	12	429	7.06
J-A	43	59	8		22	8	140	2.30
A-S	91	66	91		24	3	275	4.53
S-O	140	69	36		107	8	360	5.92
O-N	142	69	5		6	2	224	3.69
N-D	308	71	121	10	12		522	8.59
D-J	309	92	103	11	7		522	8.59
J-F	263	66	73		2	19	423	6.96
F-M	64	186	81	4		3	338	5.56
M-A	174	83	37		6	5	305	5.02
Total Consump. by sp.	3465	1367	800	29	304	111	6076	
Propn. of Tot. cons. by sp. %	57.03	22.5	13.17	0.48	5.00	1.83		

1. Corrected estimates for consumption in April-May - see text for details.

Figure 4.6.1

Monthly consumption of bait wood on 6000 m^2 grid at site M analysed by species of termites. Rainfall at HQ is given for the period between each sampling date. Numbers in each column give the percentage of the months consumption due to each species. The corrected estimates were used for April - May.

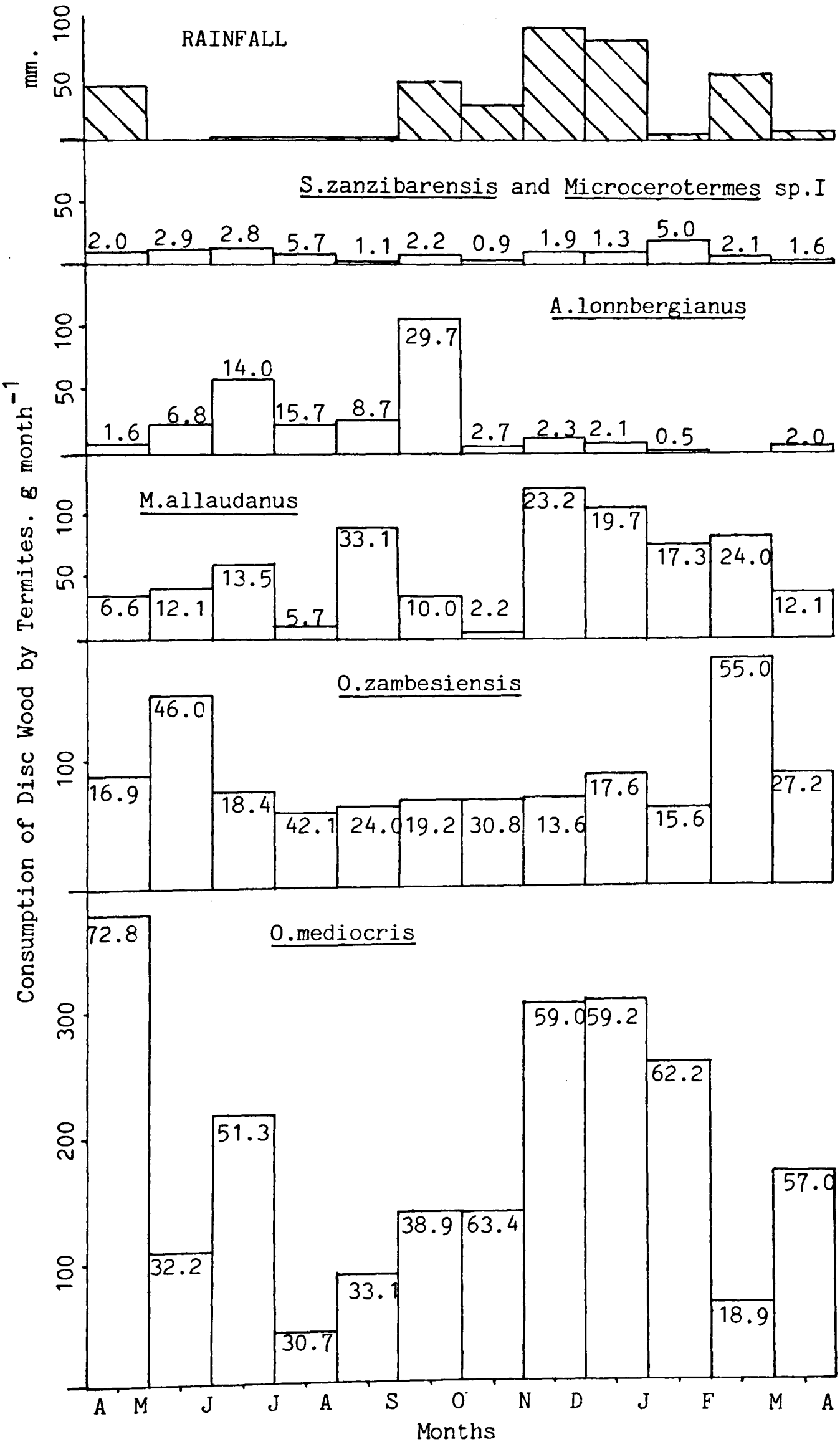


Table 4.6.2

Weight (g) of bait wood consumed on each disc transect over eleven months by each termite species and the proportion of the total for that transect.

	TRANSECT							
Species	A	B	C	D	E	F	G	M
O. mediocris	148 .38	87 .69	176 .38	25 .51	207 .37	173 .7	164 .61	73 .54
O. zambesiensis	119 .31	40 .31	49 .11	23 .47	225 .40	57 .23	106 .39	44 .33
M. allaudanus	40 .1		135 .29		16 .03			
S. zanzibarensis			24 .05					
A. lonnbergianus	30 .08		65 .14		114 .2	17 .07		17 .13
A. sciangallorum			1 .002					
Microcerotermes sp.I	49 .13		11 .02	1 .02				
Total	386	127	461	49	562	247	270	134

Figure 4.6.2

Monthly consumption of bait wood on each disc transect. Rainfall at HQ is given for the period between each sampling date.

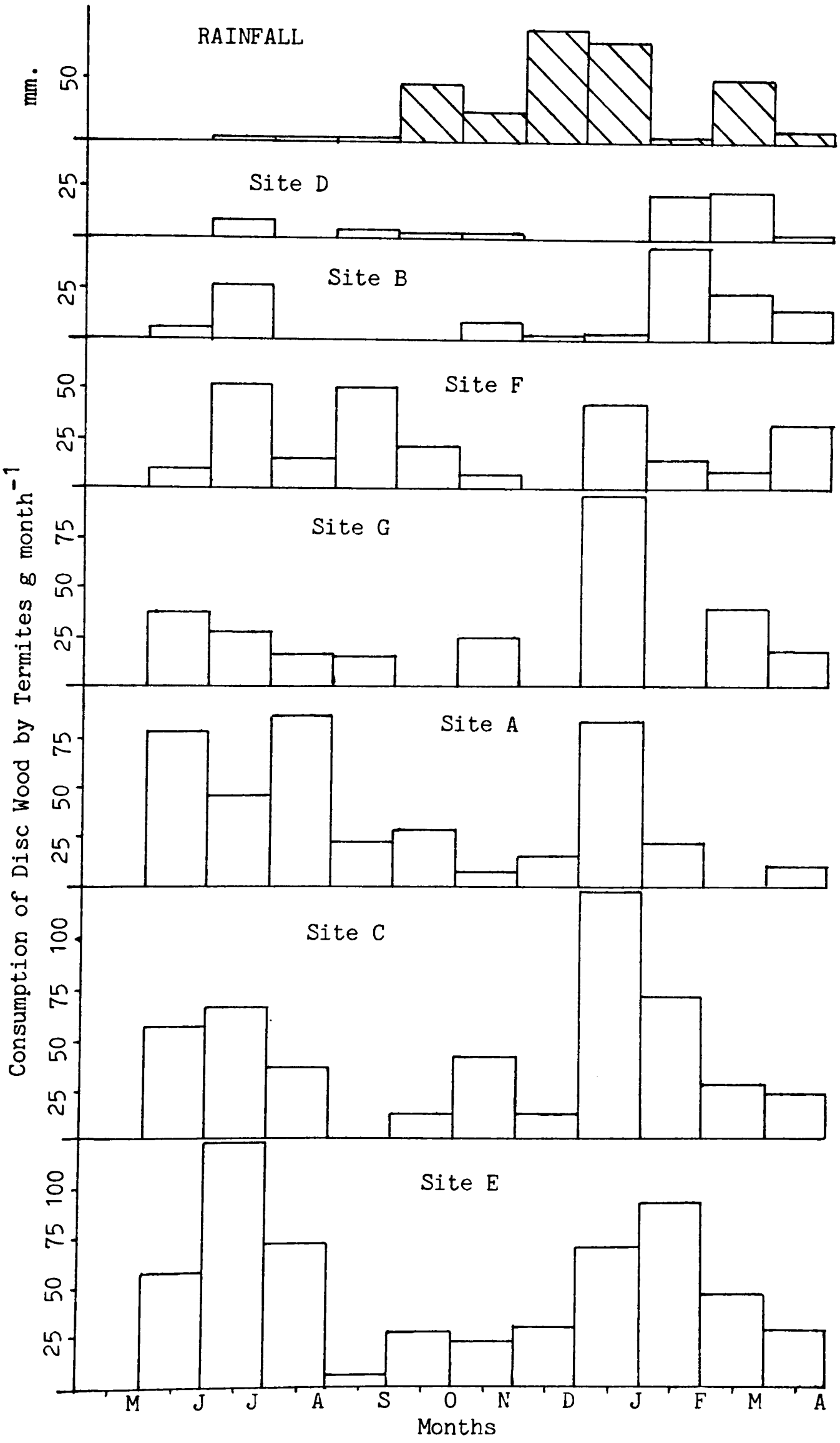


Table 4.6.3

General consumption of dead wood by each species at the main experimental site ($g\ m^{-2}\ yr^{-1}$).

Odontotermes mediocris	O. zambesiensis	Microtermes allaudanus	Synacanthotermes zanzibarensis	Amitermes lonnbergianus	Microceratermes sp.I
16.03	6.32	3.7	0.13	1.4	0.51

Table 4.6.4

Weight of wood consumed in each month by all species of termites on each disc transect (g), and the same expressed as a proportion of the total consumption on the transect.

	A	B	C	D	E	F	G	M
M-J	76 .2	5 .04	55 .12	(-4)	57 .10	9 .04	37 .14	(-6)
J-J	45 .12	26 .2	66 .14	9 .17	123 .22	52 .21	27 .1	19 .14
J-A	86 .22	(-2)	35 .08	0	71 .13	15 .06	16 .06	(-1)
A-S	21 .05	0	0	3 .06	5 .01	50 .2	15 .06	31 .23
S-O	27 .07	(-1)	11 .02	1 .02	26 .05	20 .08	0	1 .01
O-N	6 .02	9 .07	40 .09	1 .02	19 .03	6 .02	24 .09	18 .13
N-D	15 .04	3 .02	11 .02	0	27 .05	0	0	17 .13
D-J	82 .21	4 .03	122 .26	(-5)	69 .12	41 .17	98 .36	11 .08
J-F	19 .05	47 .37	70 .15	20 .28	92 .16	14 .06	(-2)	30 .22
F-M	0	22 .17	28 .06	21 .4	45 .08	8 .03	38 .14	1 .01
M-A	9 .02	14 .11	23 .05	3 .06	28 .05	32 .13	17 .06	13 .10
Total	386	127	461	49	562	247	270	134

Table 4.6.5

Estimated annual consumption of dead wood by each species of termite at each transect site (g m^{-2} yr^{-1})

	A	B	C	D	E	F	G
O. mediocris	31.2	18.5	37.0	4.7	43.9	36.5	34.8
O. zambesiensis	25.4	8.3	10.7	4.4	47.5	12.0	22.2
M. allaudanus	8.2		28.2		3.6		
S. zanzibarensis			4.9				
A. lonnbergianus	6.6		13.6		23.7	3.6	
A. sciangallorum			0.2				
Microcerotermes sp. I	10.7		1.9	0.2			
Total	82.1	26.8	96.5	9.3	118.7	52.1	57

4.6.4 DISCUSSION

The two Odontotermes species O. mediocris and O. zambesiensis were the dominant termites in all the sites examined in the study area, being responsible for at least 50% of dead wood consumption and probably equally important as consumers of grasses and other litter except in the few places where Macrotermes subhyalinus was abundant. O. mediocris was more voracious than O. zambesiensis and its foraging activities reached almost all parts of the ground surface at the main site (M) (Section 5). Foraging by O. zambesiensis was more restricted and seemed to be more faithful to particular bait locations. The very high estimate of consumption at transect site E was partly due to a colony of O. zambesiensis which attacked the same bait position very heavily for several months. There was an interesting difference between the two Odontotermes species in their response to seasons (Figure 4.8.1). O. mediocris showed strong peaks of activity in the rains, with bait wood consumption on the grid six times its minimum dry season level. On the other hand O. zambesiensis showed no increase during the main rains from November to January and peak consumption in the March rains was only two and a half times the minimum consumption. Either the populations of O. mediocris fluctuated much more than those of O. zambesiensis or they used a much wider range of foods, the alternatives to dead wood having their peak availability in the dry season. At the start of the rains all soft litter decomposed very quickly and the new growth of green grasses was generally ignored by all termites except the harvesters, Trinervitermes spp. By the end of the rains there was a considerable quantity of dead grasses and other soft litter which was attacked by both species of Odontotermes as well as being food for ungulates, Orthoptera, other termites etc. Through the dry season this food source dwindled and became increasingly patchily distributed. The very extensive foraging pattern of O. mediocris is well adapted to locating and exploiting such scattered patches of food, whereas the more restricted

activity of O. zambesiensis is much better suited to the prolonged exploitation of reasonably reliable food sources such as logs, or the steady fall of litter from single trees. These indications of different dietary preferences help to explain the coexistence of the two species of Odontotermes when there is every indication that their habitat requirements are otherwise similar and very broad.

Microtermes allaudanus was only recorded from four sites, the three sites at which total consumption of wood by termites was estimated to be highest, A, C and E and the main site (M) where the only colony was in the bait grid plot and confined to ground under a large tree. This species is clearly best adapted to woodland habitats like site C where it consumed 135 g, 29% of the disc wood eaten, and the relatively large sticks and logs it prefers are abundant. The presence of M. allaudanus at site M and the very dry site E suggest that it probably lives in any habitat with dense enough shade. Despite the low rainfall the vegetation at site E was dominated by tall bushes such as Premna resinosa and Strychnos decussata which would provide such shade. The only sites without suitable shade plants were B and F and there were very few at D. In West Africa Microtermes spp. show highly seasonal foraging, with intense activity in the rains and almost no foraging at the ground surface for most of the dry season (Wood and Johnson, in press). This does not appear to be the case in Tsavo although the long dry season is much longer and rainfall lower than in these West African sites. Activity of M. allaudanus certainly followed the pattern of the rains, but there was also considerable activity in August, before any rain had fallen. The climate of Tsavo is unpredictable, and in order to survive at all the Microtermes spp. present there may need to be able to forage when conditions are very dry because they can not rely on rain falling before all their reserves of fungus comb have been used up.

Amitermes lonnbergianus was almost universal in Tsavo East, but it was usually patchily distributed and preferred large food sources such as logs

(Section 3.3). It almost certainly occurred in sites B, D and G although it was not found on the bait discs. The species was usually not very important as a consumer of surface dead wood, but Figure 4.6.1 reveals that consumption of surface wood by A. lonnbergianus increased steadily through the dry season and fell sharply after the rain began in September-October, the peak consumption being in this month. This implies that an alternative food source became available and since Amitermes spp. are not grass feeders, but do attack rotting wood (Wood, 1976), the implication is that they turned to rotting wood such as dead roots in the ground as their main food. The availability of rotting wood is presumably confined to the time when the soil is moist, and declines during the dry season forcing the species to forage on sound wood.

The remaining species which attacked the grid bait discs were Synacanthotermes zanzibarensis and Microcerotermes sp. I; they are combined in Figure 4.8.1 as neither species ate very much of the wood. Microcerotermes sp. I ate 1.83% of the total consumption, activity appears to have declined slightly through the dry season and then it ate nothing during the two main months of the rains. It is quite likely that as with Amitermes lonnbergianus it turned to feeding underground on rotting material, dead roots etc. Active S. zanzibarensis were only found a few times on the grid discs, mainly during the rains. The signs left by this species are almost identical to those produced by Odontotermes mediocris and were recorded as O. mediocris probably leading to an underestimate of consumption by S. zanzibarensis and the seasonal peak may be spurious. Microcerotermes sp. I was widely distributed in Tsavo, its above ground foraging activity was usually concentrated on large logs and dead trees. Attacks on baits were highly predictable, and were almost all at the same bait locations month after month. The species probably occurred in all the habitats sampled by the bait method, but was only important in habitats where there were a lot of large pieces of dead wood. S. zanzibarensis was never common and had a distribution restricted to the west of the study

area; it probably occurred at site A although it was not recorded there.

The seasonal distribution of foraging at each transect site is given in Table 4.6.4 and plotted in Figure 4.6.2. Rainfall at H.Q. is also plotted in Figure 4.6.2. Foraging at all transect sites followed the same broad seasonal pattern with consumption declining throughout the long dry season and having a strong peak in the December rains. Rainfall for each site was discussed in detail in Section 4.1.2; it did not follow exactly the same pattern at all sites that it followed at H.Q., but the general form was similar and clearly consumption and rainfall were always related. Despite the clear seasonal peaks of foraging coinciding with rainfall there was still very considerable activity during the long dry season at most sites, often fluctuating strongly from month to month. Bouillon (1970) suggested that seasonal fluctuation in termite foraging activity increases as climatic variability increases. This is probably true when the climate is reasonably predictable, but the predictability of rainfall tends to fall as rainfall declines and seasonality increases. The termite species which are most successful in Tsavo are the ones which are not completely dependent on regular rainfall and can feed even on the dry material left in the dry season, and under very strong drying conditions. For instance Microtermes allaudanus in Tsavo was less seasonal than the Microtermes spp. studied by Collins (1977b) at Mokwa, Nigeria.

The Macrotermitinae, Odontotermes, Microtermes and Synacanthotermes, were responsible for at least 80% of total dead wood consumption in all the habitats examined in Tsavo. Collins (1977b) and Wood (1976) discussed the role of Macrotermitinae in tropical ecosystems, and concluded that they are numerically the dominant termites in drier ecosystems, but are replaced by lower groups and soil feeders in rain forest. In rain forest fungal and bacterial decomposition occurs rapidly making the litter a viable food source for lower termites and reducing the competitive advantage of the Macrotermitinae. A lot of the food collected by the Macrotermitinae is dissipated by the fungal

metabolism giving the group a higher weight specific consumption than other termites (Wood, 1978). This also contributes to the reduced advantage in rain forest as the Macrotermitinae must forage more intensively than other species, and they are most exposed to predators, especially ants, when they are foraging (Longhurst, 1978).

SECTION 5

TEMPORAL AND SPATIAL PATTERNS IN FORAGING ACTIVITY

5.1 INTRODUCTION

Termite activity varies with time in two ways, from hour to hour and from season to season. These variations are related to physical conditions, temperature, moisture and relative humidity (Bodot, 1967b; Collins, Haverty, LaFage and Nutting, 1973; Haverty, LaFage and Nutting, 1974; Haverty and Nutting, 1974), to changes in the food supply (Lepage, 1974; Wood, 1978) and to changes in colony composition, especially the production of alates (Bodot, 1969). For the establishment and survival of colonies given species require particular conditions, mainly related to soil, moisture and vegetation (Lee and Wood, 1971b; Bodot, 1967a). The distribution of specific conditions determines the overall occurrence of a species in a given area. The spatial pattern within suitable sites depends on the dispersion of suitable food sources in the habitat, which may lead to an aggregated distribution of foraging (Haverty and Nutting, 1975c) although competition between colonies of mound building termites can result in an over-dispersed pattern of mounds (Wood and Lee, 1971).

A variety of ways of measuring foraging activity were tried out at the main study site (M) using the grid of wooden disc baits described in section 4.6. The purpose of these studies was to try to measure the number of colonies of each termite species occuring in a given area, to assess seasonal fluctuations in foraging activity and to see how the available resources were divided up between the species present.

5.2 METHODS

Fluctuations in the foraging activity of termites were assessed from monthly changes in the numbers of termites found on wooden discs used for the grid experiment at site M (section 4.6), changes in the total number

of discs attacked, the number of foraging parties present on the sampling day and the amount of wood eaten in the month (section 4.6).

Each grid and transect disc which had termites on it at the monthly sampling was returned to the laboratory in a labelled polythene bag. The termites were separated and counted using a range of methods depending on the number, size and activity of the termites and the amount of soil present. An effort was made to keep the termites alive during separation, they were collected in labelled petri dishes and supplied with a piece of moist filter paper.

It was usually quicker to separate termites from soil and then count them than to try to sort and count at the same time, even when the sample was small. Large samples had to be subsampled for counting and the very different densities of termites and soil particles prevented random sub-sampling of the mixture so sepatation was essential.

Separation of termites and soil from the wooden disc was achieved by tapping the disc with a hammer over an enamel dish. Sometimes the disc had to be fragmented to extract all the termites, especially Microcerotermes sp.I. Hand sorting with forceps was only possible when numbers were small and was most efficient for large termites. A final hand sorting was also done on samples separated in other ways. Sometimes there was little soil on a disc or it could be scraped away leaving the termites on the wood and they were collected free from soil using an aspirator. At other times the termites were completely mixed with a large volume of soil and the extraction technique employed depended on whether they were alive or dead. Live termites would wriggle out of the soil and if the mixture was placed at the top of a sloping dish the termites rolled down the slope and could be collected relatively free from soil at the bottom. Dead termites in a large volume of soil were allowed to dry out, they would then "float" to the surface when the mixture was shaken and could be removed using an aspirator and sucking gently to produce an air flow strong enough to carry the termites but not

the soil. This technique can be mechanised, for instance electric vibrators and a vacuum cleaner have been used to separate plant debris from soil (Clark, 1977). A dust trap was added to the oral aspirator to prevent inhalation of fine soil particles (figure 5.1).

Samples of up to about 500 termites were counted complete under a binocular microscope, and were separated into castes. Larger samples were subsampled as randomly as possible to give initially four, later five, subsamples of 100 - 200 termites each. These were weighed and counted and the remaining termites were weighed. The total collection was estimated by proportionality from the subsamples. This technique usually gave reasonably accurate estimates of the total numbers, checked by total counts, but very often the estimate of the numbers of rare castes such as soldiers was very poor and had very wide confidence limits.

5.3 RESULTS

The total number of termites of each species found foraging on wooden discs are given for each month in table 5.1 together with the total numbers of discs attacked by each species and the numbers of foraging parties found on the sampling day. The weight of disc wood consumed by each species in each month is taken from section 4.6 (table 4.6.1). All these results are plotted on $\log_{10}$ scale in figures 5.2 to 5.7. Rainfall at the research station, 10 Km to the West, is also plotted for the periods between each sampling occasion.

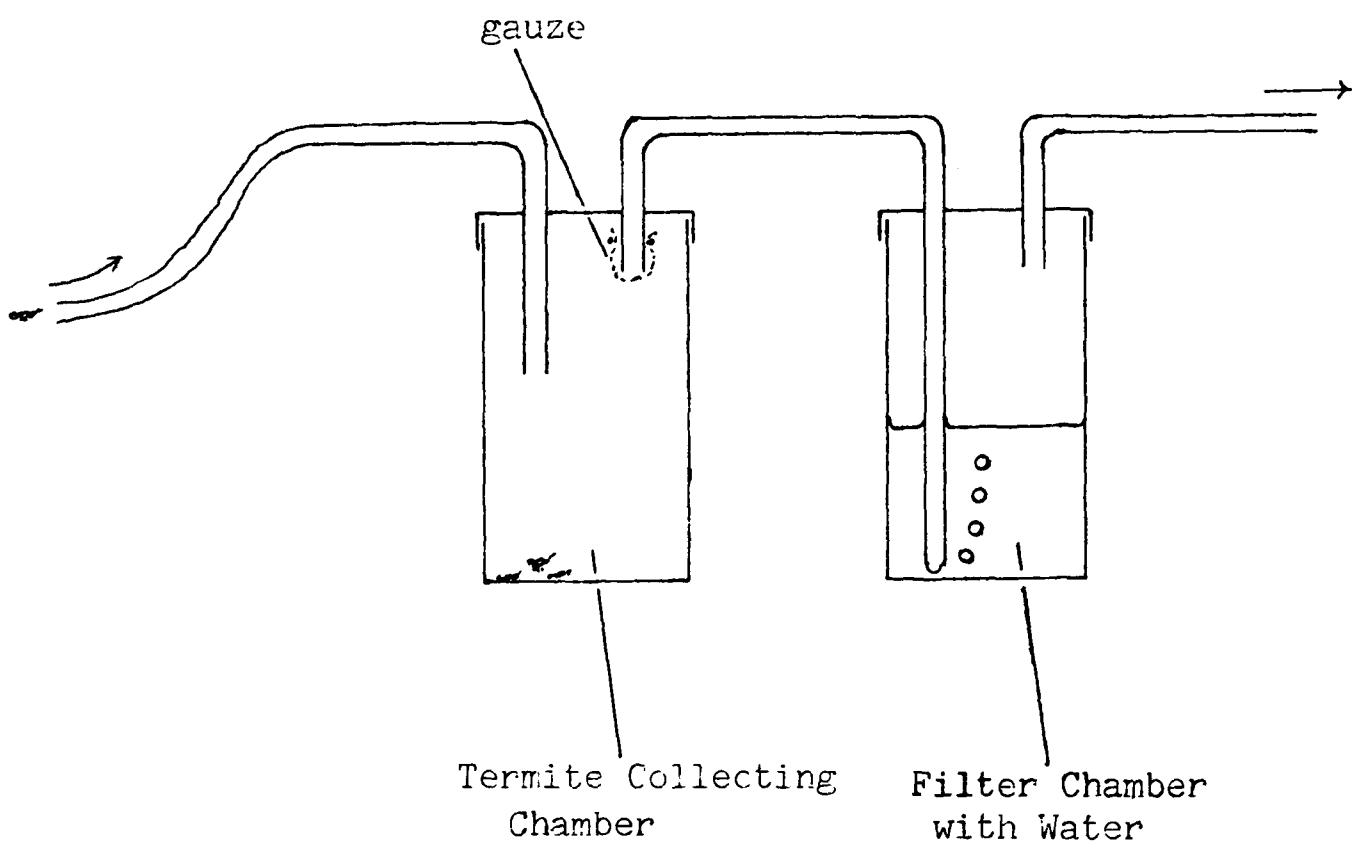
The above figures were all obtained independently. Two indications of foraging strategy can be derived from them. The mean number of termites in a foraging party (f.p.) in each month is given by

$$\text{Mean no. in foraging party} = \frac{\text{Total no. of foraging termites}}{\text{No. of f.ps.}}$$

These figures are included in table 5.1. The mean duration of attack on a particular food item (wooden disc) is given by

Figure 5.1

Diagram of a modified aspirator used for separating dead termites from dry soil. The air was filtered through water to remove dust.



$$\text{Mean duration of attack} = \frac{30 \times \text{no. of f.ps. at sampling}}{\text{total no. of discs attacked in month}}$$

These figures are included in table 5.1 . They suffer from the limitation that 30 days is the longest period of foraging they can indicate and some species foraged continuously at the same point for much longer than this.

The results of the different measures of activity given in table 5.1 and figures 5.2 to 5.7 can be used to make a number of deductions about the feeding strategies of each species. Four factors are likely to have influenced the results obtained. 1) Experimental errors including incorrect attribution of attacks and inadequate sampling. The results for Synacantho-termes zanzibarensis are probably badly affected by both these sources of error. 2) Seasonal changes in population size produce synchronous fluctuat-ions in all the measures of activity. 3) Seasonal changes in the food materials eaten may also produce synchronous fluctuations in all the activity measures, but not necessarily in phase with 2. 4) Seasonal changes in foraging pattern, including changes in the area over which food materials are attacked by members of a given colony, changes in the time of day when foraging occurs and variations in the period over which any one food source is attacked.

The Macrotermitinae usually showed synchronous fluctuations in wood consumption, the numbers of foragers, the number of foraging parties and the number of discs attacked. Peak activity usually occurred in the rains. This pattern is however broken particularly by Microtermes allaudanus which has a peak in the number of foraging termites in the long dry season when the numbers of foraging parties and discs attacked are at a minimum. Activity of Amitermes lonnbergianus (figure 5.6) and Microcerotermes sp.I. (figure 5.7) was greatest in the long dry season and fell during the rains implying an alternative source of food. These results will be discussed species by species in section 5.4.

The spatial pattern of foraging was examined by recording the number

of months in which each bait location on the grid was attacked by each species of termite. These attack frequencies have been plotted on transparent material (figures 5.8 to 5.11) so that the distribution of the foraging areas of each species can be readily compared with the other species. The frequencies were analysed using the General Purpose Contouring Program published by Calcomp and available on file at the Oxford University Computing Centre. The programme produced maps of the dispersion of the foraging frequencies of three species, Microtermes allaudanus (figure 5.9), Odontotermes zambesiensis (figure 5.10) and O.mediocris (figure 5.11). These were plotted onto the same figures as the attack frequency data. The original maps were visually baffling many of the contours were therefore omitted in the figures. The 5 and 10 frequency contours were retained for M.allaudanus all contours were kept for O.zambesiensis and the 3 and 5 contours for O.mediocris. The decision as to which contours to retain was arbitrary and based on visual grouping of the numerical data. Three species, Synacanthotermes zanzibarensis (S), Amitermes lonnbergianus (A) and Microcerotermes sp.I. (M) were too infrequent for mapping to clarify the distribution of foraging. The attack frequencies for these three species are given in figure 5.8.

Table 5.1

Seasonal Fluctuations in Termite Activity at the Main Experimental Site (M) as measured by: 1) The consumption of dead wood (table 4.6.1); 2) The total number of foraging termites collected at the monthly sampling; 3)The number of discs attacked in the month and 4) The number of foraging parties (f.ps.) collected. The mean duration of attack was calculated from

$$\text{Mean duration} = \frac{\text{No. of f.ps. at sampling} \times 30}{\text{Total no. of discs attacked}}$$

	Total no. of foragers	No. of discs attacked	No. of f.ps. collected	Mean no. in f.p.	Mean duration of attack (days)
		Odontotermes mediocris			
M	2116	241	23	92	2.9
J	1136	132	4	284	0.9
J	3526	139	12	294	2.6
A	566	92	6	94	2.0
S	221	72	3	74	1.2
O	691	221	9	77	1.2
N	344	134	2	172	0.4
D	1877	353	19	99	1.6
J	3345	274	17	197	1.9
F	1678	144	5	336	1.0
M	1357	113	9	151	2.4
A	1770	121	24	74	6.0

Table 5.1 (cont.)

	Total no. of foragers	No. of discs attacked	No. of f.ps. collected	Mean no. in f.p.	Mean durat-. ion of attack (days)
		Odontotermes zambesiensis			
M	1117	24	10	112	12.5
J	168	46	4	42	2.8
J	0	13	0	0	-
A	33	23	2	16	2.6
S	202	10	4	50	12.0
O	81	31	3	27	2.9
N	0	10	0	0	-
D	669	29	5	134	5.2
J	818	24	4	204	5.0
F	39	38	1	39	0.8
M	598	27	8	75	8.9
A	160	24	4	40	5.0
		Microtermes allaudanus			
M	7335	26	18	407	20.8
J	12079	8	7	1726	26.2
J	18769	2	1	18769	15.0
A	0	1	0	0	-
S	30104	3	2	15052	20.0
O	7889	15	10	789	20.0
N	2539	4	3	846	22.5
D	12738	24	21	607	26.2
J	13686	25	19	720	22.8
F	13657	6	4	3414	20.0
M	16734	17	14	1195	24.7
A	6034	10	10	603	30.0

Table 5.1 (cont.)

	Total no. of foragers	No. of discs attacked	No. of f.ps. collected	Mean no. in f.p.	Mean durat-. ion of attack (days)
		Synacanthotermes zanzibarensis			
M	0	0	0	0	-
J	143	1	1	143	30.0
J	0	0	0	0	-
A	51	1	1	51	30.0
S	0	0	0	0	-
O	0	0	0	0	-
N	0	0	0	0	-
D	1216	1	1	1216	30.0
J	4805	3	2	2402	20.0
F	0	0	0	0	-
M	2267	3	3	756	30.0
A	206	2	2	103	30.0
		Amitermes lonnbergianus			
M	953	11	9	106	24.5
J	3227	3	3	1076	30.0
J	3759	4	3	1253	22.5
A	3827	3	3	1276	30.0
S	4035	4	2	2017	15.0
O	2077	7	7	297	30.0
N	2124	4	4	531	30.0
D	1416	7	5	283	21.4
J	755	4	3	252	22.5
F	393	2	1	393	15.0
M	281	1	1	281	30.0
A	298	2	2	149	30.0

Table 5.1 (cont.)

	Total no. of foragers	No. of discs attacked	No. of f.ps. collected	Mean no. in f.p.	Mean duration of attack (days)
		Microcerotermes sp.I.			
M	5296	2	2	2648	30.0
J	2445	3	2	1222	20.0
J	2159	4	3	720	22.5
A	3057	3	2	1528	20.0
S	2003	3	3	668	30.0
O	2787	2	2	1393	30.0
N	1533	1	1	1533	30.0
D	0	0	0	0	-
J	0	0	0	0	-
F	1448	1	1	1448	30.0
M	1515	2	1	1515	15.0
A	1020	1	1	1020	30.0

Figure 5.2

Seasonal fluctuations in foraging activity of Odontotermes mediocris at site M.

1) Consumption of dead wood. 2) Total number of foragers collected
3) Number of foraging parties. 4) Number of discs attacked.
5) Mean number in foraging party.

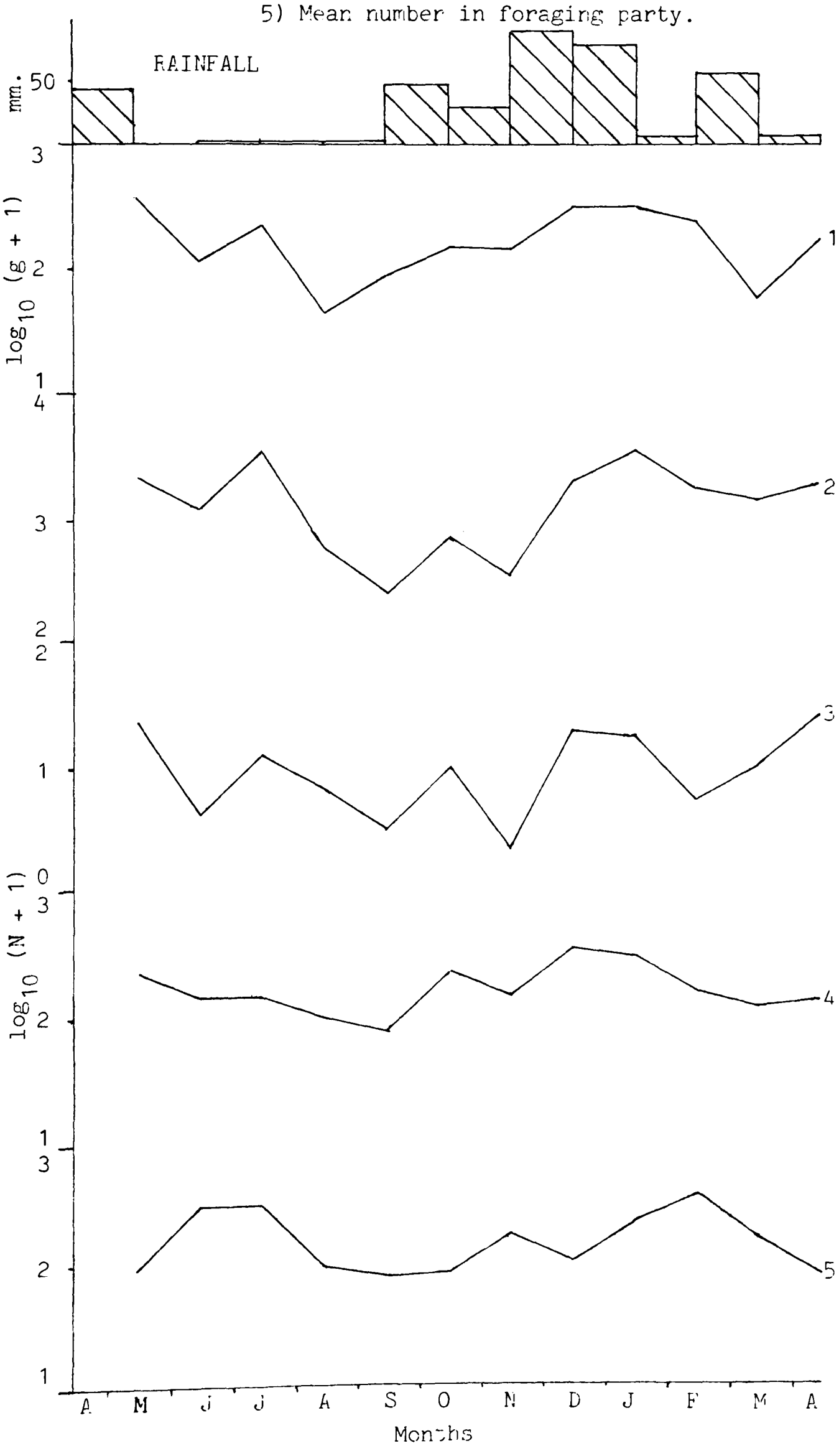


Figure 5.3

Seasonal fluctuations in the foraging activity of Odontotermes zambesiensis at site M.

See figure 5.2 for key.

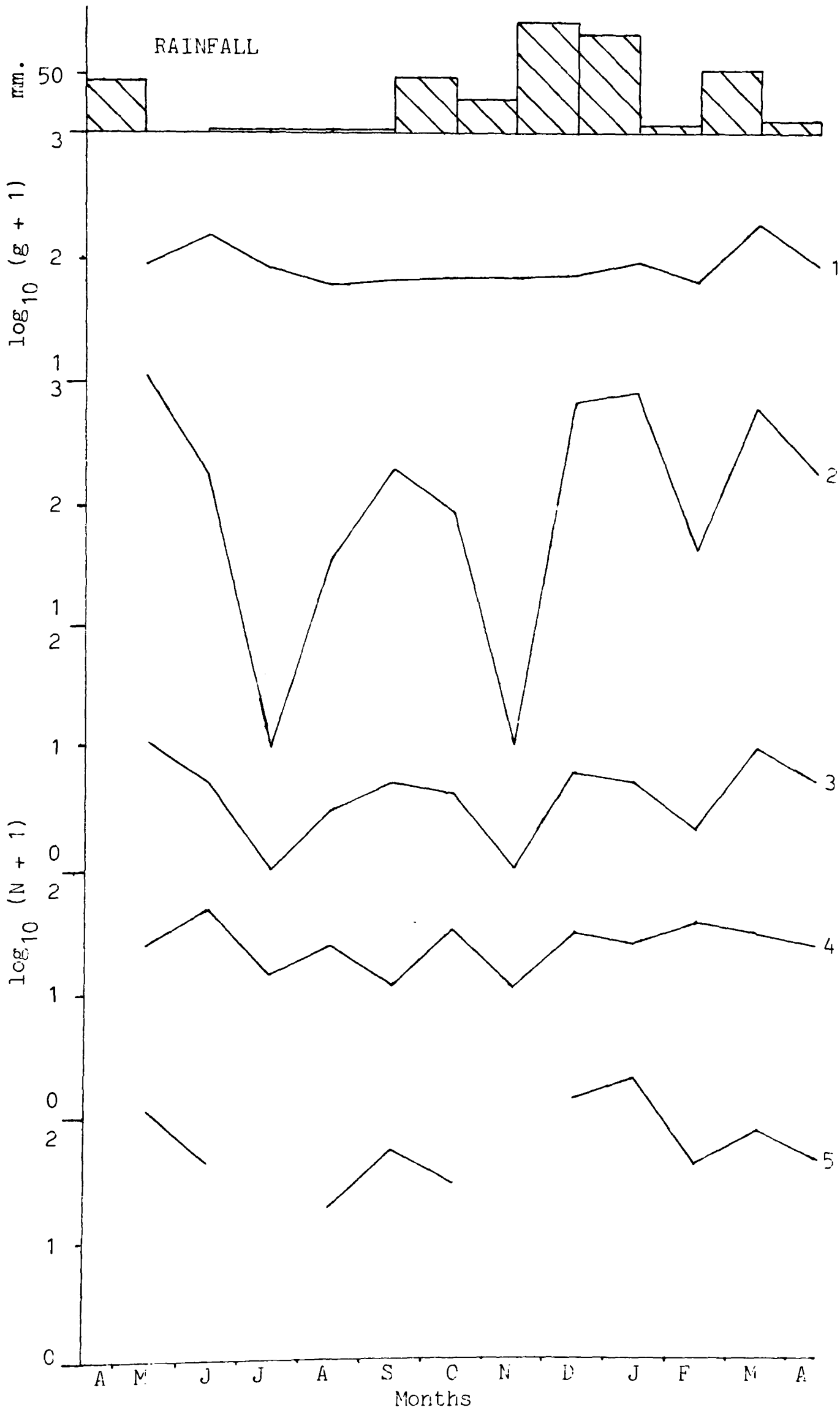


Figure 5.4

Seasonal fluctuations in the foraging activity of Microtermes allaudanus at site M.

See figure 5.2 for key.

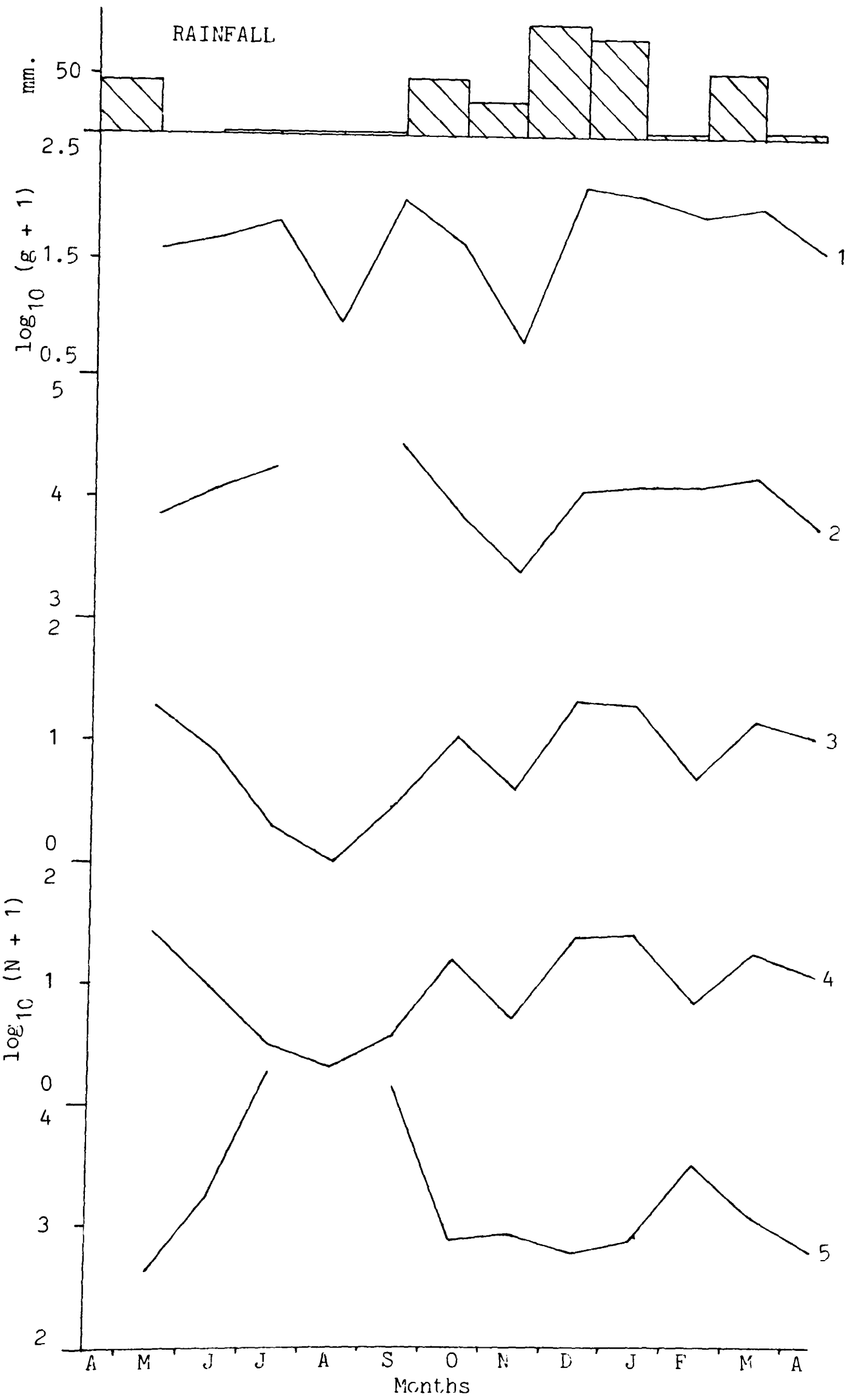


Figure 5.5

Seasonal fluctuations in the foraging activity of Synacarthotermes zanzibarensis at site M.

See figure 5.2 for key.

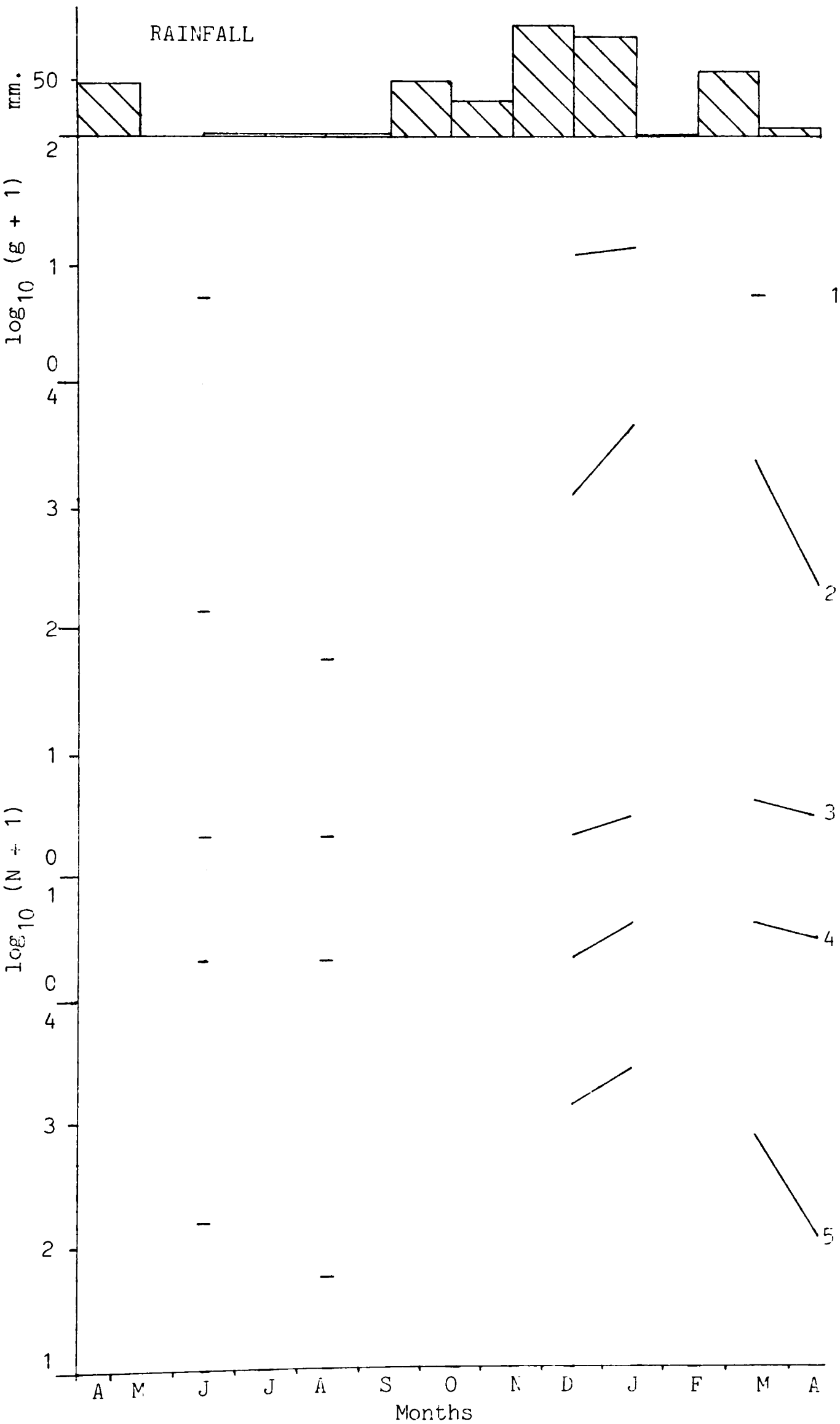


Figure 5.6

Seasonal fluctuations in the foraging activity of Anitermes lonrbergianus at site M.

See figure 5.2 for key.

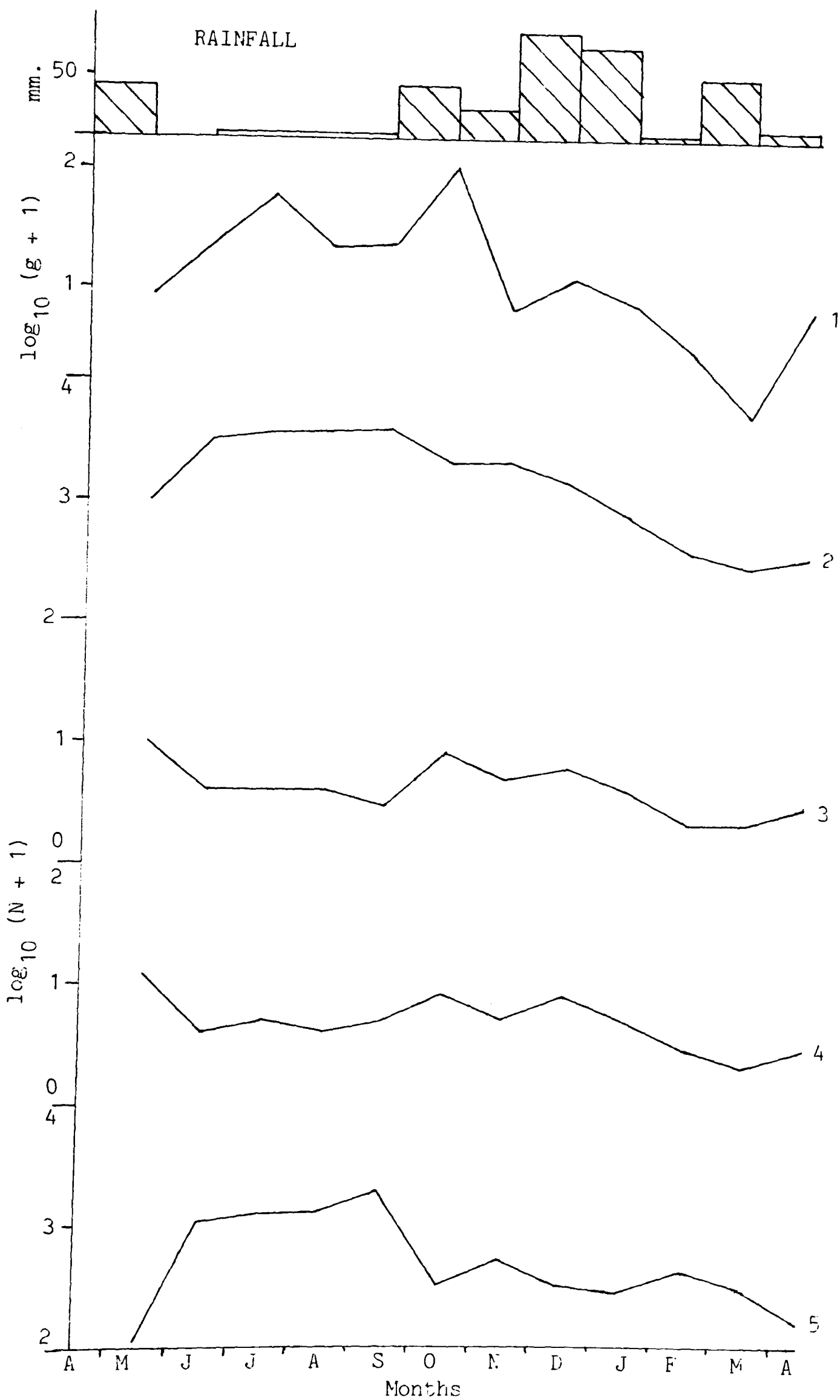
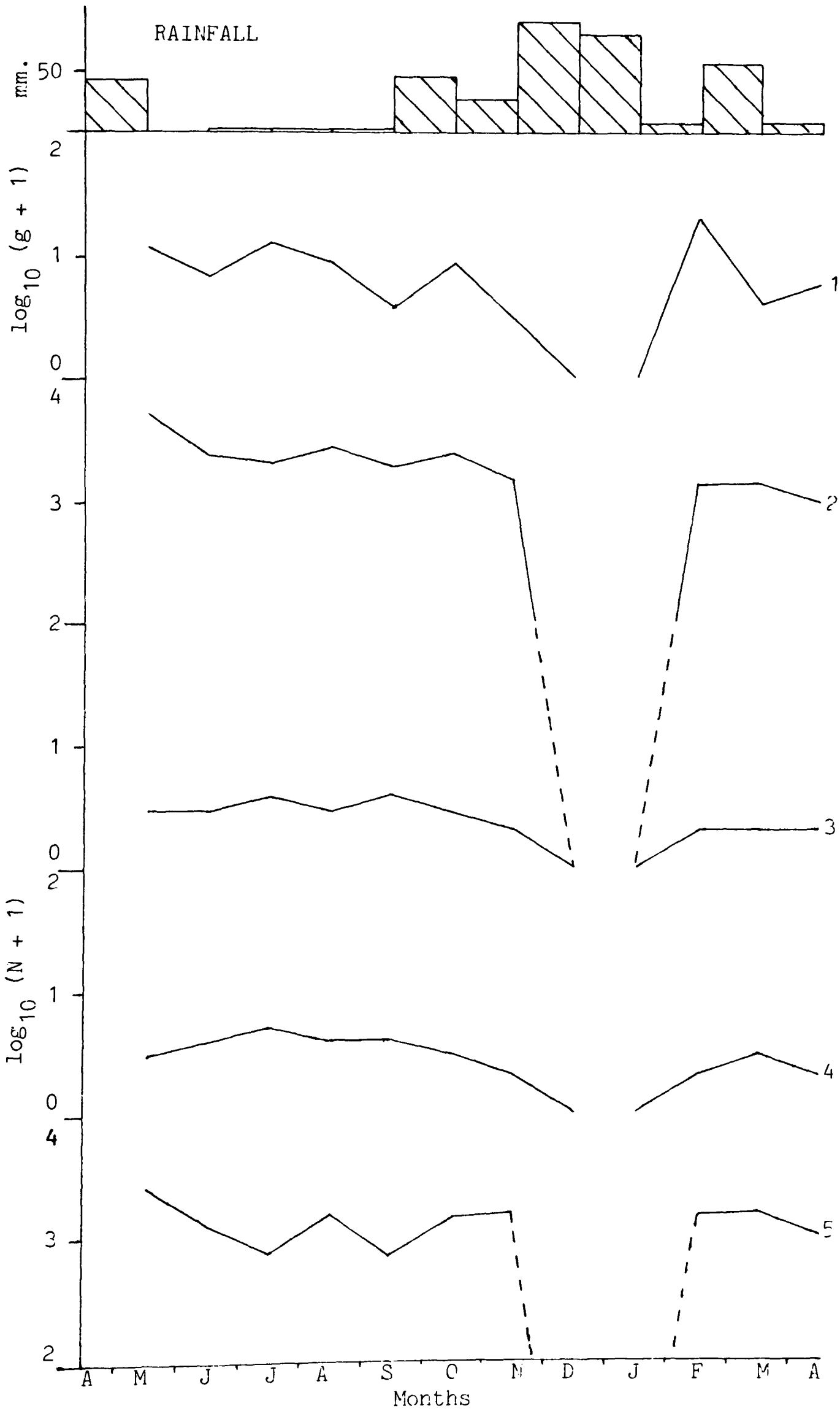
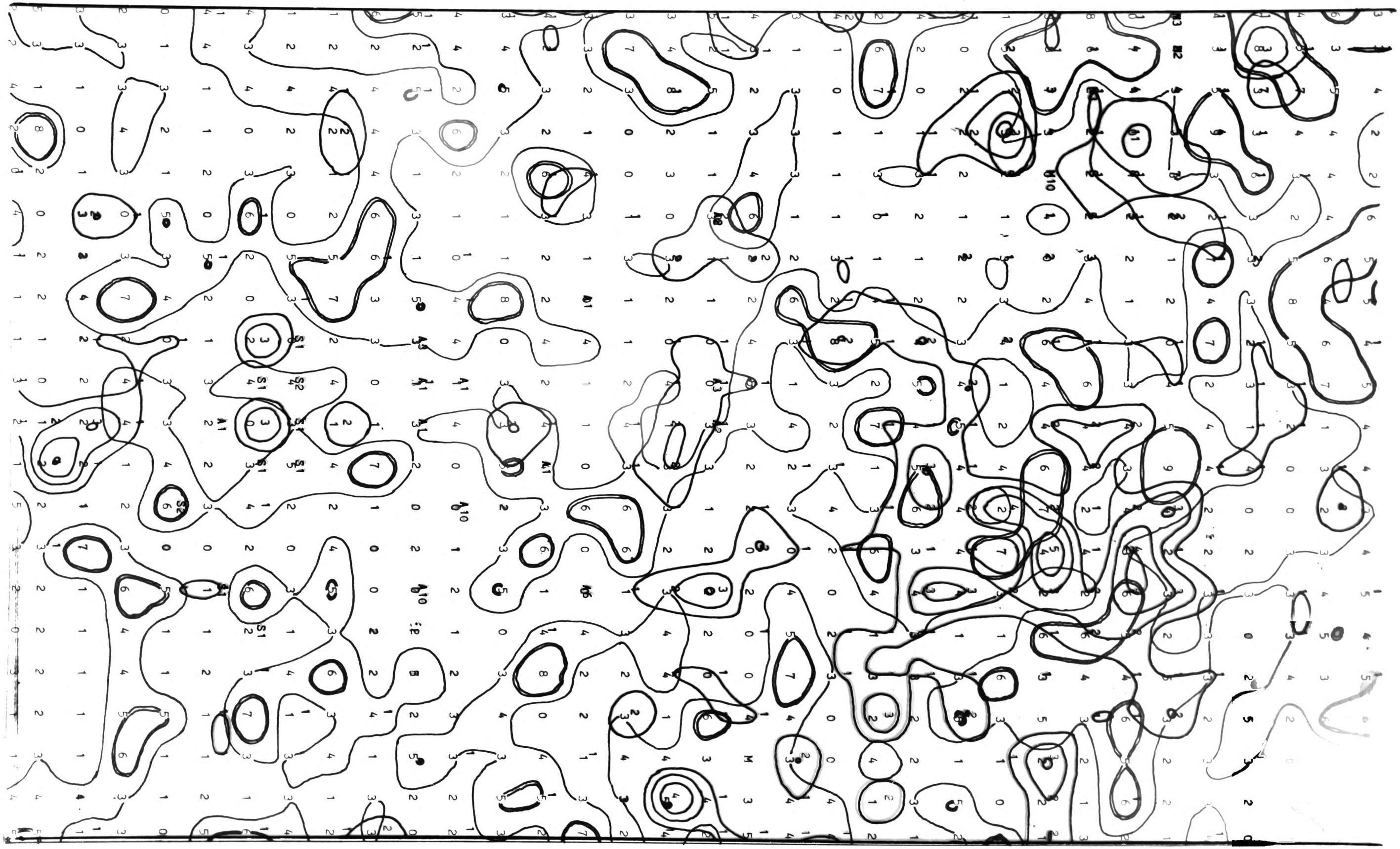


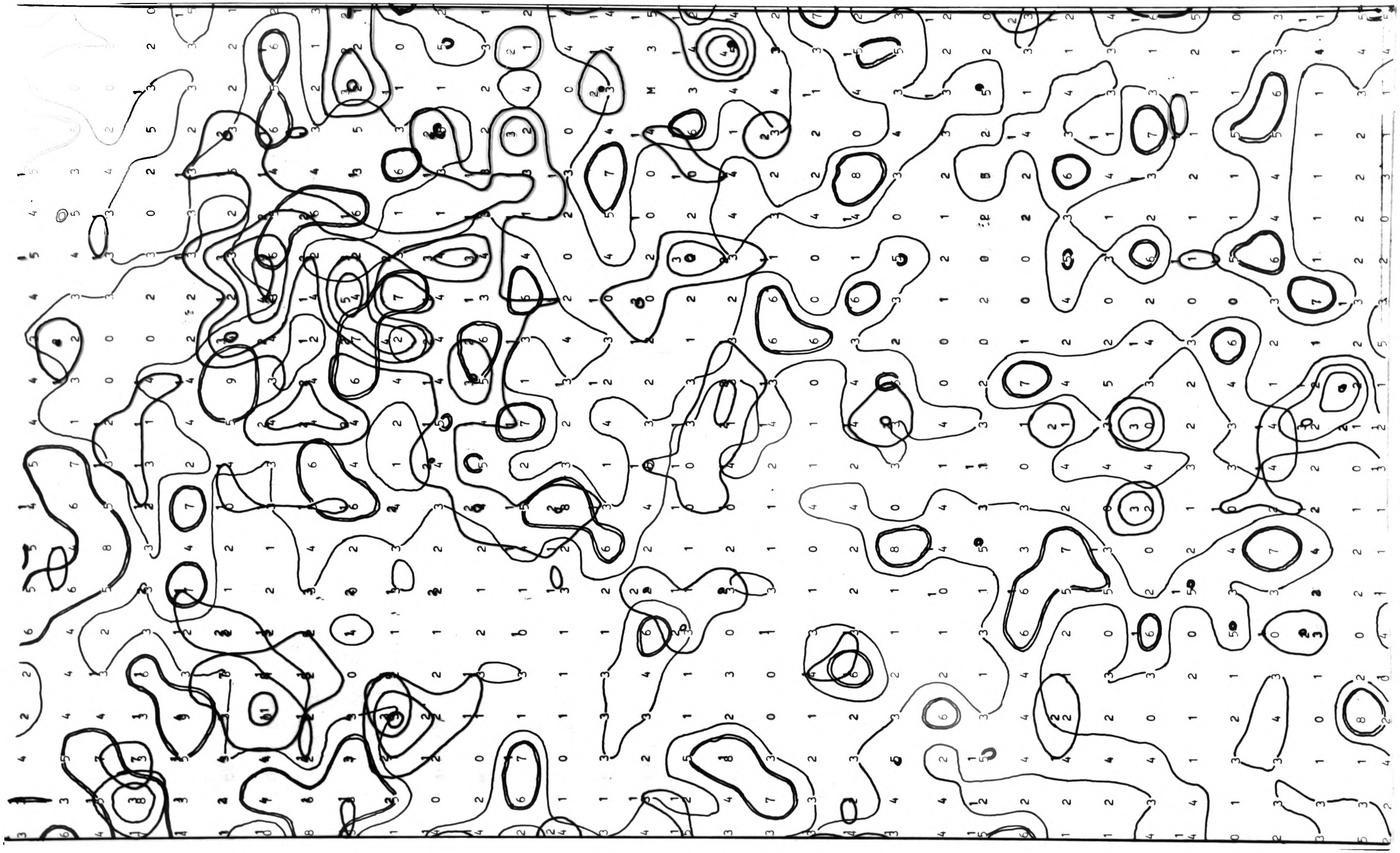
Figure 5.7

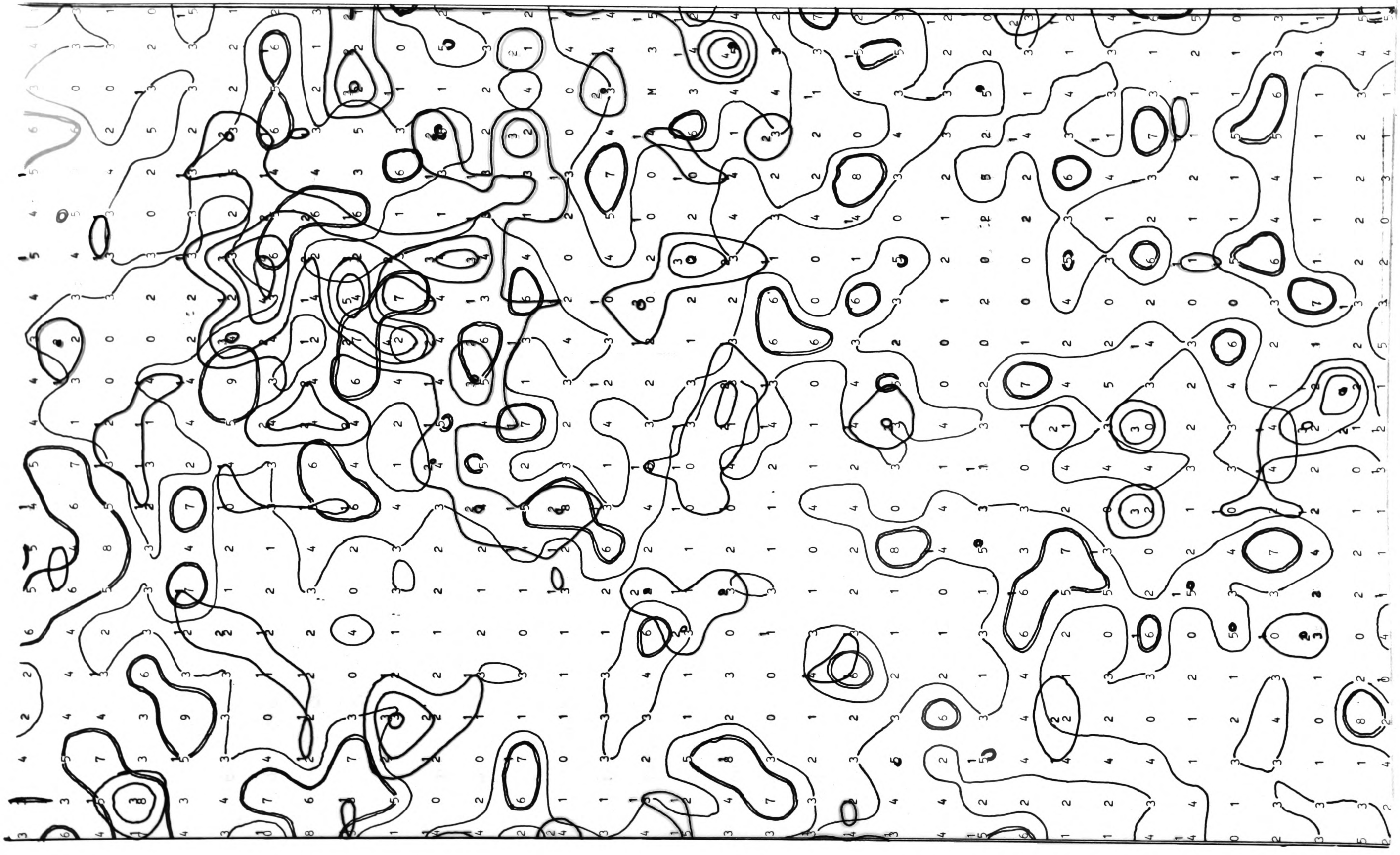
Seasonal fluctuations in the foraging activity of Microcerotermes sp.I at site M.

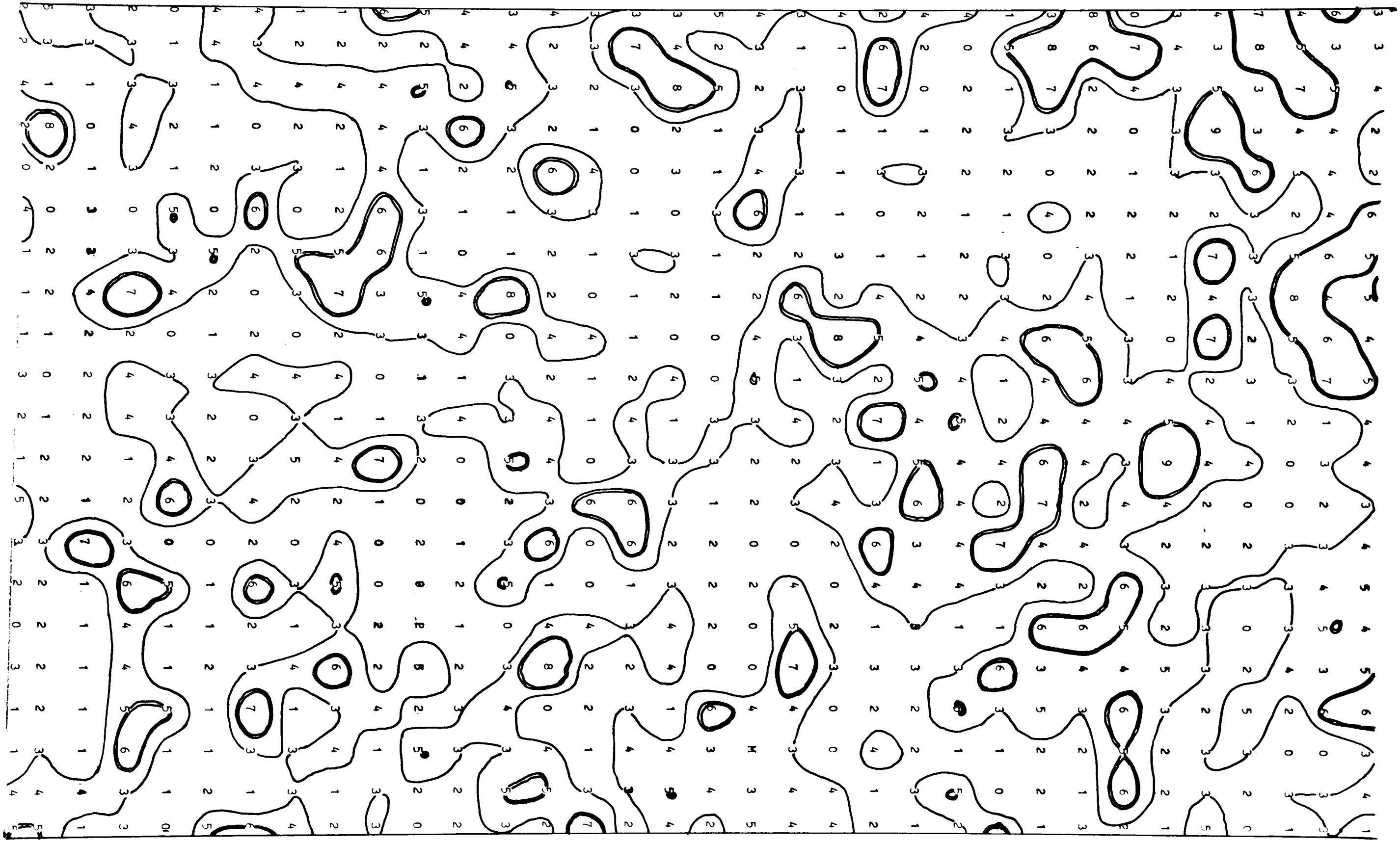
See figure 5.2 for key.











5.4 DISCUSSION

Six species of termites were found foraging on wooden discs in an area of 6000 m^2. They were potentially competing for dead wood to feed on. Does the data presented in this section provide any evidence of behaviour tending to reduce competition ?

Odontotermes mediocris (figures 5.2 and 5.11) shows synchronous fluctuations in the numbers of foraging termites, foraging parties, attacked discs and the weight of wood eaten, the main peaks of activity being in the rains with a marked reduction in the dry seasons. It forages extensively on dead grasses after the rains, but dead wood was the only food source available for much of the 1976 long dry season. The decline in activity on wood may therefore be interpretable as a fall in the population. There is no reliable indication of the scale of this change. The amount of wood eaten varied by a factor of nine between May and August 1976, but consumption can not be related directly to the population, particularly in species which have food stores. The fungus combs of O.mediocris may be used as a store and be depleted during the long dry season. Wood and Johnson (in press) reported that Microtermes spp. used their fungus combs in this way in Southern Guinea Savanna in Nigeria where they are the principal dead wood eating termites. The other measures of activity are all related to foraging and subject to the same objection as indices of population change.

The mean size of foraging parties of O.mediocris varied seasonally in parallel with the other measures of activity, but the peak was two months later than the peak in consumption and attack. Foraging parties remained small in the early part of the rains although many parties were found. This implies that the species searches extensively for high quality food sources at this time, but consolidates its attacks at the end of the rains. Attacks by O.mediocris lasted a mean of 2.0 days (S.E. 0.41, N = 12), the minimum was 0.4 days in November supporting the suggestion of wide searching at the beginning of the rains.

Figure 5.11 shows that almost all of the study plot was visited by O.mediocris at least once during the year but the habitat was not exploited evenly. Without further information on the behaviour of this species it is not possible to determine whether discrete areas of intense exploitation represent the foraging territories of single colonies. However if areas delineated by the three attacks contour can be interpreted in this way there were probably between five and ten colonies of O.mediocris foraging in the study area (6000 m^2).

Odontotermes zambesiensis shows a much more stable level of consumption of dead wood throughout the year than O.mediocris. In section 4.6.4 it was suggested that this was an indication that O.zambesiensis has a more stable population and a more restricted food supply than O.mediocris. Examination of figure 5.3 reveals that the numbers of foragers, number of attacked discs and number of foraging parties fluctuated wildly. Some of the peaks of activity occurred during the rainy season, others in the dry season. The mean size of foraging parties peaked at the end of the rains in January. The mean duration of foraging on one disc was 5.7 days (S.E. 1.28, N = 10) but also fluctuated wildly and could not be calculated for two months when no foraging parties were found. It seems likely that the instability in these data is partly due to incorrect identification of attacks on discs where termites were not present, but this can not explain the fluctuations in the numbers of foragers and foraging parties. The minimum numbers in January and February may be explicable by a switch to grasses which were abundant at these times and the November minimum may represent a minimum population or intensive feeding from fungus combs, or perhaps foraging parties returned under-ground earlier in the day before the discs were sampled.

Figure 5.10 shows that O.zambesiensis had a restricted foraging distribution compared with O.mediocris. The areas exploited may represent parts of the foraging territories of two or three colonies. The main

foraging area overlapped an area of intense foraging by O.mediocris although in other parts of the plot there are weak indications of segregation. This implies that there was a particularly rich food source in the principal area of overlap. This area was underneath a large Delonix elata tree which did produce a steady fall of twigs and branches. Some of the instability shown in figure 5.3 may be due to competition and interference between the two species in this area.

Figure 5.9 shows that there was one large colony of Microtermes allaudanus in the area covered by the grid of discs and possibly one very small colony. In the dry season they were only found on a group of three adjacent discs month after month. These discs were close to the base of a second large D.elata tree. In the rains foraging spread out concentrically from the tree to attack a maximum of 27 discs in May and 25 discs in December and January. The total number of foraging termites collected showed a peak in September at the end of the long dry season and a second peak in February at the end of the short dry season when the numbers of foraging parties were at their lowest. Mean foraging group size therefore declined in the rains and increased in the dry season as the foraging range expanded and contracted. The mean duration of foraging on one disc was 22.57 days (S.E. 1.23, N = 11), the minimum in July is probably spurious being caused by the small sample size (2 attacked discs, 1 foraging party collected). The foraging strategy adopted by M.allaudanus is one of persistent feeding on a few proved food sources supplemented by exploration during wet conditions. Foraging continues throughout the dry season in contrast to the species of Microtermes studied by Wood and Johnson (in press) in Nigeria. Comparison of figures 5.9, 5.10 and 5.11 shows that M.allaudanus mainly forages in areas poorly exploited by Odontotermes mediocris and O.zambesiensis. Taking into account the intense foraging by the latter two species under the other large tree on the plot it looks as if M.allaudanus can exclude them in competition.

Very little can be said about the foraging activities of Synacantho - termes zanzibarensis except that there appears to be a peak of foraging during the rains. The signs of attack on discs by S.zanzibarensis were indistinguishable from those of O.mediocris so that the figures for the consumption of dead wood, the total number of discs attacked in each month and the duration of foraging on one disc are highly unreliable. All the discs attacked by S.zanzibarensis were in a small area (figure 5.8) indicating that only one colony occurred in the study plot. The contribution of S.zanzibarensis to total consumption and activity was probably very small.

In section 4.6.4 it was argued that consumption of disc wood by Amitermes lonnbergianus declines in the rains because they turn to foraging on rotting wood in the soil. There is nothing in figure 5.6 to refute this suggestion. The mean duration of attacks was 25.1 days (S.E. 1.69, N = 12), but figure 5.8 shows that half the total number of attacks (41) by this species occurred at two bait positions suggesting that the true duration is probably several months at a reliable food source. The numbers of discs attacked increased at the beginning of the rains although the total number of foragers and the consumption of disc wood were already falling. This suggests that A.lonnbergianus behaves in a similar way to O.mediocris and M.allaudanus, exploring for new food sources after rain. The foraging parties encountered on the discs probably all came from the same colony.

The most noticeable feature of the behaviour of Microcerotermes sp.I. (figure 5.7) is its complete disappearance from the wooden discs during the main wet months December and January. It was suggested in section 4.6.4 that this species switches to feeding underground on rotting roots etc. during the rains. It is extremely faithful to single bait locations from month to month (figure 5.8) although the mean duration of foraging was only estimated as 25.7 days (S.E. 1.83, N = 10) for each attacked bait. The discrepancy is partly due to the very small sample size in each month, a total of four bait locations being attacked over the whole year, one of them in every month

when the species was active. All foragers probably came from one colony. Microcerotermes sp.I. does not appear to have an exploratory phase at the beginning of the rains.

Seasonal fluctuations in termite foraging activity have been reported by a number of authors. Bouillon (1970) suggested that foraging seasonality increases with latitude as the seasonality of rainfall increases with latitude in West Africa. Collins (1977b) found two types of response to seasons among the Southern Guinea Savanna termites in Nigeria. Large species such as Odontotermes and Macrotermes foraged more or less steadily throughout the year whereas small species such as Ancistrotermes and Microtermes foraged mainly in the rains. In the long dry season these species used their fungus combs as stored food. At the end of the dry season the stores were almost entirely used up in areas where maize had been cultivated for a long time, but only about half was used in woodland where dead roots were available as an alternative food source (Wood, Johnson, Ohiagu, Collins and Longhurst, 1977). Bodot (1964, 1967b) found a similar difference between large and small species in Ivory Coast. Trinervitermes spp. and Ancistrotermes cavithorax showed strong peaks of activity during the short rains. Macrotermes bellicosus also had a peak at this time and a minimum in the long dry season but the fluctuation was much less marked.

Haverty and Nutting (1974) did a laboratory study of the foraging rates and survival of Paraneotermes simplicicornis and Heterotermes aureus in relation to temperature and they tested the results for H.aureus in the field using baits (Haverty, LaFage and Nutting, 1974). They found that foraging was related to temperature in both species in the lab and in the field with maxima at 28^{o} C for P.simplicicornis and 36^{o} C for H.aureus, but rain provided an enormous stimulus to foraging by H.aureus. Foraging by this species was best described by the relationship

$$\ln Y = -0.985 - 0.0761\,T + 2.928 \ln T + 0.327 \ln R$$

where Y is the number of foragers above ground (presumably in 1200 m^2, the

area of their study plot), T is the temperature at the bait - soil interface and R is daily rainfall. These results were used in a predictive model of foraging activity by H.aureus (Haverty and Nutting, 1975b).

Odontotermes zambesiensis was the largest termite on the bait experiment plot in Tsavo and, if consumption is taken as the measure of activity, it did fluctuate less seasonally than the other species. However small species continued to forage at a high level throughout the dry season (except S.zanzibarensis for which the sample is very small) and the non-Macrotermitinae, which probably fed on other materials in the rains, showed peaks of surface wood feeding activity in the long dry season. No data are available to separate the effects of temperature and rainfall on the foraging activities of termites in Tsavo.

The densities and spatial relationships of mound building termites have been the subject of a considerable number of studies (eg. Hesse, 1955; Glover, Trump and Wateridge, 1964; Bodot, 1967a; Bouillon, 1970; Lee and Wood, 1971a and b; Wood and Lee, 1971; Pomeroy, 1976, 1977 and 1978; Collins, 1977b). Subterranean termites are harder to study (Sands, 1972b) and fewer studies have been made of their numbers, distribution patterns and activity. Most studies have used modifications of the bait or "graveyard" methods (LaFage, Nutting and Haverty, 1973; Nutting et al.,1973; Haverty et al., 1975; Lepage, 1974; Usher, 1975). Nel (1968) working with the grass harvester Hodotermes mossambicus in South Africa devised a direct method of determining whether foraging termites at two neighbouring points come from the same or different colonies. He put a sample from each foraging party in a container and watched them to see if they fought. The areas from which they were friendly were always discrete and fighting was always observed between termites from different areas. Josens (1972) dug up a large number of 25 and 16 m^2 plots to a depth of 25 cm and recorded the positions, species and contents of all termite chambers encountered. Soil core sampling has been used in several studies of subterranean termites

(Strickland, 1944 and 1945; Salt, 1952; Harris, 1963; Maldague, 1964; Bodine and Ueckert, 1975; Wood and Johnson, in press; Wood, Johnson and Ohiagu, in press). The earlier studies used shallow cores which did not sample the whole population. Wood et al. (in press) used hand augurs to sample to 2 m depth and achieved good population estimates when enough samples were taken.

Most of these studies indicate that at any place one species of termite is more or less dominant, exploring if not exploiting most of the ground surface, but often eating very little from any particular food source. In Sahel Savanna in Senegal Psammotermes hybostoma was most widespread (Lepage, 1974); in fallow farmland scrub in Ghana Ancistrotermes spp. were dominant (Usher, 1975) and in Arizona Gnathamitermes perplexus visited almost every bait location (96%) (LaFage, et al., 1973). In the same sites other species were patchily distributed, and usually exploited a few bait positions intensively. For instance Heterotermes aureus visited 14% of bait locations on the same plot where G.perplexus attacked 96% in Arizona (LaFage et al., 1973); Coptotermes spp. and Odontotermes spp. were found on few baits in Ghana (Usher, 1975) and in Tsavo Microtermes allaudanus, Amitermes lonnbergianus and Microcerotermes sp.I. all attacked particular baits for longer than Odontotermes mediocris and O.zambesiensis, sometimes for months on end.

Intraspecific competition between colonies of mound building termites has been deduced from over-dispersed distributions of the mound of eg. Amitermes spp. in Australia (Wood and Lee, 1971) and Odontotermes sp. in Kenya (Glover et al., 1964). In other places mounds have been found to be randomly dispersed or clumped (Collins, 1977b; Pomeroy, 1976; Sands, 1965c). Data on the dispersion patterns of subterranean termites are not sufficient to make similar deductions, however intraspecific competition is most likely to occur between colonies of a species which has more or less saturated its environment. There is no evidence to sugest that O.mediocris

was spatially saturated on the bait plot in Tsavo, many baits were visited less than three times in the year.

Interspecific competition has been inferred from mutual overdispersion of mounds of more than one species in an area. For instance Nasutitermes exitiosus and Coptotermes lacteus were mutually overdispersed on plots in South Australia (Wood and Lee, 1971). In most of the studies of subterranean termite communities there is evidence that different species avoid competition either by feeding on different materials or by spatial segregation. Josens (1972) found that the four commonest subterranean Macrotermitinae in Southern Guinea Savanna in Ivory Coast were largely segregated on the basis of their feeding habits. Microtermes toumodiensis chiefly foraged under-ground on dead roots, occasionally feeding on dead wood at the ground surface; Ancistrotermes cavithorax foraged on woody litter above ground, making extensive use of soil sheeting; a species of Odontotermes fed mainly on grasses and Pseudocanthotermes militaris was an opportunist feeder on all these materials but probably avoided competition by feeding on each resource only when it was abundant. In Usher's (1975) study area Ancistrotermes spp. appear to be the widely distributed generalist feeders. Two species of Macrotermes were spatially segregated and various other species were rare and widely spaced.

In Arizona most termite species ate dead wood at the ground surface, but Haverty and Nutting (1975a) found preferences for different species of wood. Heterotermes aureus prefered Opuntia spinosior wood and Paraneotermes simplicicornis prefered Acacia greggii wood, but Gnathamitermes perplexus showed no preferences and was the species which visited 96% of the baits but ate little of each.

There was little spatial separation of the species in the Tsavo study plot except that the non-Macrotermitinae, Amitermes lonnbergianus and Microcerotermes sp.I. appear to avoid, or preclude, the Macrotermitinae at a few points. These two species also had distinctly different wet season

food preferences from the Macrotermitinae. Microtermes allaudanus was a specialist feeder on dead wood on the ground surface at sites where conditions suited it well, and may be able to exclude the opportunist Odontotermes spp.. Both species of Odontotermes were opportunists although O.mediocris was more widely dispersed than O.zambesiensis. There are strong indications that these two species compete, or at least interfere, with eachother at rich food sources and the question arises as to how they manage to coexist. A possible answer lies in the instability of the Tsavo climate. If one species is better adapted to very dry conditions than the other they may coexist in a state of competition as long as the climate changes sufficiently often that neither species dies out completely. There is therefore some evidence of behaviour tending to reduce competition in Tsavo, but segregation is far from complete.

SECTION 6

FEEDING HABITS AND SPECIES COMPOSITION OF TERMITE COMMUNITIES IN RELATION TO RAINFALL

Typically termites feed on vegetable material ranging from living trees and grasses through matter in all stages of decomposition to humus (Wood, 1976). Any one species is normally restricted to one part of this range and may be specialised in other ways for instance as a grass feeder. The feeding habits of each species found in Tsavo have been given in section 3.3 and are summarised in table 6.1. It will be seen from this table that the majority of termites in Tsavo feed on sound dead wood and some, such as the Kalotermitidae are obligate specialists. Specialists dedicated to other materials are few and in terms of numbers very rare. This is chiefly because other food sources either do not occur at all or they are extremely seasonal in availability. Grasses only grow in the rainy seasons and are eaten by large numbers of large mammals and grasshoppers as well as by termites. The specialist grass feeding Trinervitermes are scarce compared with wetter African habitats (Sands, 1965b), being limited by availability of grass in the long dry season. Coe (1972) estimated that the production of elephant dung was 8.7×10^3 Kg $Km^{-2}Yr^{-1}$ dry weight at an elephant population density of 1 Km^{-2}. Elephant distribution is seasonal (Cobb, 1976) and during the rainy seasons dung beetles rapidly remove all the dung from the ground surface (Kingston, 1977). During the dry season a little microbial decomposition occurs (Anderson and Coe, 1974) but a great deal of dung is available locally for termites (Kingston, 1977). Grass and dung are therefore complementary in their seasonal and spatial availability to termites. There are therefore no dung specialists among the termite fauna of Tsavo but large amounts are removed by polyphagous species. Ferrar and Watson (1970) came to the same conclusion in Australia, but possibly the reason for the absence of specialists there is that they have not yet

evolved a close association with the dung of the recently introduced species which produce most of the faecal material. Kemp (1955) found Angulitermes truncatus feeding in middens of the dikdik, a small antelope, in Mkomazi, 100 Km from the present study area. Dikdik are common in Tsavo but Angulitermes was not recorded. Amitermes spp. and Microcerotermes sp.I may feed on rotting roots (sections 4.6.4 and 5.4) but they appear to require sound wood in the dry season. Very little organic matter is incorporated in the soil in Tsavo (Van Wijngaarden, in prep.) so the specialist humivorous termites Cubitermes spp.and Promirotermes spp. are rare. The Macrotermitinae are gastronomically the most accomplished generalists in Tsavo, so they are the most abundant termites.

A number of studies have been made of termite communities in West Africa. From these Wood (1976) found a relationship between latitude and the total number of ground living termite species and the proportion of species having different feeding habits. In table 6.2 the results of the present study are compared with the data given by Wood (1976). The Kalotermitidae are omitted. The number of species in Tsavo and their feeding behaviour is almost identical to the numbers and feeding habits in Sahel Savanna (Lepage, 1974) where the rainfall was nearly the same as in Tsavo. With increasing rainfall the percentage of Macrotermitinae declines and of humivores increases. Wood (1976) believes that this is due to increasing rates of microbial and fungal decomposition making more material available for termites which prefer rotting matter at the expense of Macrotermitinae which normally avoid it.

Within the present study area eight experimental sites were chosen in places with five year mean rainfalls varying from 200 to 500 mm. At each site 30 wooden discs were used to measure termite activity (section 4.3). Although they did not provide a complete sample of all the wood eating termite species at each site it is useful to compare the numbers of species attacking the discs and their relative importance as consumers (table 6.3,

figure 6.1). In figure 4.3.1 (section 4.3.4) the total consumption by termites was found to be positively related to the mean rainfall at the site. If sites E and F are ignored, for the reasons given in section 4.3.4, a clear relationship is found between the number of species attacking the discs and rainfall (mm yr^{-1}.) (AP)

$$\text{No. of spp. on 30 discs} = 0.016\ AP - 2.4$$

the proportion consumed by Macrotermitinae declines

$$\%\ \text{Consumed by Macrotermitinae} = 117.8 - 0.069\ AP$$

When the number of species attacking the discs, and the proportion consumed by Macrotermitinae are plotted against total consumption (C) (g dry weight) the relationships are even clearer and sites E and F fit the trends of the rest of the data (figure 6.2)

$$\text{No of spp. on 30 discs} = 1.9 + 0.029\ C$$

$$\%\ \text{Consumed by Macrotermitinae} = 100.4 - 0.18\ C$$

The sampling procedure did not include the whole termite fauna at any of the eight sites so it is not possible to compare these studies directly with Wood's (1976) complete community analyses. However the results do demonstrate that the principles of increasing species richness and declining importance of Macrotermitinae with rainfall can be tested experimentally using simple techniques. The results are detectable over a fairly small range of rainfall in sites within 50 Km of eachother. The same techniques could be used to explore other relationships between the composition of the termite fauna and various environmental variables.

Table 6.1

Feeding Habits of the Termite Species Collected in

in Tsavo During the Present Study

1 = Minor Consumption, 2 = Major Consumption, ( ) = Assumed

Species	Grass	Tree Snags	Ground Wood	Dead Roots	Eleph. Dung	Other Dung	Soil
Epicalotermes kempae		2					
Neotermes meruensis		2					
Cryptotermes sp.I		2					
Unidentified sp.		2					
Coptotermes amanii			2				
Cubitermes glebae							2
Cubitermes umbratus							2
Promirotermes bellicosi							2
Microcerctermes sp.I			2	(1)			
Amitermes lonnbergianus			2	(1)			
Amitermes unidentatus			2	(1)			
Amitermes sciangallorum				(1)	1	1	
Amitermes messinae				(1)			
Amitermes somaliensis	1			(1)			
Trinervitermes gratiosus	2		1				
Trinervitermes bettonianus	2						
Trinervitermes dispar	2						
Macrotermes subhyalinus	2		2		1		
Odontotermes badius	2				2		
Odontotermes zambesiensis	2		2		2	1	
Odontotermes mediocris	2		2		2	1	
Microtermes allaudanus			2		1		
Microtermes vadschaggae			2				
Microtermes sp.I			1				
Synacanthotermes zanzibarensis			2		1		

Table 6.2

Number of Termite Species and their Feeding Habits in Various Places in Africa

Place	Author	Latitude	Rainfall mm yr^{-1}	Total no. of spp.	Living wood fresh woody litter	Grass & herb litter	Decomposing wood	Soil
Sahel Savanna Senegal	Lepage, 1974	16.5° N	375 - 400	19	11	8	0	3
Northern Guinea Savanna Nigeria	Sands, 1965c	11° N	1120 - 1220	19	9	11	1	5
Southern Guinea Savanna Nigeria	Wood et al., in press	9° N	1175	23	10	10	2	8
Derived Savanna Ivory Coast	Josens, 1972	6° N	1290	36	18	11	3	13
Rain Forest Cameroon	Collins, 1977c	4.5° N	3800	43	8	2	8	31
Tsavo Kenya	Present Work	4° S	200 - 500	20	11	7	0	3

Table 6.3

Number of Termite Species Attacking Wooden Discs at Eight Sites in Tsavo and the Importance of Macrotermitinae in Relation to Rainfall and Total Consumption at each Site

Site	Mean Rainfall 1972 - 1976 mm yr^{-1}.	Total Consumption by Termites g m^{-2} yr^{-1}.	Total No. of Species Attacking Discs	No. of Spp. of Macrotermitinae Attacking Discs	% of Total Disc Wood Eaten Consumed by Macrotermitinae
C	496	97.4	7	4	83
A	458	82.0	5	3	79
G	426	57.0	2	2	100
M	352	28.1	3	2	87
B	327	26.8	2	2	100
D	265	9.3	3	2	98
F	236	52.2	3	2	93
E	213	118.7	4	3	80

Figure 6.1

Relationship between rainfall and 1) the number of species of termites present on wooden baits in Tsavo and 2) the proportion of the total wood consumption which was eaten by Macrotermitinae.

1) Y = 0.016 AP - 2.4 (lower case letters)

2) Y = 117.8 - 0.069 AP (upper case letters)

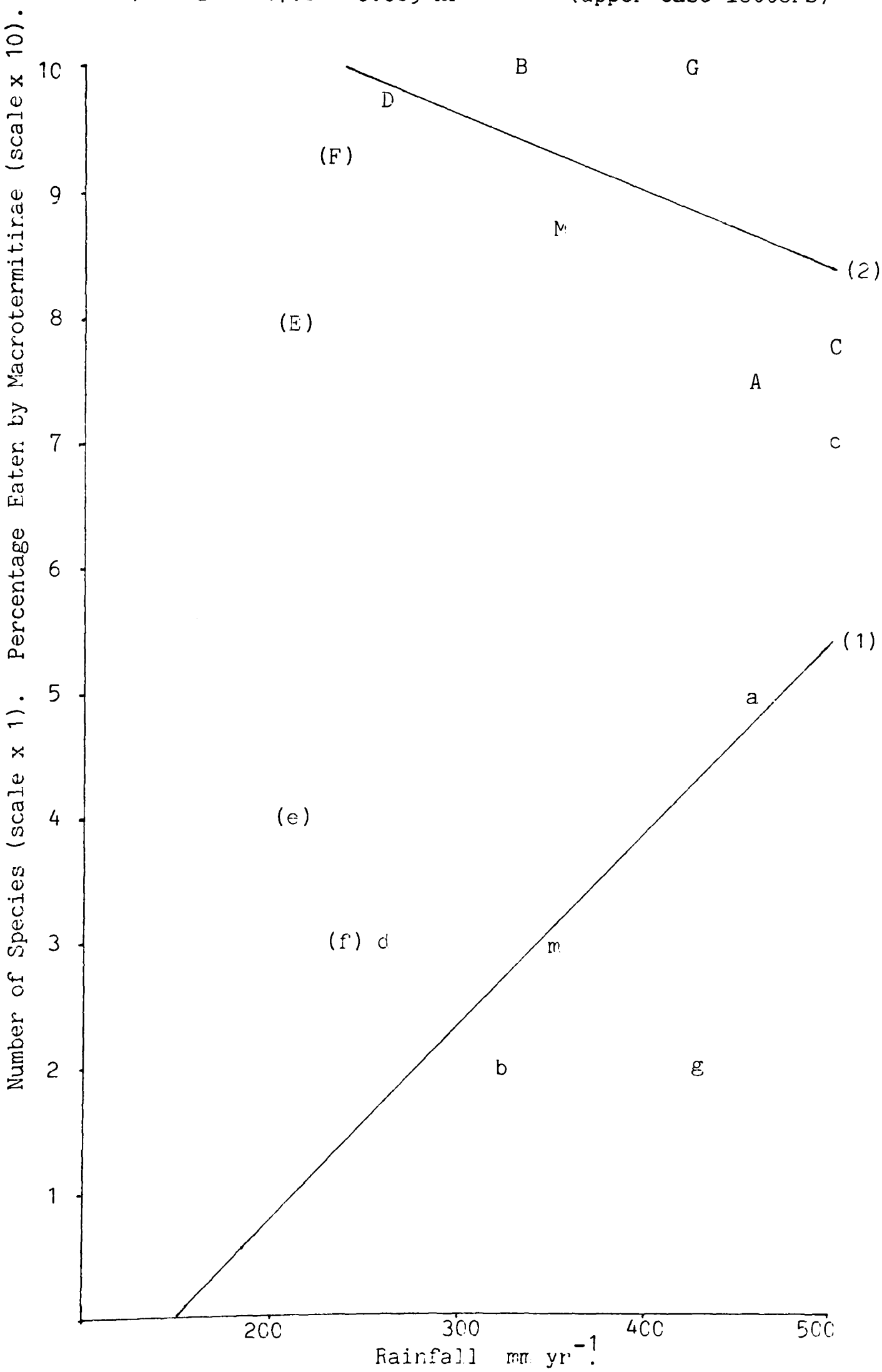
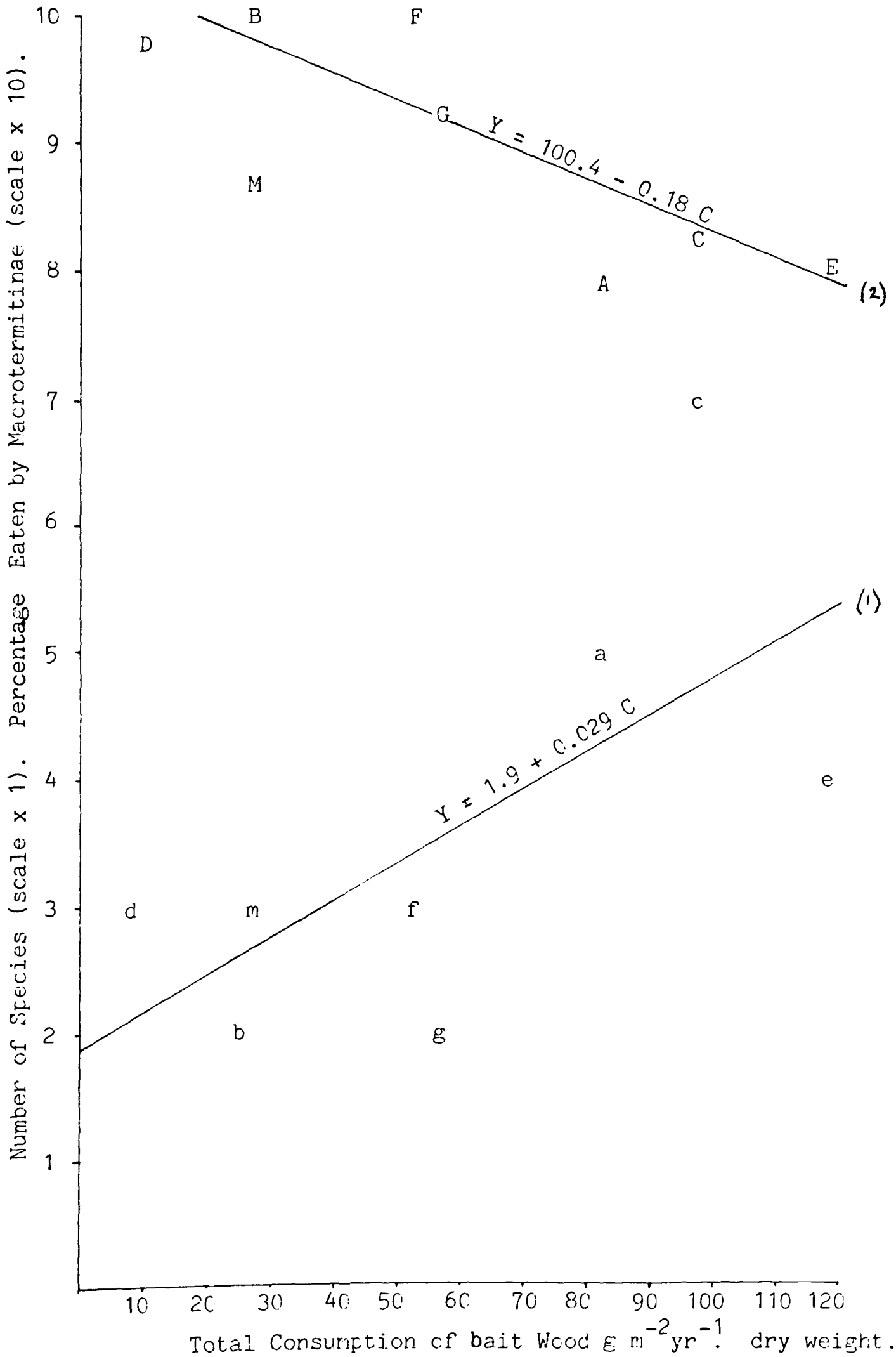


Figure 6.2

Relationship between total consumption of dead wood from baits and 1) the number of species of termites present on the baits and 2) the proportion of the total wood consumption which was eaten by Macrotermitinae.

Conventions as figure 6.1.



SECTION 7

OBSERVATIONS ON SUBTERRANEAN TERMITE NEST CHAMBERS

Termites build nests in a variety of places and from a variety of materials, these structures have been examined and reviewed by Noirot (1970) and Lee and Wood (1971a).

The design of termite nests is a compromise between three requirements, efficient access to food, protection from predators and environmental regulation to give optimum conditions for growth. The simplest compromise adopted by for instance the Kalotermitidae is to live inside the dead wood on which they feed, preserving an outer shell of wood as a defence. Very little control of environmental conditions is possible and once the food source is used up the colony dies. Elaboration of nests outside the food source avoids this problem and allows improved regulation, but both require additional energy expenditure. Elaborated nest structures may be arboreal, subterranean or mound structures. They range from relatively simple soil or carton constructions to the giant complex mounds of Macrotermes spp.. Every improvement in the defensive and homeostatic properties of the structure has an energetic cost. The termites must forage over wider areas to meet this cost, reducing the foraging efficiency of the colony. In other words increasingly elaborate defence and control mechanisms lead to increasingly inefficient foraging. One way out of this vicious circle is to decentralise the nest and place the parts of it in naturally well protected places with relatively stable conditions as close as possible to the optimum. Deep in the soil conditions are usually relatively stable, and a divided nest is unlikely to be completely over-run by predatory ants. Individual chambers can be sited within easy reach of important food supplies.

Table 7.1 shows that in Tsavo five termite species build mounds. Only two of these species are widespread and common, Macrotermes subhyalinus and Trinervitermes gratiosus . Various secondary occupants have been found

in the eroded skirts of M.subhyalinus mounds but none in the central nest area. Amitermes messinae was found occupying a T.gratiosus mound and Microtermes allaudanus sharing a Cubitermes glebae mound. The five kalotermitids occupy typical sites for the group, dead wood high up on living and dead trees. The majority of termites in Tsavo however live underground.

An opportunity to make observations on subterranean nest chambers arose in February 1977 when some sections of a pipeline were replaced. A large pipe supplying water to Mombasa passes through the western edge of the study area, and the new sections were laid to the side of the old in previously undisturbed ground. The ditches were examined for signs of termite chambers. Several of the ditches were in black bottom-land clay soil and deep brown alluvial soil neither of which showed any signs of termite chambers, but one section was in deep red soil on the south side of Irima Hill. The ditch was over 300 m long, 2 m deep and 2 m wide. The soil appeared to be uniform dark red rhodic ferralsol ontop of recrystalised limestone and gravel at a depth of 180 - 200 cm. Chambers in both faces of a 300 m length of ditch were examined several days after the ditch had been dug, they were measured and the contents recorded.

One hundred and sixteen chambers were found of which only 30 could unequivocally be assigned to occupants. Of these 10 belonged to dung beetles, 17 to termites and 3 contained ants' middens. The mean diameter of four measured dung beetle chambers was 4.5 cm and of 14 measured termite chambers was 11.4 cm. The distribution of the diameters of 109 measured chambers is shown in figure 7.1. There are three peaks in the distribution at 5, 10 and 15 cm diameters. All chambers less than 8 cm diameter were ascribed to dung beetles, and those 8cm and above to termites unless signs were present to contradict this assignment. No chambers were found which had been built by the giant dung beetles Heliocopris spp., although they did occur in unsampled parts of the ditch. The results of dividing the 116 chambers on the basis of diameter were 60 dung beetle chambers, 53 termite chambers and

3 chambers with ant middens. If we assume that the line transect represented by 600 m of ditch face represents a belt transect 11.4 cm wide (the mean diameter of the known termite chambers) then the density of all chambers ascribed to termites is 0.77 m^{-2}. The 14 chambers definitely identified as belonging to termites were found at depths ranging from 10 to 200 cm, the mean depth being 91.4 cm ($\pm$ 34.8 cm, 95% limit). The lowest of these chambers was excavated in a dense gravel layer and although it is unlikely that many chambers were deeper than this it is not impossible.

The upper 95% limit of the mean depth of termite chambers is 56.6 cm. Glover (1972) recorded soil temperatures (table 2.3) and found that the annual range of temperature at 60 cm depth was 7.5^{o} C from 25.3^{o} C minimum to 32.5^{o} C maximum. The annual mean was 28.9 - 29.0^{o} C fluctuating by only 0.1^{o} C through the day. Below 60 cm the annual range decreased and the mean stabilised to 28.9^{o} C throughout the day. The optimum temperature for the growth of Termitomyces spp. fungi is 28 - 30^{o} C (Dr M.J.Swift pers. comm. to Collins, 1977b) and the nests of Macrotermes spp. are maintained at about 30^{o} C (Luscher, 1961; Collins 1977b). The termite chambers in the soil in Tsavo are therefore situated at the depths where conditions are stable and most favourable for development of both the termites and their symbiotic fungi. Collins (1977b) showed that one of the functions of the elaborate system of air passages in Macrotermes bellicosus mounds is to dissipate the excess heat produced by the fungus combs. Heat loss from subterranean combs can not be accelerated in this way, so that large combs would probably overheat, small combs with diameters no more than 10 - 15 cm probably have a high enough surface area to volume ratio to lose heat fast enough to avoid overheating.

Of the 14 chambers definitely identified as belonging to termites 12 contained fungus comb. In ten of these the diameter of the pellets making up the fungus comb was 0.1 - 0.15 mm, Odontotermes mediocris workers and soldiers were found with some of these combs. The other two fungus combs

had pellet diameters of .025 to .075 mm and one was associated with Microtermes allaudanus workers and soldiers. All these chambers containing O.mediocris and M.allaudanus were close to 10 cm diameter and it is possible tentatively to suggest that most of the 39 chambers with 8 - 12 cm diameters belonged to these two species. Of the 14 larger chambers one contained the remains of a nest resembling structures built above ground by Cubitermes spp. and one had a black faecal lining reminiscent of structures occupied by Amitermes spp., the rest can not be ascribed to any particular termite.

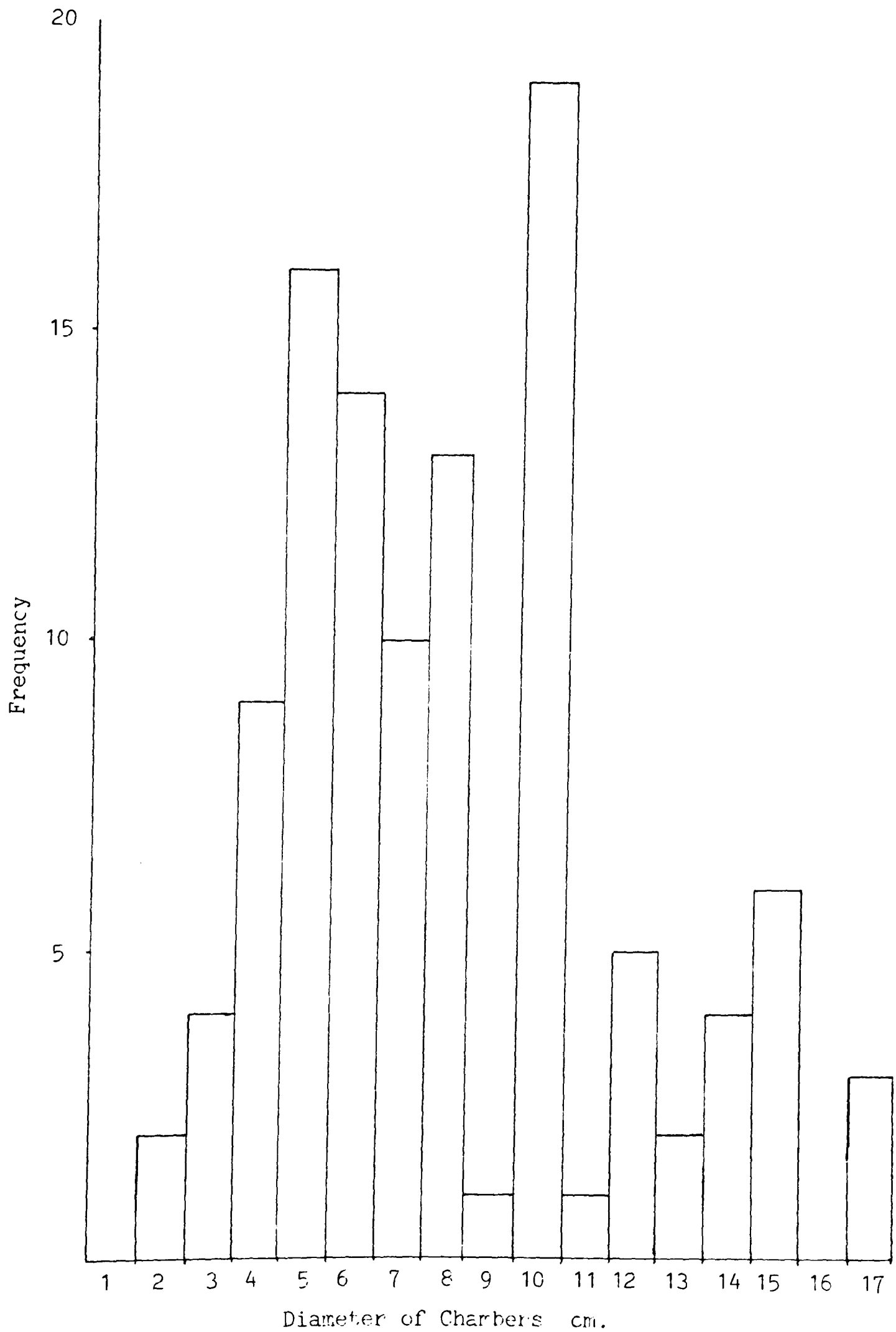
Table 7.1

Nesting Sites of Termite Species Recorded in Southern Tsavo East

Species	Snags on Trees	Ground Dead Wood	1° Mound Builder	2° Mound Occupant	Sub-terra-nean
Epicalotermes kempae	1				
Neotermes meruensis	1				
Cryptotermes sp.I	1				
Bifiditermes azaniae	1				
Unidentified sp.	1				
Coptotermes amanii		1			1
Cubitermes glebae			1		
Cubitermes umbratus			1		
Promirotermes bellicosi					1
Promirotermes massaicus					1
Microcerotermes sp.I					1
Amitermes lonnbergianus					1
Amitermes unidentatus					1
Amitermes sciangallorum					1
Amitermes messinae				1	1
Amitermes somaliensis					1
Trinervitermes gratiosus			1		
Trinervitermes dispar					1
Trinervitermes bettonianus					1
Macrotermes subhyalinus			1		
Odontotermes badius			1		
Odontotermes zambesiensis					1
Odontotermes mediocris					1
Microtermes allaudanus		1		1	1
Microtermes vadschaggae					1
Microtermes sp.I					1
Synacanthotermes zanzibarensis					1

Figure 7.1

Distribution of the diameters of 104 chambers in the two faces of a ditch 300 m long and 2 m deep.



SECTION 8

MONITORING FLIGHT OBSERVATIONS ON THE DISTRIBUTION OF MACROTERMES SUBHYALINUS MOUNDS

8.1 INTRODUCTION

In some parts of Tsavo, notably in Tsavo East south of the Galana River, there are a great many unoccupied Macrotermes subhyalinus mounds, but living colonies are rare. The impression gained from examining the mounds was that many colonies had died recently. Elephants have caused such marked changes in the habitat (section 1) that it was thought that they might be responsible directly or indirectly for changes in the Macrotermes population, if indeed the population had changed. A regular programme of aerial counts of large mammals was initiated by Cobb (1976), and the opportunity was taken to count termite mounds on one of these flights in September 1976. The results of the count could be directly compared with Cobb's (1976) figures for various habitat parameters as well as the distribution and numbers of large mammals.

8.2 METHODS

The description which follows is taken from Cobb (1976).

The monitoring flights in Tsavo were designed to provide as complete a survey as possible of the range occupied by the Tsavo elephant population, and the best estimate possible of the populations of the large mammal species in the area. They covered an area of 43,900 Km^2 including both parts of Tsavo National Park and about an equal area outside it (figure 8.1).

The area was divided into 10 x 10 Km squares using the Kenya national grid. North and South transects were flown over the centres of the grid squares. Large mammals were counted by two observers in the back of the

aeroplane, the sample strip to be counted being marked by a pair of streamers attached to each wing strut. The plane was flown at 61 m above ground level giving sample strip widths of 135 m at the ground and together the two sampling strips covered 2.7% of the total area. A constant speed of 200 Km h^{-1} was maintained so that each 10 Km square was traversed in three minutes. The data were collected in one minute periods, so that each unit of data represented a rectangle 10 Km wide and 3.33 Km long. An observer in the front of the plane kept records of vegetation condition and cover and various other parameters. While doing this job I was able to make sample counts of termite mounds in the sampling strip on one side of the aircraft.

At the beginning of each minute all termite mounds within the sample strip on the right side of the plane were counted for approximately 10 seconds. The numbers of live and dead mounds were recorded separately and the actual counting time noted. On the ground it is often only possible to tell whether a termite mound is occupied or not by breaking it open. In this survey the mounds recorded as alive all had sharp outlines and chimneys, those recorded as dead were rounded and often obviously eroded. The sites of old termite mounds remain recognisable for a very long time in Tsavo, these sites were not counted, only dead mounds with a recognisable central nest structure were included in the survey. The ten second samples each covered 7.5 ha, 0.225% of the area of the 10 x 3.33 Km rectangle represented by the sample.

Several sources of error and bias affect estimates of animal populations made from data gathered in this way (Jolly, 1969a; Graham and Bell, 1969; Pennycuick and Western, 1972; Caughley, 1974). Among the causes of error are: the visibility of the animals, affected by eg. light conditions, observer alertness and behaviour of the animals; fluctuations in the area sampled caused by variations in the altitude and attitude of the aircraft and timekeeping; and accuracy of counting which depends on the area

searched in a given time, distribution of the animals etc.. All these factors affected the mound counts, particularly lighting. A strong shadow thrown towards the observer highlighted each mound, but without a visible shadow they blended with the background, they were also often obscured by trees. Attempting to count both live and dead mounds made it hard to keep tally accurately at high densities. These errors all tended to cause under-counting, and were accentuated at high densities and in woodland habitats, but no independent estimate of the errors was made so no correction factors can be applied to the sample counts.

8.3 RESULTS

The numbers of live and dead termite mounds recorded in each 10 s count are given in appendix C. The numbers of mounds were compared with figures given by Cobb (1976) for: soil type (figure 8.2) only distinguished as red or non-red; rainfall (figure 2.4); damage to vegetation by elephants (figure 8.3) and the dry season numbers of elephants (figure 8.4). Dry season elephant numbers were used because competition for food between elephants and Macrotermes would be expected to be greatest in the dry season and show up as a reduction in mound numbers if it occurs at all. Cobb (1976) recorded these measurements by 10 Km squares, not by the original sampling units. The three sample mound counts in each 10 Km square were therefore added together for analysis, the resulting patterns of mound distributions are shown in figures 8.5, 8.6 and 8.7.

The most striking result to emerge from the analysis is that Macrotermes subhyalinus has a strong preference for red soils in Tsavo. The mean number of both live and dead mounds counted per 10 Km square on red soils was about 8 (0.36 ha^{-1}.) whereas on non-red soils it was 3.4 (0.15 ha^{-1}.) alive and 4.4 (0.20 ha^{-1}.) dead, the difference between soil types being highly significant (table 8.1). The analysis was extended to the total number of mounds with the same result. The actual mean densities

are given in table 8.2.

Table 8.3 shows the distribution of mound numbers in relation to rainfall, red and non-red soils being treated separately. Analysis of variance (table 8.6) indicates that there were significant trends between rainfall and mound density, but the only strong relationship was an increase in the total mound count on non-red soils as rainfall increased. Mound densities, live and dead, did in general increase with increasing rainfall, except on red soils where dead mounds became fewer as rainfall increased.

The density of live mounds and total density were positively related to elephant damage to vegetation on red soils, but analysis of variance showed the relationship to be much weaker on non-red soils (tables 8.4 and 8.6) although the means showed the same increasing trend with damage.

No relationship was found between the density of termite mounds and the dry season distribution of elephants (tables 8.5 and 8.6).

Figure 8.1

The area covered by the Tsavo Monitoring Flights (from Cobb (1976) figure 1.6.1). The hatched area covers the Taita Hills which were not sampled.

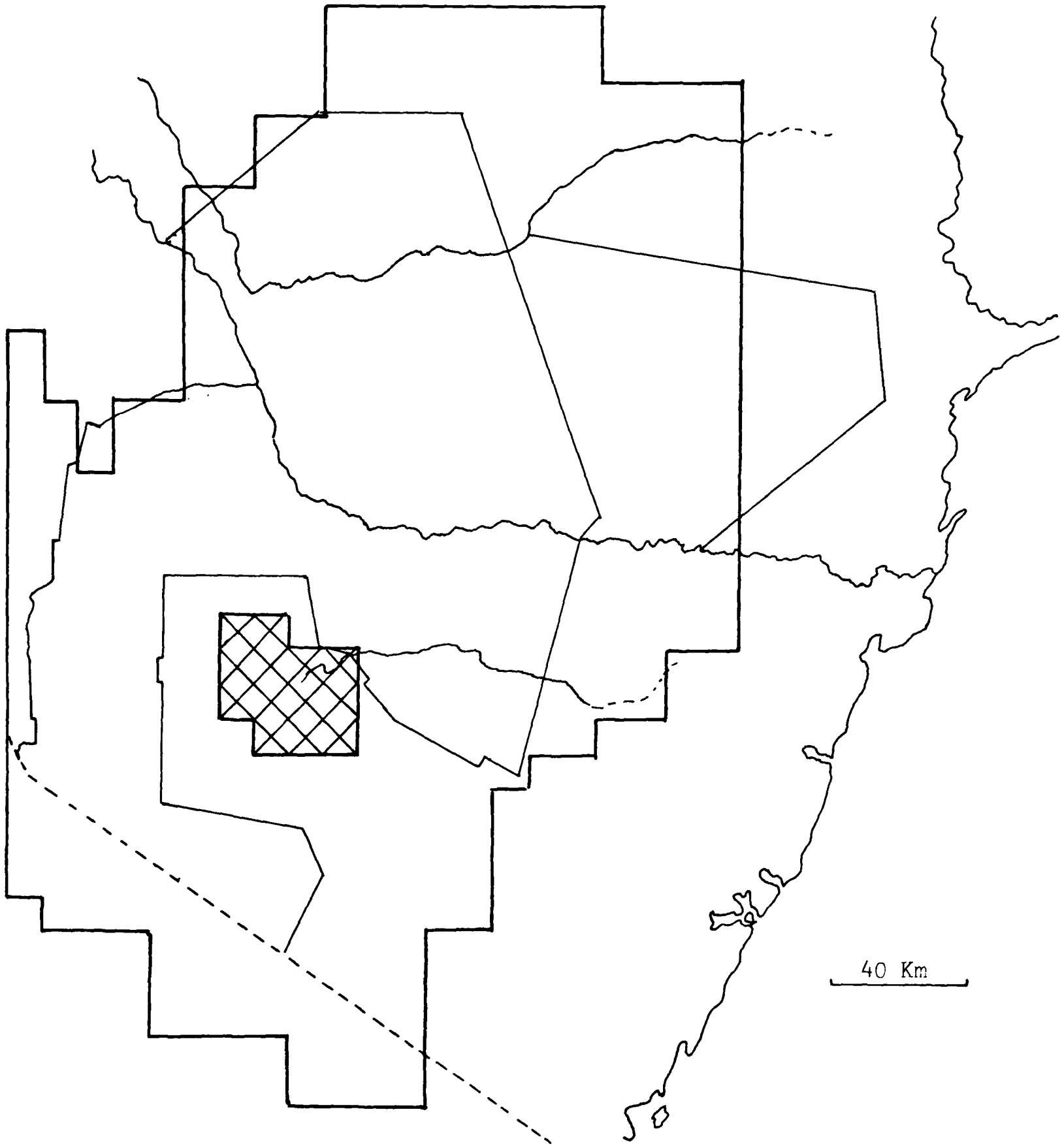


Figure 8.2

The presence or absence of red soils in each 10Km square covered by the Tsavo Monitoring Flights (from Cobb (1976) figure 2.2.3).

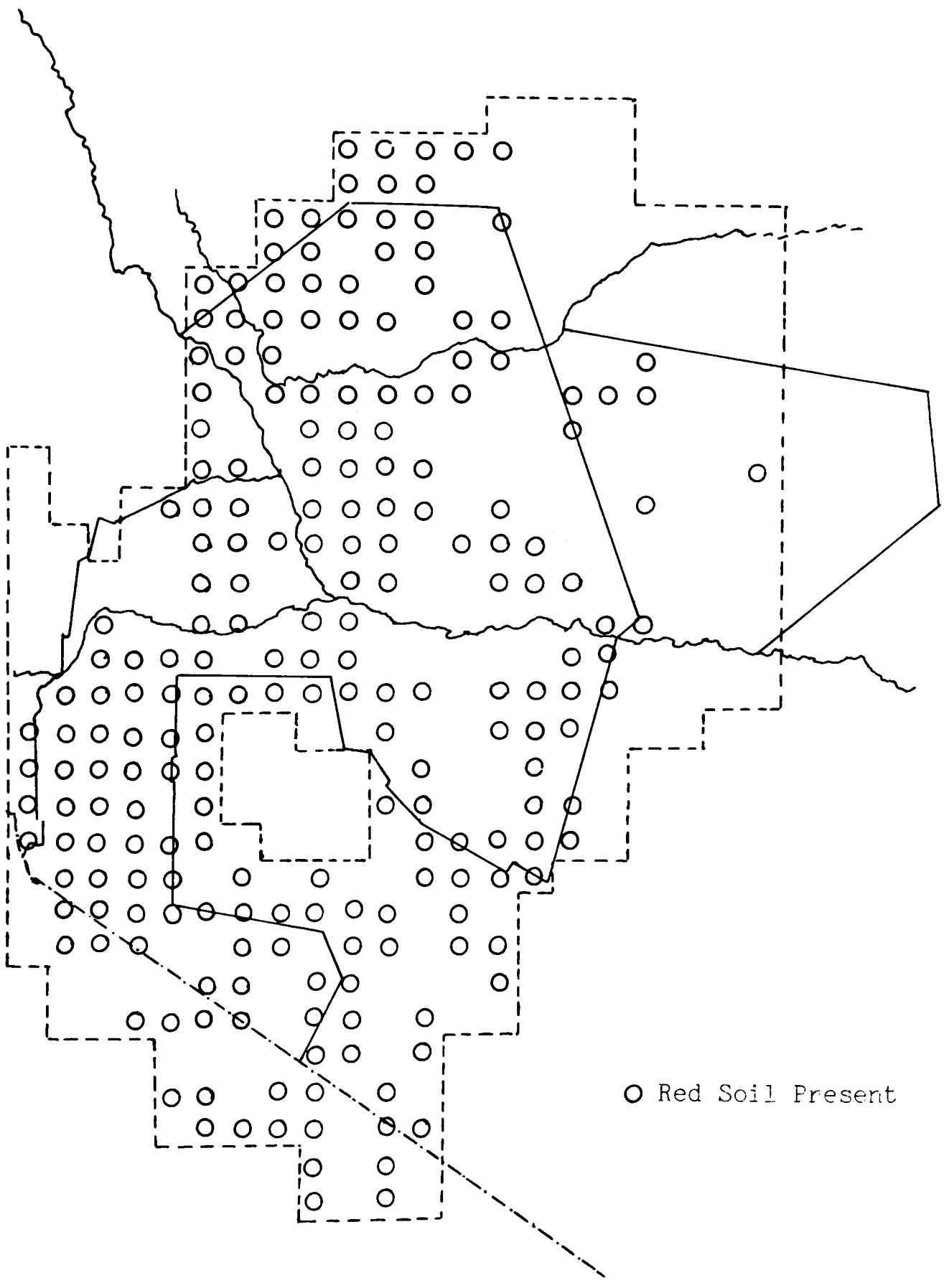


Figure 8.3

Distribution of elephant damage to vegetation in the area covered by the Tsavo Monitoring Flights (from Cobb (1976) figure 2.4.5).

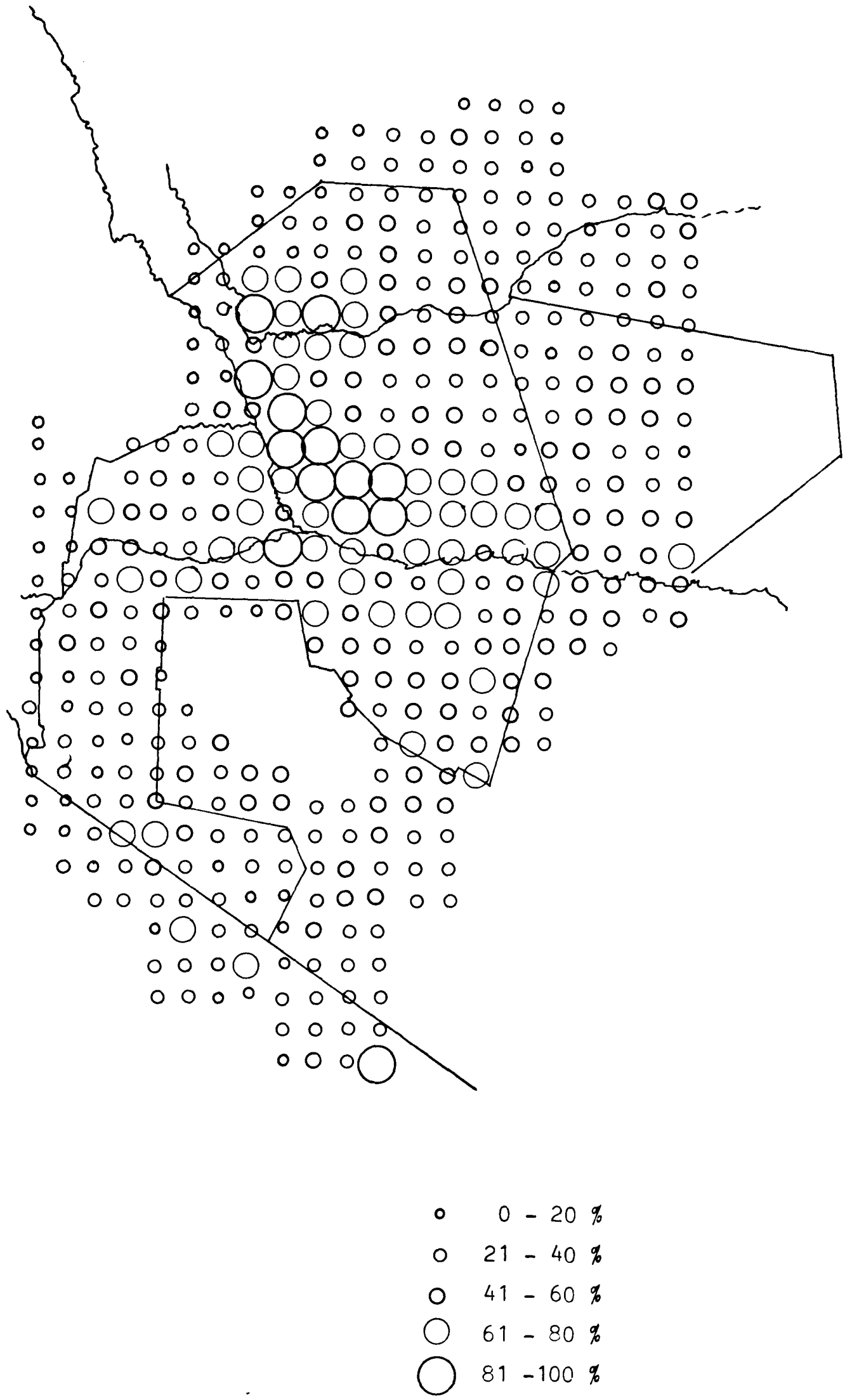
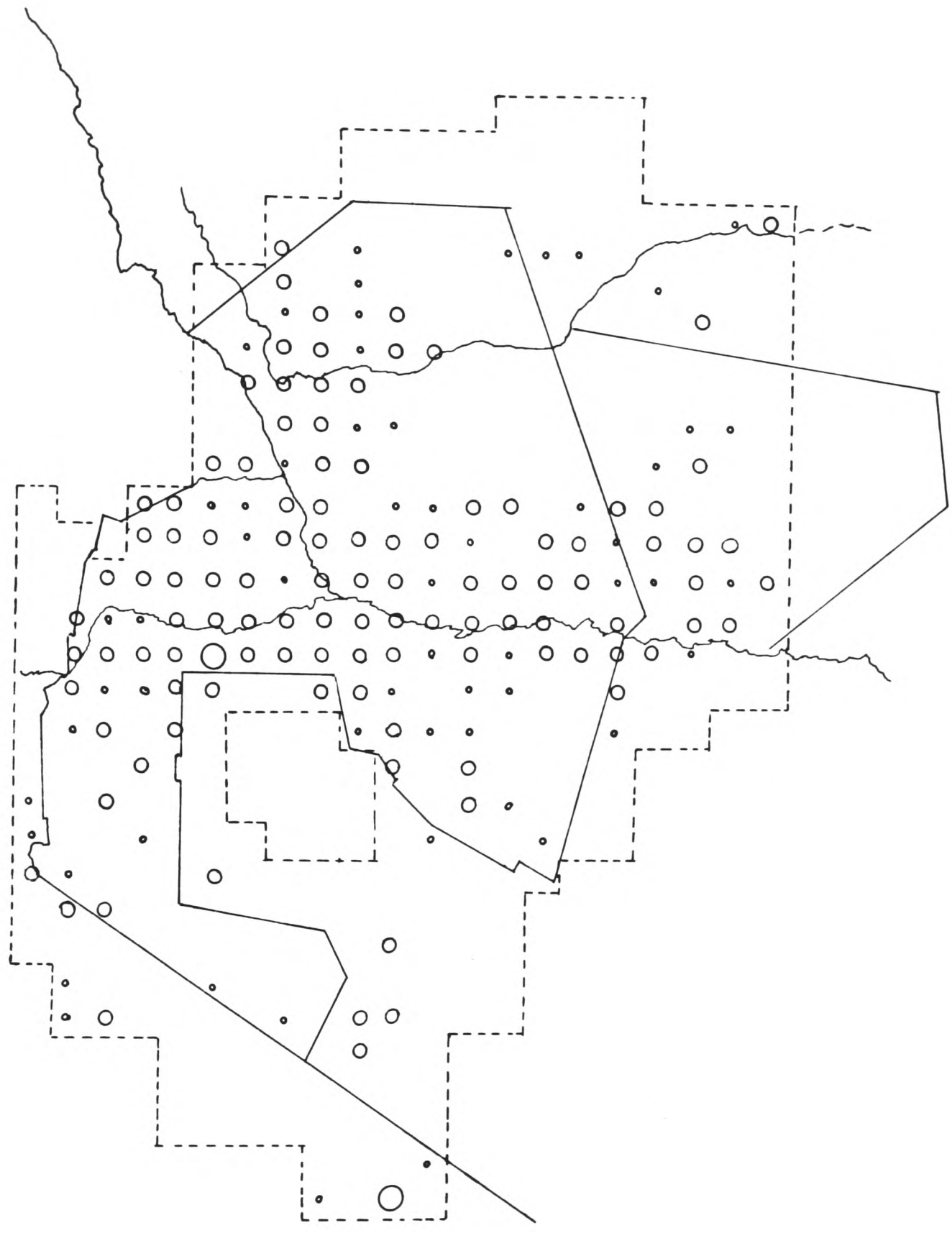


Figure 8.4

Dry season elephant distribution in the Tsavo area (from Cobb (1976) figure 3.3.1).



- 0.1 - 0.99 elephants Km^{-2}.
- 1.0 - 9.99 elephants Km^{-2}.
- 10.0 - 99.99 elephants Km^{-2}.

Table 8.1

Numbers of *Macrotermes subhyalinus* Mounds in Red and Non-Red Soil Areas (Nos. 22.5 ha^{-1})

	Red Soil		Non-Red Soil			
	Mean	S.E.	Mean	S.E.	d	p
Live Mounds	8.14	0.677	3.44	0.355	6.144	<.001
Dead Mounds	8.03	0.518	4.35	0.432	5.455	<.001
All Mounds	16.18	0.885	7.80	0.658	7.598	<.001
N	221		218			

Table 8.2

Densities of *Macrotermes subhyalinus* Mounds on Red and Non-Red Soils (No. ha^{-1} $\pm$ S.E.)

	Red Soil	Non-Red Soil
Live Mounds	0.36 $\pm$ .059	0.15 $\pm$ .031
Dead Mounds	0.35 $\pm$ .045	0.20 $\pm$ .038
All Mounds	0.72 $\pm$ .077	0.34 $\pm$ .057

Table 8.3

Numbers of Live and Dead Macrotermes subhyalinus Mounds in Relation to Rainfall (Nos. 22.5 ha^{-1})

	Red Soil			Non-Red Soil		
Rainfall mm	Mean	S.E.	N	Mean	S.E.	N
			Live Mounds			
200	6.87	2.04	8	1.25	0.49	16
300	9.83	1.58	65	3.04	0.36	112
400	6.88	0.84	109	3.75	0.85	59
500	11.41	1.78	27	6.57	1.87	21
600	4.00	1.11	12	3.2	0.89	10
			Dead Mounds			
200	13.87	4.71	8	3.19	0.91	16
300	8.97	0.79	65	3.69	0.51	112
400	6.96	0.70	109	4.20	0.78	59
500	9.00	1.59	27	8.38	2.23	21
600	6.58	2.93	12	6.1	2.92	10
			All Mounds			
200	20.75	6.56	8	4.44	1.04	16
300	18.8	1.63	65	6.72	0.69	112
400	13.84	1.15	109	7.95	1.36	59
500	20.41	2.69	27	14.95	3.54	21
600	10.58	3.71	12	9.3	3.66	10

Table 8.4

Numbers of Macrotermes subhyalinus Mounds in Relation to an Index of Vegetation Damage by Elephants (Nos. 22.5 ha^{-1})

	Red Soil			Non-Red Soil		
Damage	Mean	S.E.	N	Mean	S.E.	N
			Live Mounds			
1	5.77	0.87	44	1.21	0.51	29
2	6.78	0.88	87	3.54	0.38	98
3	7.35	1.38	48	3.42	0.74	69
4	14.35	2.65	34	5.78	2.11	18
5	14.37	3.91	8	7.25	3.79	4
			Dead Mounds			
1	6.07	1.30	44	2.14	0.88	29
2	7.59	0.81	87	4.30	0.70	98
3	7.98	0.89	48	4.74	0.73	69
4	10.74	1.33	34	6.33	1.42	18
5	12.5	2.99	8	6.25	3.06	4
			All Mounds			
1	11.84	1.81	44	3.34	1.06	29
2	14.37	1.28	87	7.84	0.95	98
3	15.33	1.58	48	8.16	1.24	69
4	25.09	2.66	34	12.11	2.64	18
5	26.87	4.76	8	13.5	6.45	4

Table 8.5

Numbers of Macrotermes subhyalinus Mounds in Relation to an Index of the Dry Season Density of Elephants (Nos. 22.5 ha^{-1})

	Red Soil			Non-Red Soil		
Elephant density	Mean	S.E.	N	Mean	S.E.	N
			Live Mounds			
0	7.05	0.69	132	3.12	0.35	136
1	9.59	2.34	27	2.72	0.72	32
2	9.82	1.67	60	4.80	1.12	50
3	10.50	1.50	2			
			Dead Mounds			
0	7.70	0.71	132	3.88	0.57	136
1	8.52	1.26	27	4.12	0.91	32
2	8.53	0.95	60	5.78	0.90	50
3	8.00	4.00	2			
			All Mounds			
0	14.76	1.07	132	7.00	0.81	136
1	18.11	2.45	27	6.84	1.43	32
2	18.35	1.93	60	10.58	1.56	50
3	18.5	5.50	2			

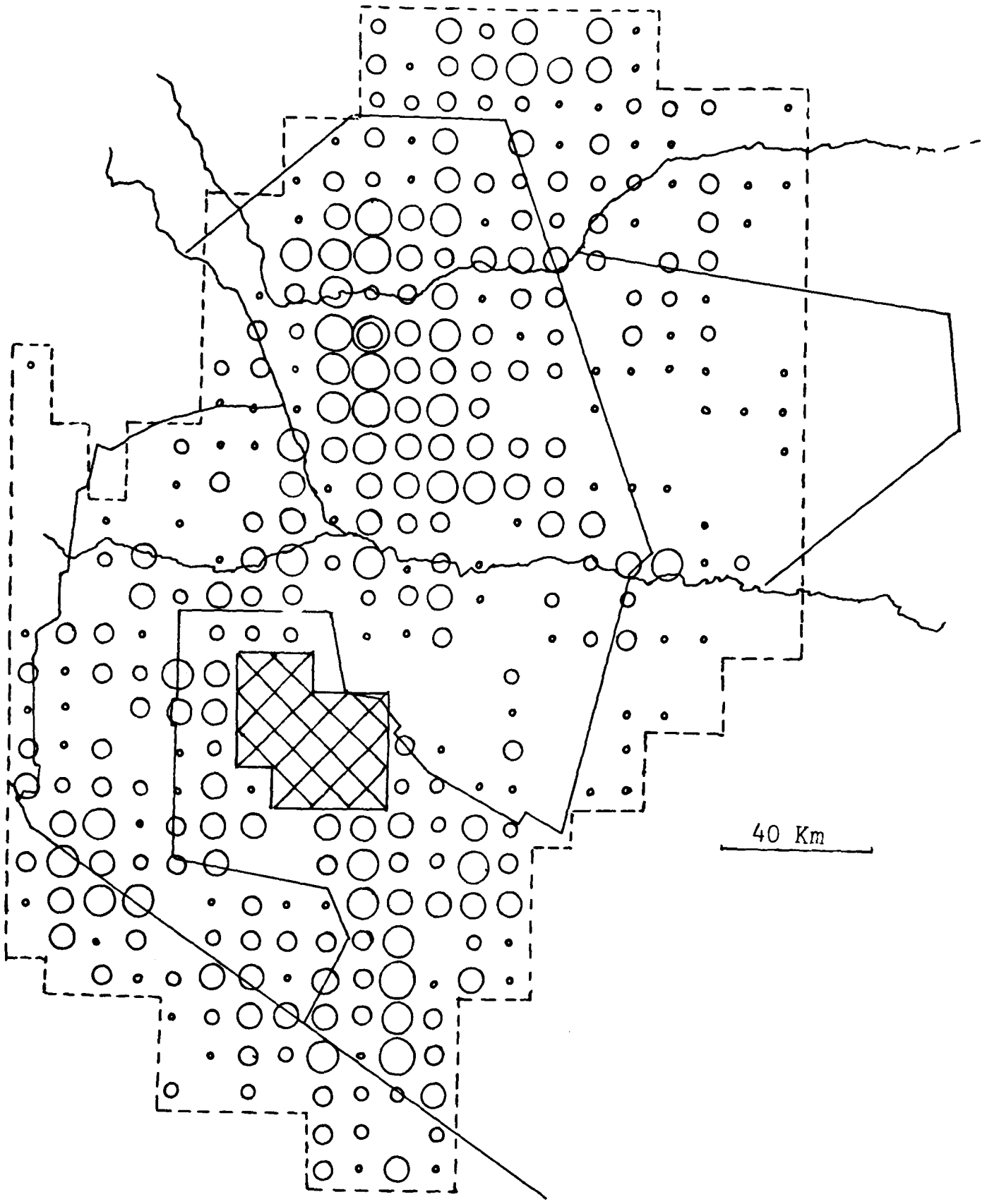
Table 8.6

Analysis of Variance of Mound Numbers in Relation to Rainfall, Damage and Dry Season Elephant Density

	Red Soil		Non-Red Soil	
Mounds	F-Ratio	p	F-Ratio	p
	Rainfall			
Live	2.180	<.05	2.883	<.05
Dead	2.175	<.05	2.823	<.05
All	3.098	<.05	3.937	<.01
	Damage			
Live	5.495	<.001	2.834	<.05
Dead	2.581	<.05	1.477	N.S.
All	7.716	<.001	2.878	<.05
	Dry Season Elephant Density			
Live	0.968	N.S.	1.121	N.S.
Dead	0.148	N.S.	0.819	N.S.
All	0.954	N.S.	1.341	N.S.
	$F_1 = 4$ $F_2 = 214$		$F_1 = 4$ $F_2 = 217$	

Figure 8.5

The distribution of live Macrotermes subhyalinus mounds in the area covered by the Tsavo Monitoring Flights.



Key: Numbers of Mounds Seen in each 10Km Square.

1 and 2	•
3 and 4	o
5 - 8	o
9 - 16	o
17 - 32	o
33 - 64	o
> 64	o

Figure 8.6

The distribution of dead Macrotermes subhyalinus mounds in the area covered by the Tsavo Monitoring Flights.

See figure 8.5 for key.

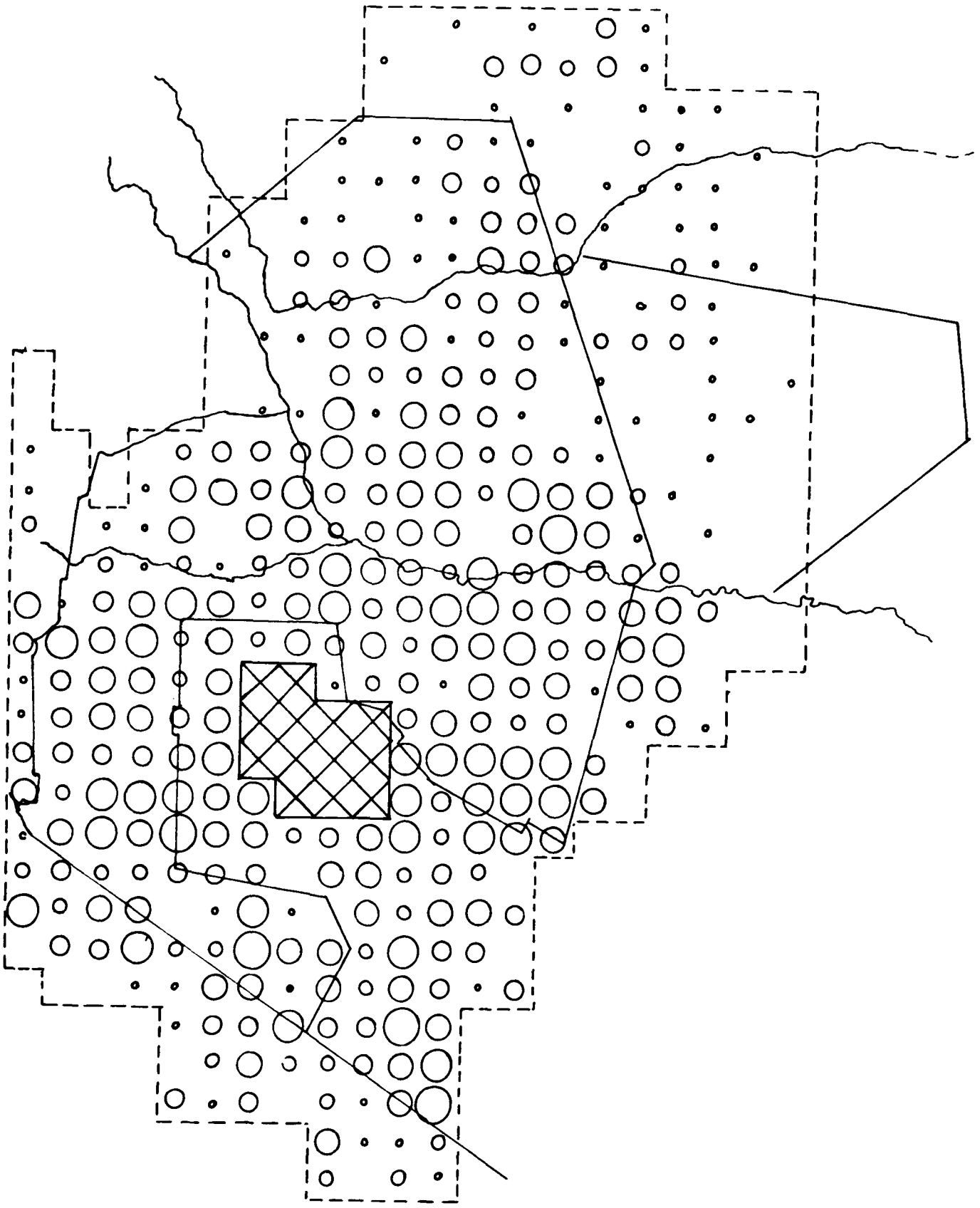
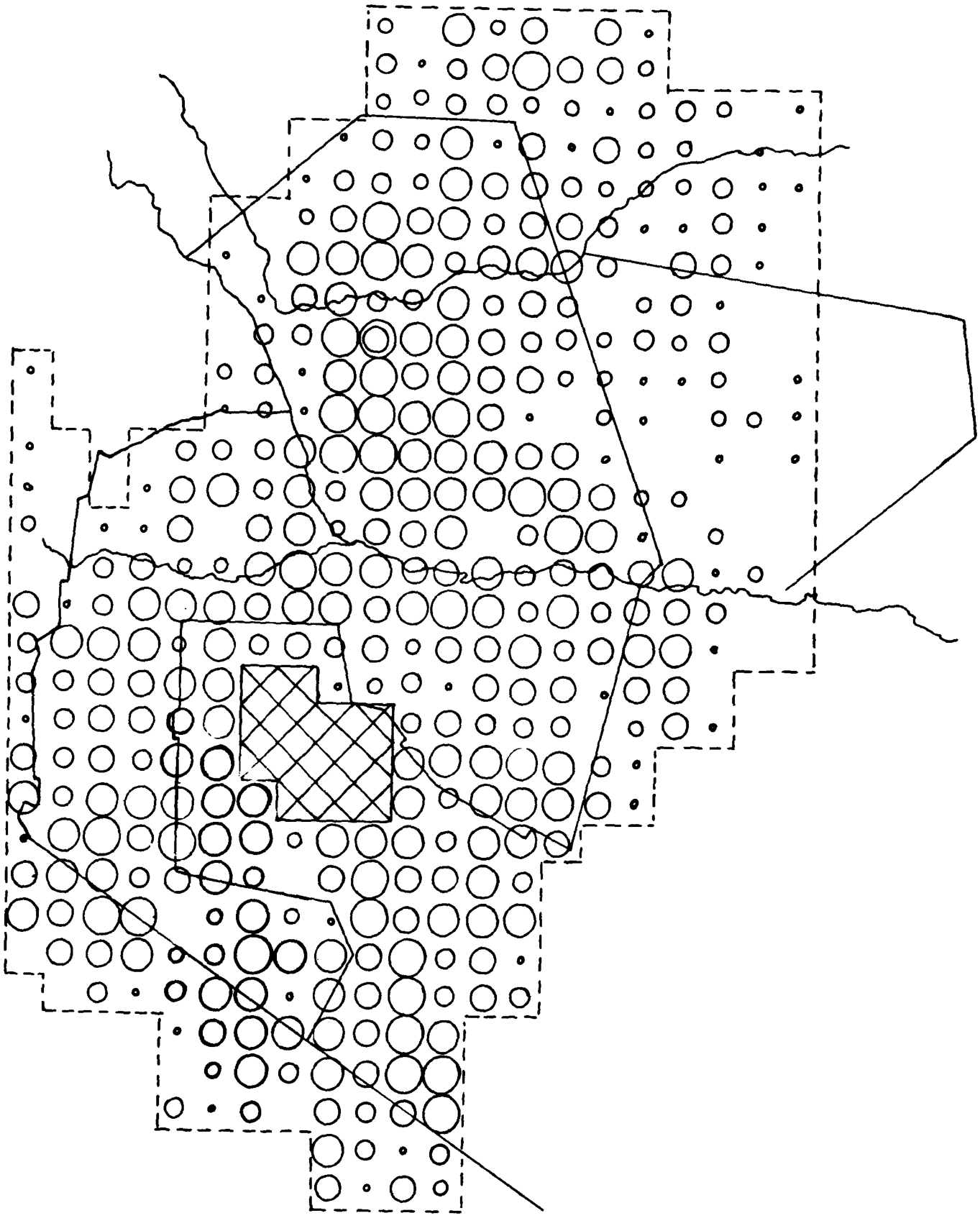


Figure 8.7

The distribution of all Macrotermes subhyalinus mounds in the area covered by the Tsavo Monitoring Flights.

See figure 8.5 for key.



8.4 DISCUSSION

A variety of sampling techniques have been used for estimating the abundance of termite mounds. These studies fall into two groups, those designed to describe the population of one place in detail, eg. Bodot (1966, 1967a), Lepage (1974) and Collins (1977b) and those designed to try to explain the distribution and abundance of the termites, eg. Pomeroy (1977, 1978), Bouillon and Kidieri (1964). The sampling methods used for the two purposes differ in the amount of time spent sampling a given area and the total area covered by the samples. Collins (1977b) carefully searched an area of 6 ha, plotting all Macrotermes bellicosus mounds, with estimates of their heights and diameters. Josens (1972) searched 19 0.25 ha plots. Lepage (1974) used the positions of foraging covers of M.subhyalinus on line transects to calculate the mean diameter of a foraging territory and he used nearest neighbour techniques and discrete plot methods to estimate mound densities, he also recorded the occupancy and condition of each mound. Pomeroy (1977, 1978) sampled mounds of M.bellicosus and M.subhyalinus beside roads throughout Uganda. He used timed counts from a vehicle moving at a set speed, and only counted large mounds within a visually estimated fixed distance from the road-side. The results were related to features of the climate and soils recorded separately. Bouillon and Kidieri (1964) counted mounds of M.bellicosus on aerial photographs of savanna in Zaire.

The present study falls into the second category of low intensity extensive studies. There were several potential sources of error in the collection of the data so that the estimates of mound densities are much less reliable than the differences found between habitat types.

Compared with most other estimates of the density of Macrotermes mounds the estimates from Tsavo are very low (table 8.7). The mean density over the whole area covered by the monitoring flights was 0.26 live mounds ha^{-1}, 0.28 dead mounds ha^{-1} the total being 0.54 mounds ha^{-1}. This gives a

total estimated population of live Macrotermes subhyalinus mounds of 1,133,778. Unfortunately no figures are available for the populations within these colonies so the estimate can not be extended to make an estimate of the total population and biomass of M.subhyalinus in the Tsavo ecosystem. About half the mounds counted were recorded as being dead, although the range was from 0 to 100% dead, the extremes normally occuring when sample numbers were small. Lepage (1974) recorded that 90% of mounds were dead in Sahel Savanna where conditions were in many respects similar to those in Tsavo. He included later erosional stages of mounds in his estimates accounting for some of the discrepancy. Sands (1965c) found that in two disturbed habitats he examined in Northern Guinea Savanna woodland all the M.bellicosus mounds were dead, but in undisturbed woodland 60% were alive. Pomeroy (1977) found that 33 - 100% of M.subhyalinus mounds and 38 - 82% of M.bellicosus mounds were alive in a variety of habitats in Uganda. The higher rainfall in most of Uganda probably causes dead mounds to disappear much faster than they do in Tsavo.

Pomeroy (1978) made an extensive analysis of the distribution of both M.subhyalinus and M.bellicosus in Uganda in relation to 14 environmental variables encompasing features of climate, soil properties and human population. In most cases he found that the relationship between the density of mounds and a particular environmental variable was parabolic, reflecting the existence of an optimum condition. Detailed spatial data are not yet available from Tsavo for most of the variables used by Pomeroy (1978) so his analysis can not be repeated on the density data from Tsavo. However sufficient data are available to make a crude comparison between Pomeroy's (1978) optimum conditions for M.subhyalinus and the conditions prevailing in red and non-red soils in Tsavo (table 8.8). Pomeroy (1978) found a strong relationship between mound densities and rainfall. In Tsavo this relationship is not very pronounced (tables 8.3 and 8.6) possibly because

of the unpredictability of the climate all over Tsavo and the occurrence of prolonged droughts. The rainfall is in any case very close to the 300 mm yr^{-1} considered by Pomeroy to be the lower limit for the species and rainfall of the area is almost certainly directly or indirectly the reason for the low mound population density in the area. The mean annual maximum and minimum temperatures at Voi town (figure 2.3) are close to the optima recorded by Pomeroy for M.subhyalinus but temperatures in much of Tsavo are probably considerably higher. Red soils by and large have physical properties closer to the optima than most of the common non-red soils (table 8.8), a lower percentage of clay probably being particularly important. Live mounds are abundant on some non-red soils often where the clay fraction is minimal for instance on exposed limestone. Conversely M.subhyalinus is completely absent from heavy aluvial clay soils.

Sands (1965c) and Wood et al.(1977) have investigated changes in termite faunas associated with clearing of savanna woodlands for agriculture. M.bellicosus became scarcer and disappeared completely under intense cultivation. The opposite change was observed in Tsavo in relation to elephant damage to vegetation (table 8.4 and 8.6), numbers of live and dead mounds approximately doubled between areas with least damage and with greatest damage. Some of this increase may have been due to an increase in mound visibility from the air, but this does not seem to be adequate to explain the marked jump in live mound numbers between damage levels 3 and 4, without a strong increace in dead mound numbers. The implication is that a wave of new mounds appeared sufficiently recently that the colonies have not yet completed a life cycle, so the wave has not passed on to affect the population of dead mounds. Such a phenomenon must have a recent origin, within the last 5 - 15 years. The most likely explanation for the increased population is that the destruction of woody vegetation provided an initial surplus of food in the form of dead wood. This was followed by increased grass production on the cleared areas sustaining the higher M.subhyalinus

population.

M.subhyalinus distribution was found to be unrelated to elephant dry season density which implies that they do not compete significantly for food.

Table 8.7

Some Estimates of *Macrotermes* mound densities from various parts of Africa

Author	Species	Mound Density Nos. ha^{-1}	Place
Collins, 1977b	*M.bellicosus*	5.5 - 7.2	Southern Guinea Savanna, Nigeria
Pomeroy, 1976	*M.bellicosus*	1.4 - 4.2	Old farmland, Uganda
Pomeroy, 1977	*M.bellicosus* *M.subhyalinus*	1.45 - 9.0 0.75 - 13.25	Throughout Uganda
Hesse, 1955	*Macrotermes* spp.	3 - 4	Savanna, East Africa
Bouillon and Kidieri, 1964	*M.bellicosus*	2 - 3	Savanna, Zaire
Lepage, 1974	*M.subhyalinus*	0.41 - 0.49 alive (10%) 4.46 dead (90%)	Sahel Savanna, Senegal
Sands, 1965c	*M.bellicosus*	0.5 - 2.5	Northern Guinea Savanna, Nigeria
Present study	*M.subhyalinus*	0.15 - 0.36 alive 0.20 - 0.35 dead	Modified Dry Woodland Savanna, Kenya

Table 8.8

Physical Conditions in Tsavo (from van Wijngaarden, pers. comm.) compared with the optimum conditions for *Macrotermes subhyalinus* described by Pomeroy (1978)

	Pomeroy Optima	Red Soil	Non-Red Soil
Rainfall (mm yr^{-1})	1200	200 - 600	200 - 600
Precipitation / Evaporation	0.7	-	-
Mean Minimum Temperature (^{o}C)	16	19.3	19.3
Mean Maximum Temperature (^{o}C)	28	30.5	30.5
% Sand in Topsoil	70	high	< red
% Clay in Topsoil	20	low	> red
% Sand in Subsoil	80+	high	< red
% Clay in Subsoil	60-	low	> red
Total Exchangeable bases (m. equiv. 100 g^{-1})	16	14	28 - 95
pH	6	5.5	5.8-7.8
% Carbon in Soil	2.5	0.7	0.6-1.3
% Nitrogen in Soil	0.2	0.06	0.07 - 0.17
C/N	12	11.7	7.6 - 9

SECTION 9

CONCLUSIONS

Termites are responsible for removing almost all of the dead wood which disappears from the surface of the ground in Tsavo, at least when the climate is in a "dry" phase. At the main study site (mean rainfall 350 mm yr^{-1}.) the mean standing crop of dead wood on the ground was 316.7 g m^{-2} dry weight. Annual dead wood litter fall was 30.8 g m^{-2} dry weight and 28.1 g $m^{-2}yr^{-1}$. dry weight disappeared. An average piece of dead wood took about ten years to decompose completely. Studies at eight other sites, with mean rainfall varying from 200 to 500 mm yr^{-1}, indicate that consumption (C) (g $m^{-2}yr^{-1}$.) of dead wood by termites in Tsavo can be related to rainfall (AP) (mm yr^{-1}.) by the equation

$$C = 0.39\ AP - 101.78$$

Using the data from several other studies in Africa as well a more general result was obtained

$$C = 0.13\ AP - 12.94$$

The fungus growing termites, Macrotermitinae, were the most important consumers of dead wood at all nine experimental sites, but their importance declined as rainfall increased. The percentage of total consumption eaten by Macrotermitinae (MC) was related to total consumption by termites (C) (g $m^{-2}yr^{-1}$.) by

$$MC = 100.4 - 0.18\ C$$

Some differences in food preferences and foraging strategies between species were noted. The Macrotermitinae foraged most intensively on dead wood during the rains whereas other termites ate most dead wood during the long dry season. Differences in resource exploitation between different species of Macrotermitinae are more subtle and probably depend on the ability of some species, eg. Microtermes allaudanus to hold a monopoly in

restricted "favourable" sites while other species forage widely but less intensively eg. Odontotermes mediocris.

Macrotermes subhyalinus mounds never occurred at the high densities observed in other parts of Africa (table 8.7). Their distribution was related to soil types, rainfall and damage to trees by elephants. Subterranean nest chambers of other termite species occurred at a density of 0.77 chambers m^{-2} in a limited ditch sample.

APPENDIX A

Preliminary analysis of vegetation of Tsavo National Park East (South of Galana) by structural and floristic types. From: W. van Wijngaarden, Legend to Preliminary Vegetation Map, September 1976.

The vegetation was described by the relevee method (Braun - Blanquet). The vegetation types are then established by working out these relevees in tables. From the tables the differential species appear which are used for the mapping. So the main mapping units are based on the botanical composition of vegetation. Some of the major mapping units are subdivided on base of differences in dominant species.

The classification of the structure of the vegetation is the same as used by the Kenya Soil Survey (see figure 2.2 p.9).

The tables give:

I The differential species for each of the vegetation types, where:

- o means: occuring in more than 50% of the relevees
- . means: occuring in less than 50% of the relevees, but more than one.

II The dominant species in the most important layers of the vegetation types and subtypes.

Due to practical reasons very little attention is paid so far to the herbs. They are not recognisable 10 months a year and the botanical knowledge of them is far from complete.

Letters in first column refer to grass species (g), shrubs (s) and trees (t).

Part I Differential species Vegetation type		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of relevees		31	7	13	11	10	12	9	7	5	11	8	8	4	1	4	2
Over % tree cover		3	3	2	2	1	1	+	0	0	1	1	+	28	30	20	15
Over % shrub cover		16	30	8	14	12	18	9	1	1	15	25	14	17	20	15	20
Over % grass cover		40	30	35	45	25	35	40	65	60	35	30	40	20	30	50	20
Vegetation structure		BG	B	BG	BG	BG	BG	BG	G	G	BG	B	BG	BW	BW	BW	WB
s	Dirichletia glaucescens	Hiern	o	o	.	.	.					o	o	.				o
g	Eragrostis caespitosa	chiov.	o	.	.	.	.					.	.	.	.			
g	Latipes senegalensis	kunth	o	.	o	.	o					.	o	o	.			
s	Premna holstii	Guerke	o	o											.			.
s	Ochna inermis	(Forsk.)	o	.											.			
s	Strychnos decussata	(Pappe)	o	.											o			o
s	Erythrococca atrovirens	(Pax)	.	.														
s	Hymenodictyon parvifolium	Oliv.	.	.											.			
s	Lannea alata	(Engl.)	.	.											o			o
s	Bauhinia taitensis	Taub.		o									o					.
s	Erythrochlamys spectabilis	Guerke		o									o					.
s	Disperma kilimandscharica	(Lindau)		.						.		.						.
s/t	Dobera glabra	(Forsk.)			o	o	o	.					o		.	o		
s	Anisotes parvifolius	Oliv.				o	o	.					.			.		
s	Maerua denhardtiorum	Gilg				.	.								.	o		
s	Salvadora persica	L.				.	.	.								o		
s	Lycium europaeum	L.					.	.										
s	Maerua subcordata	(Gilg)					.	.								.		
s	Croton dichogamus	Pax					.	.							.			o

Part I	Differential species (cont.)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
s	Cadaba ruspolii	Gilg						o	.	.				.				
s	Cadaba glandulosa	Forsk.						.	o		.			.				
s	Blepharispermum fruticosum	klatt & Schinz						o	.	.				.				
s	Sericocomopsis hildebrandtii	(c. B. Cl.)						.	.	.				o				
s	Grewia tenax	(Forsk.)						o	o	.				.				
s	Terminalia parvula	Pamp.						.	.	o				.				
s	Acacia zanzibarica	(S. Moore)							.	o	o							
s	Maerua sp.C.								.		.							
g	Sporobolus helvolus	(Trin.)						.	o	.	o							
g	Schoenefeldia transiens	(Pilg.)							o	.	o							
g	Pennisetum massaicum	Stapf									o							
g	Enteropogon somalensis	Chiov.									o							
s	Combretum aculeatum	Vent.			.	.	.	o	o	o								o
s	Caucanthus albidus	(Nied.)						.	.	o		.						.
s	Caesalpinia trothae	Harms						.		o								.
g	Schmidtia bulbosa	Stapf						o	o	o								o
t	Mature Commiphora sp.										o	o						o
t/s	Boswellia hildebrandtii	Engl.									o	.						.
t	Terminalia spinosa	Engl.									o	.						
t	Newtonia hildebrandtii	(Vatke)											o					
t	Tamarindus indica	L.											.					
s	Lawsonia inermis	L.											o					
g	Cynodon dactylon	(L.)											o					
s	Tarenna graveolens	(S. Moore)																o
t	Ficus sp.												.					o
s/t	Boscia salicifolia	Oliv.																.

Part II Dominant species

Veg. type	Veg. Struct.	Dominant trees	Dominant shrubs	Dominant grasses
1^a	G	———	———	Chrysopogon aucheri (Boiss.)
1^b	BG	———	Sericocomopsis pallida (S. Moore)	Latipes senegalensis Aristida adscensionis L.
1^c	B	Delonix elata (L.) Platycelyphium voense (Engl.)	Strychnos decussata	Eragrostis caespitosa
1^d	B	Delonix elata Platycelyphium voense Melia volkensii Guerke	Premna holstii Premna resinosa (Hochst.)	Eragrostis caespitosa Chloris roxburghiana schult. Aristida adscensionis
2	B	Delonix elata	Premna holstii Premna resinosa Bauhinia taitensis	Chloris roxburghiana Aristida adscensionis
3^a	BG	———	Sericocomopsis pallida	Chrysopogon aucheri Cymbopogon pospischilii (K. schum.)
3^b	BG	———	Boscia coriacea Pax Cordia gharaf (Forsk)	Chloris roxburghiana Digitaria macroblephara (Hack.) Aristida adscensionis
4	BG	Delonix elata	Boscia coriacea Premna resinosa Cordia gharaf	Chloris roxburghiana Bothriochloa radicans (Lehm.)
5^a	BG	———	Sericocomopsis pallida	Chloris roxburghiana Latipes senegalensis Aristida adscensionis

Part II Dominant species (cont.)

Veg. type	Veg. Struct.	Dominant trees	Dominant shrubs	Dominant grasses
5[b]	BG	———	Cordia gharaf	Aristida adscensionis
5[c]	B	———	Anisotes parvifolius	Aristida adscensionis
6	BG	———	Boscia coriacea Cordia gharaf Grewia tenax	Chrysopogon aucheri Chloris roxburghiana
7	BG	———	Cordia gharaf Cadaba glandulosa	Chrysopogon aucheri Chloris roxburghiana Tetrapogon bidentatus Pilg.
8	G	———	Acacia zanzibarica	Chrysopogon aucheri
9	G	———	———	Schoenefeldia transiens Pennisetum massaicum Enteropogon somalensis
10	BG	———	Boscia coriacea Premna resinosa	Schmidtia bulbosa Aristida adscensionis
11	B	Delonix elata	Bauhinia taitensis Premna resinosa	Schmidtia bulbosa Aristida adscensionis
12	BG	———	Boscia coriacea Premna resinosa Ehretia teitensis Guerke	Chloris roxburghiana
13	BW	Mature Commiphora sp. Boswellia hildebrandtii	Strychnos decussata Lannea alata	Chloris roxburghiana

Part II Dominant species (cont.)

Veg. type	Veg. Struct.	Dominant trees	Dominant shrubs	Dominant grasses
14	BW	Mature Commiphora sp.	Croton dichogamus Combretum sp.	Chloris roxburghiana Aristida adscensionis
15[a]	W	Dobera glabra Newtonia hildebrandtii	Lawsonia inermis	———
15[b]	G	———	———	Cynodon dactylon
16	WB	Euphorbia quinquecostata Volkens Mature Commiphora sp.	Combretum aculeatum Tarenna graveolens	Schmidtia bulbosa

APPENDIX B

Weight losses by transect discs attributable to termite attack g.

Numbers in brackets refer to calculations made when there was a negative estimate of weight loss. These bracketed figures were used in the main analysis (section 4.3).

Abbreviations used for species names:

O.m. = Odontotermes mediocris

O.z. = Odontotermes zambesiensis

Mi. = Microtermes allaudanus

Syn. = Synacanthotermes zanzibarensis

A.l. = Amitermes lonnbergianus

A.s. = Amitermes sciangallorum

Mc. = Microcerotermes sp.I.

A mean of 3 g. was lost by discs taken as controls and this has been subtracted from the overall weight loss by each disc to give the figure for consumption by termites.

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
A	June	O.m.	233	227	3		
			221	219	(-1)	3 (2)	
		O.z.	219	190	26		
			185	170	12		
			170	162	5		
			110	108	(-1)		
			216	213	0	43(42)	
		Mi.	265	225	37		
			221	219	(-1)	37(36)	
		Mc	151	152	(-4)	(-4)	83 (76)
	July	O.m.	204	201	0		
			167	156	8		
			213	204	6		
			210	206	1		
			190	184	3		
			152	147	2		
		(+Mi.)	132	104	25	45	45
	Aug.	O.m.	339	333	3		
			186	177	6		
			261	259	(-1)		
			162	159	0	9 (8)	
		O.z.	271	207	61		
			413	403	7	68	
		Mc.	151	141	7		
			134	128	3	10	87 (86)
	Sept.	O.z.	147	142	2		
			166	163	0		
			328	328	(-3)	2(-1)	
		A.l.	139	114	22		
			226	223	0	22	24 (21)
	Oct.	O.m.	211	186	22		
			184	184	(-3)	22(19)	
		A.l.	379	374	2	2	
		Mc.	441	432	6	6	30 (27)
	Nov.	O.m.	181	175	3		
			216	214	(-1)		
			403	402	(-2)	3 (0)	
		A.l.	230	223	4		
			180	175	2	6	9 (6)
	Dec	O.m.	204	203	(-2)		
			208	203	2		
			125	120	2		
			151	147	1		
			173	171	(-1)	5 (2)	
		O.z.	179	177	(-1)		
		(+A.l.)	218	205	10		
			156	154	(-1)	10 (8)	
		Mi.	150	150	(-3)	(-3)	
		Mc.	259	248	8	8	23 (15)
	Jan	O.m.	575	562	10		
			272	239	30		
			223	219	1		
			161	152	6		
			319	310	6	53	
		A.l.	484	482	(-1)	(-1)	
		Mc.	338	305	30	30	83 (82)

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
A cont.	Feb.	O.m.	286	283	0		
			144	137	4		
			335	331	1		
			208	201	4		
			250	245	2	11	
		Mi.	266	262	1		
			174	164	7	8	19
	March	O.m.	270 179	264 177	3 (-1)		
			185	183	(-1)	3 (1)	
		Mi.	149	147	(-1)	(-1)	
		A.l.	237	233	1	1	
		Mc.	201	199	(-1)	(-1)	4 (0)
	April	O.m.	183	182	(-2)		
			107	102	2		
			231	227	1		
			217	211	3		
			160	157	0		
			148	144	1		
			146	145	(-2)		
			285	278	4	11 (7)	
		O.z.	365	360	2	2	13 (9)
					11 Month total		420 (388)
B	June	O.m.	252	244	5	5	5
	July	O.m.	220	217	0	0	
		O.z.	165	136	26	26	26
	Aug.	O.m.	185	184	(-2)	(-2)	(-2)
	Oct.	O.m.	163	158	2		
			286	286	(-3)	2(-1)	2 (-1)
	Nov.	O.m.	262	250	9	9	9
	Dec.	O.m.	234	229	2		
			445	441	1	3	3
	Jan.	O.m.	223	216	4	4	4
	Feb.	O.m.	268	256	9		
			261	257	1		
			271	257	11		
			291	284	4		
			266	256	7		
			229	215	11		
			244	237	4	47	47
	March	O.m.	372	361	8	8	
		O.z.	333	316	14	14	22
	Arpil	O.m.	352	345	4		
			198	198	(-3)		
			217	209	5		
			190	186	1		
			253	243	7	17(14)	17 (14)
					11 Month total		135 (127)

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
C	June	O.m.	321	315	3		
			308	301	4	7	
		O.z.	455	435	17	17	
		Mi.	550	514	33	33	
		A.l.	388	390	(-5)		
			241	238	0	(-5)	57 (52)
	July	O.m.	398	396	(-1)		
			344	340	1		
			326	323	0		
			789	778	8		
			248	240	5		
			216	211	2		
			249	229	17	33(32)	
		O.z.	182	178	1	1	
		A.l.	198	166	29	29	
		A.s.	251	247	1	1	
		Mc.	309	303	3	3	67 (66)
	Aug.	O.z.	384	379	2		
			334	328	3		
			320	317	0	5	
		Mi.	328	305	20	20	
		A.l.	325	327	(-5)		
			229	211	15	15(10)	40 (35)
	Sept.	O.m.	465	462	0	0	
		A.l.	202	199	0	0	0
	Oct.	O.m.	349	343	3		
			326	316	7		
			173	171	(-1)	10 (9)	
		Mi.	251	250	(-2)		
			418	408	7		
			196	195	(-2)	7 (3)	
		A.l.	178	177	(-2)		
			274	270	1	1(-1)	18 (11)
	Nov.	O.m.	226	214	9		
			224	221	0		
			364	360	1		
			402	397	2	12	
		Mi.	388	379	6		
			252	247	2		
			253	249	1		
			148	139	6	15	
		Syn.	244	232	9	9	
		A.l.	280	273	4	4	40
	Dec.	O.m.	234	232	(-1)		
			107	97	7		
			388	382	3		
			377	367	7		
			106	106	(-3)		
			164	159	2		
			228	228	(-3)	19 (12)	
		O.z.	177	174	0	0	
		Mi.	241	239	(-1)		
			211	206	2		
			128	120	5		
			280	283	(-6)		
			102	100	(-1)		

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
C cont.	Dec. cont.	Mi.cont.	333	332	(-2)	7(-3)	
		A.1.	171	170	(-2)		
			343	336	4	4 (2)	30 (11)
	Jan.	O.m.	663	649	11		
			244	229	12		
			210	202	5		
			251	221	27		
			313	308	2		
			430	406	21		
			152	150	(-1)	78(77)	
		O.z.	307	282	22	22	
		Mi.	357	352	2		
			172	166	3	5	
		Syn.	265	261	1	1	
		A.1.	247	242	2		
			119	107	9		
			329	320	6	17	123(122)
	Feb.	O.m.	158	147	8		
			191	189	(-1)		
			148	146	(-1)		
			211	208	0		
			450	454	(-7)	8(-1)	
		Mi.	185	183	(-1)		
			227	224	0		
			205	180	22		
			238	219	16		
			237	229	5		
			270	258	9	52(51)	
		Syn.	187	175	9	9	
		A.1.	289	275	11		
			453	458	(-8)	11 (3)	
		Mc.	187	184	0		
			239	228	8	8	88 (70)
	March	O.m.	209	201	5		
			329	326	0		
			210	206	1		
			214	213	(-2)		
			180	177	0		
			281	273	5		
			296	290	3	14(12)	
		O.z.	268	267	(-2)		
			298	296	(-1)		
			222	222	(-3)		
			178	165	10	10 (4)	
		Mi.	323	321	(-1)		
			320	316	1		
			154	145	6	7 (6)	
		A.1.	206	200	3	3	34 (25)
	April	O.m.	180	174	3		
			263	251	9		
			106	105	(-2)		
			175	173	(-1)		
			292	285	4	16(13)	
		Mi.	190	188	(-1)		
			128	124	1		
			192	188	1		

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
C cont.	April cont.	Mi.	102	94	5		
		cont.	189	187	(-1)	7 (5)	
		Syn.	261	253	5	5	28 (23)
					11 Month total		525 (455)
D	June	O.m.	418	418	(-3)	(-3)	
		O.z.	401	402	(-4)		
			343	337	3	3(-1)	3 (-4)
	July	O.m.	180	174	3		
			435	430	2		
			227	222	2		
			190	185	2	9	9
	Sept.	O.m.	179	173	3	3	3
	Oct.	O.m.	209	205	1	1	1
	Nov.	O.z.	266	262	1	1	1
	Jan.	O.m.	212	211	(-2)		
			192	192	(-3)		
			247	246	(-2)		
			173	172	(-2)		
			119	112	4	4(-5)	4 (-5)
	Feb.	O.m.	106	105	(-2)		
			201	194	4	4 (2)	
		O.z.	128	107	18	18	26 (20)
	March	O.m.	235	215	17		
			114	111	0		
			300	294	3	20	
		Mc.	162	158	1	1	21
	April	O.m.	294	291	0		
			249	247	(-1)		
			208	207	(-2)		
			113	112	(-2)		
			108	102	3		
			196	194	(-1)		
			256	252	1	4(-2)	
		O.z.	225	217	5	5	9 (3)
					11 Month total		77 (49)
E	June	O.m.	271	270	(-2)		
			340	336	1		
			281	271	7		
			281	275	3		
			659	655	1	12(10)	
		O.z.	297	281	13		
			355	320	32		
			574	575	(-4)	45(41)	
		A.1.	244	235	6	6	63 (57)
	July	O.m.	301	295	3		
			211	202	6	9	
		O.z.	190	115	72	72	
		A.1.	170	125	42	42	123

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
E cont.	Aug.	O.m.	271	272	(-4)		
			225	221	1	1(-3)	
		O.z.	470	441	26		
			252	236	13		
			108	103	2	41	
		A.l.	362	326	33	33	78 (71)
	Sept.	O.m.	239	229	7		
			109	106	0	7	
		A.l.	135	134	(-2)	0(-2)	7 (5)
	Oct.	O.m.	228	207	18	18	
		A.l.	202	191	8	8	26
	Nov.	O.z.	153	148	2		
			225	215	7		
			514	504	7	16	
		A.l.	198	192	3	3	19
	Dec.	O.m.	239	239	(-3)		
			143	140	0		
			328	325	0		
			538	513	22		
			369	359	7	29(26)	
		A.l.	158	154	1	1	30 (27)
	Jan.	O.m.	312	298	11		
			162	149	10		
			170	166	1		
			191	179	9		
			210	201	6		
			204	172	29	66	
		A.l.	521	515	3	3	69
	Feb.	O.m.	125	121	1		
			211	209	(-1)		
			441	430	8		
			463	430	30	39(38)	
		O.z.	277	220	54		
			109	106	0		
			104	101	0	54	93 (92)
	March	O.m.	271	251	17		
			245	236	6		
			165	159	3		
			111	109	(-1)	26(25)	
		A.l.	222	202	17		
			316	310	3	20	46 (45)
	April	O.m.	250	245	2		
			321	308	10		
			196	194	(-1)		
			297	294	0	12(11)	
		O.z.	515	511	1	1	
		Mi.	253	234	16	16	29 (28)
					11 Month total		583 (562)

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
F	June	O.m.	136	125	11		
			465	465	(-3)		
			339	335	1	12 (9)	12 (9)
	July	O.m.	248	245	0		
			138	112	23	23	
		O.z.	369	337	29	29	52
	Aug.	O.m.	228	210	15	15	15
	Sept.	O.m.	294	289	2		
			330	307	20	22	
		O.z.	343	312	28	28	50
	Oct.	O.m.	235	229	3	3	
		A.l.	278	258	17	17	20
	Nov.	O.m.	227	218	6	6	6
	Jan.	O.m.	338	323	12		
			348	325	20		
			272	268	1		
			121	110	8	41	41
	Feb.	O.m.	253	247	3		
			230	225	2		
			229	217	9	14	14
	March	O.m.	258	250	5		
			200	195	2		
			312	310	(-1)		
			209	205	1		
			355	351	1	9 (8)	9 (8)
	April	O.m.	375	364	8		
			265	261	1		
			371	359	9		
			111	112	(-4)		
			377	356	18	36(32)	36 (32)
					11 Month total		255 (247)

G	June	O.m.	271	261	7		
			423	413	7		
			336	334	(-1)		
			463	445	15	29(28)	
		O.z.	400	388	9	9	38 (37)
	July	O.m.	163	147	13		
			191	191	(-3)		
			216	204	9		
			140	129	8	30(27)	30 (27)
	Aug.	O.m.	233	230	0	0	
		O.z.	374	355	16	16	16
	Sept.	O.m.	250	250	(-3)	(-3)	
		O.z.	396	382	11		
			286	276	7	18	18 (15)
	Nov.	O.m.	516	502	11	11	
		O.z.	258	242	13	13	24
	Dec.	O.m.	272	270	(-1)		
			205	198	4		
			401	401	(-3)	4 (0)	4 (0)

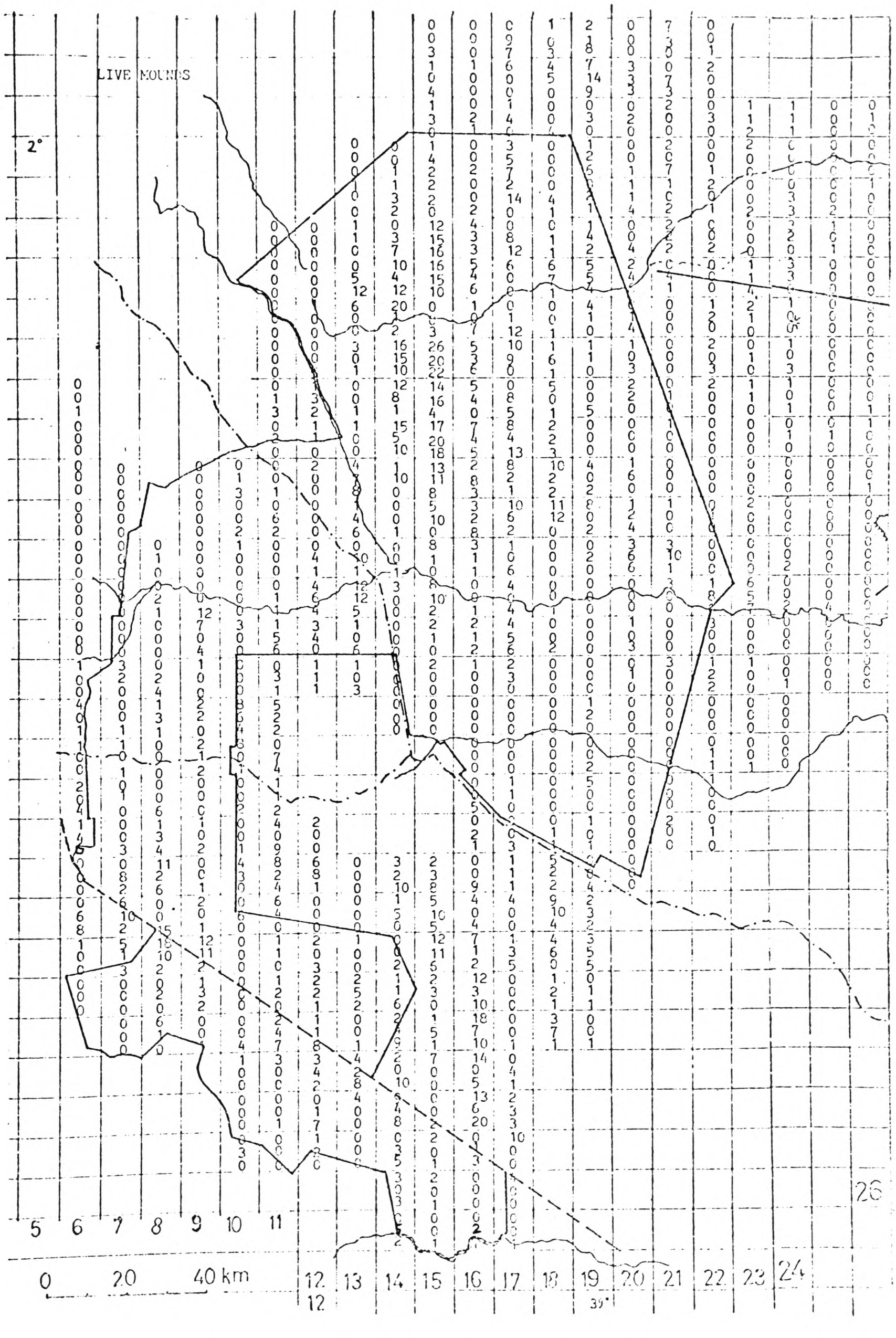
Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
G cont.	Jan.	O.m.	446	418	25		
			308	300	5		
			206	185	18		
			240	232	5		
			191	188	0		
			211	210	(-2)		
			156	158	(-5)	53(46)	
		O.z.	413	395	15		
			408	376	29		
			194	183	8	52	105 (98)
	Feb.	O.z.	208	206	(-1)		
			276	274	(-1)	(-2)	(-2)
	March	O.m.	401	385	13		
			187	182	2		
			161	146	12		
			155	152	0		
			195	193	(-1)		
			215	208	4		
			155	144	8	39(38)	39 (38)
	April	O.m.	222	208	11		
			128	125	0		
			175	173	(-1)		
			188	183	2		
			102	97	2		
			335	332	0		
			110	108	(-1)		
			117	114	0		
			202	201	(-2)		
			137	135	(-1)		
			257	247	7	22(17)	22 (17)
					11 Month total		296 (270)

M	June	O.m.	168	162	1		
			228	229	(-4)		
			390	390	(-3)		
			253	251	(-1)	1(-7)	
		O.z.	333	328	2	2	3 (-5)
	July	O.m.	196	190	3		
			232	226	3		
			200	187	10		
			149	143	3	19	19
	Aug.	O.m.	110	105	2	2	
		O.z.	340	340	(-3)	(-3)	2 (-1)
	Sept.	O.z	157	153	1		
			417	384	30	31	31
	Oct.	O.m.	410	410	(-3)		
			236	230	3	3 (0)	
		O.z.	108	104	1	1	4 (1)
	Nov.	A.l.	112	91	18	18	18

Tsct.	Month	Species	Initial dry wt.	Final dry wt.	Consump. by tmts.	Species Total	Month Total
M cont.	Dec.	O.m.	122	113	6		
			276	268	5		
			778	767	8		
			211	209	(-1)		
			179	175	1	20(19)	
		O.z.	122	118	1		
			129	126	0	1	
		A.l.	175	172	0		
			112	112	(-3)	0(-3)	21 (17)
	Jan.	O.m.	357	349	5	5	
		O.z.	243	236	4	4	
		A.l.	286	281	2	2	11
	Feb.	O.m.	250	245	2		
			379	375	1		
			212	190	19	22	
		O.z.	134	128	3		
			339	331	5	8	30
	March	O.m.	418	414	1	1	1
	April	O.m.	203	196	4		
			223	219	1		
			218	215	0		
			201	199	(-1)		
			234	222	9	14(13)	14 (13)
					11 Month total		154 (134)

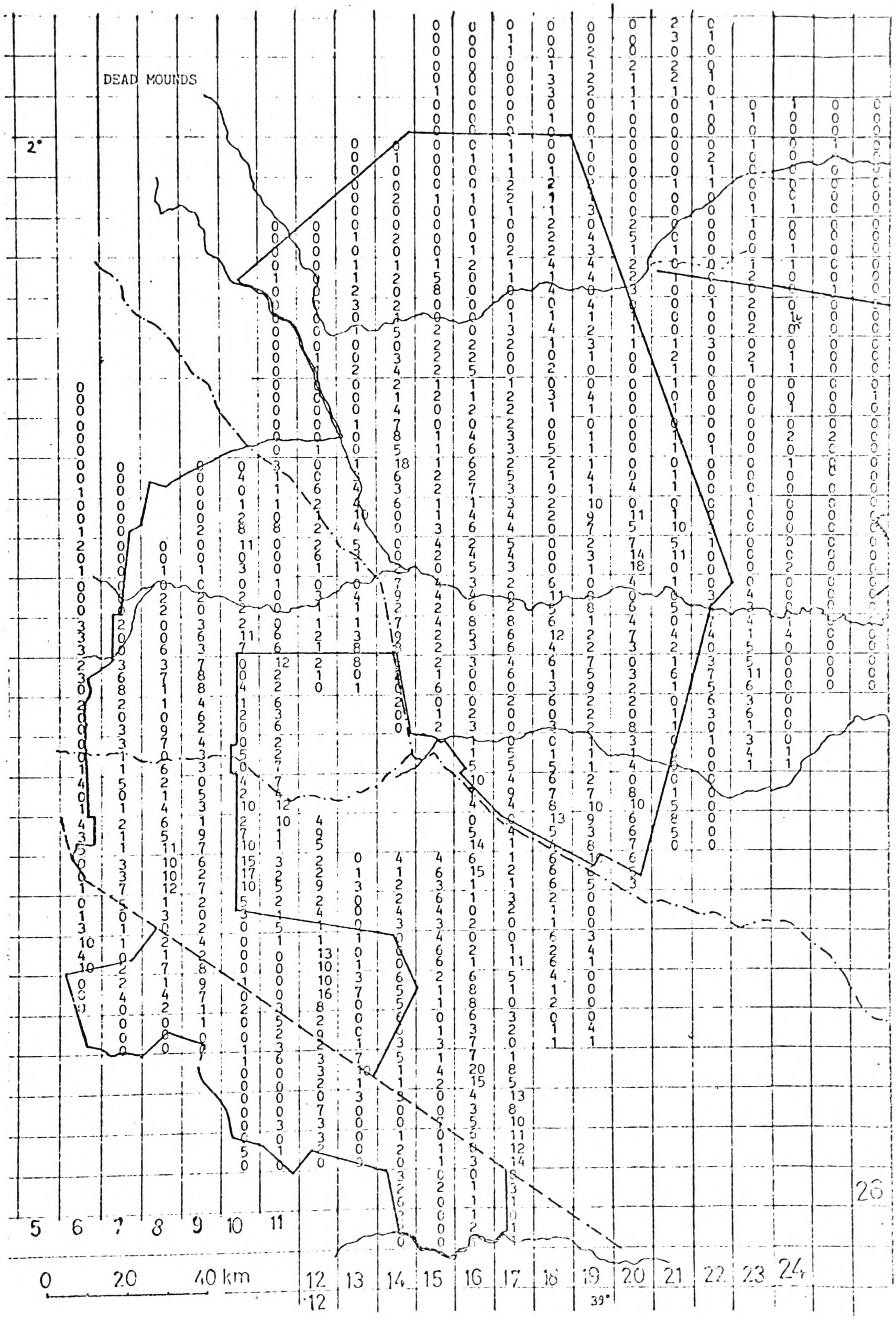
Appendix C

Data from the monitoring flight counts of live and dead Macrotermes subhyalinus mounds. Numbers counted in each 10s sample.



Appendix C (cont.)

Data from the monitoring flight counts of live and dead Macrotermes subhyalinus mounds. Numbers counted in each 10s sample.



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