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THE ROLE OF TERMITES IN LITTER DECOMPOSITION AND
SOIL TRANSLOCATION WITH SPECIAL REFERENCE TO
ODONTOTERMES IN ARID LANDS OF NORTHERN KENYA

BY

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I declare that this thesis is my original work
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S U M M A R Y

This research work on the role of termites in an arid ecosystem covered eleven months (August 1981 to June 1982). It was conducted at the site of the UNESCO integrated project in Arid Lands (UNESCO - IPAL). This area is in Western Marsabit district, Kenya. About 80% of this area is semi-arid thorn bush scrubland and receives annual rainfall from about 100 to 600 mm.

A survey of the termite fauna as a whole was carried out around most of the IPAL Field camps. Main investigation sites were located at Balesa Kulal and Olturot. The two sites lie about 8 km from each other, Olturot being more to the south eastern slopes of Mt. Kulal than Balesa Kulal. Balesa Kulal lies in riverine woodland vegetation while Olturot is at the boundary of annual grassland and dense woodland vegetation. The woodland vegetation where my experiments were located is not typical of the IPAL area as a whole, which has 3.5% woodlands and even in woodland my sites were perhaps comparatively productive. Rainfall occurs in two seasons (in April and in November) at both sites and maximum daily temperatures are often above 30°C.

Ad hoc collecting of termite species was made. Five sub-families were recorded: Kalotermitinae: Nasutitermitinae: Termitinae; Amitermitinae and Macrotermitinae. A total of 15 species were recorded and their habitats described in relation to elevation, annual rainfall, soils and vegetation.

The quadrat method was used to estimate the standing crop of dead and live plant materials. This information was gathered in order to understand the food resources available to termites. At Olturot where most of the study took place, mean standing crop of grass litter, woody (less than 4 cm diameter) litter, standing grass and standing shrubs were estimated as 90.4 g, 70.0g and 132.4 g per m² respectively. Net primary production was estimated at 488 g per m² per year. Termites were found to consume about 430 gm⁻² yr⁻¹ of the estimated primary production, which is about 87% consumption. However the consumption of plant materials varied from month to month. There was a general decline of grass litter from August to November 1981 and then from January to April 1982. Also the amount consumed by termites declined simultaneously. This indicated that termites are resource limited.

The foraging activity of termites measured in terms of soil brought up for covering food portions had the highest peaks in September to October, then December to January and lastly April to June. These peaks appeared after or before rains. Rainfall and other environmental variables influenced the foraging activity as demonstrated in this study. The consumption of plant materials by termites was assessed by weighing a known quantity of plant litter before placing it on the ground and re-weighing after termite attack. Rate of plant litter consumption by termites mainly Odontotermes was estimated at $1.08 \text{ g m}^{-2} \text{ d}^{-1}$ for grass litter while $0.09 \text{ g m}^{-2} \text{ d}^{-1}$ was estimated for woody litter.

Food preference studies were carried out using the bait sampling technique. The results indicated that termites do not show statistical preference at plant species level, but preferred grasses to woody materials. This was found to be significant at $p = 0.01$. Odontotermes were the most common termites occurring in the study sites and therefore responsible for 90% of attacks on plant materials.

The assessment of soil translocated by termites mainly Odontotermes was made using (i) randomly located foraging strips, (ii) a paired sample technique (two open-ended tins). The results revealed that an enormous quantity of soil about 13 tons per hectare per year was used for covering food portions on the surface. It was shown that the amount of soil used for covering food resources is related to the amount of food consumed at that particular place. A regression of soil translocated against grass consumption gave the relation $\bar{y} = 14.6x - 653$, $r = 0.921$, $N = 11$, indicating that termites are important as plant consumers and in soil movement. The foraging density of termites was estimated by counting individuals within 2 x 20 m plots during peak foraging hours (morning and evenings). The density was estimated as 145.84 m^{-2} for Odontotermes workers while the mean surface foraging biomass was 125 g per hectare.

This study showed that termites play a key role in the arid ecosystem. Their percentage consumption of net primary production is higher than those reported for camels, sheep and goats combined (7%) Field (1979), and grasshoppers (acridids) 2.51%

by Okelo (1981), in the riverine woodland ecosystem at Balesa Kulal. Although their main resources are dead plants, they sometimes consume standing and live plant materials when the habitat is denuded of plant litter by overgrazing. At this stage termites may come into direct competition with grazing mammals.

Termites play a positive role in nutrient recycling, but where fungus growing termites occur much of the nutrients are locked in the fungus gardens which serve as reserve food. Nutrients are also channelled through predation. Soils used for constructing surface sheetings are often eroded by wind and rain in these arid conditions where soils are loose and poorly structured. Loss of soil fertility leads to poor plant growth which may significantly encourage desertification.

CHAPTER ONE

1. INTRODUCTION

1.1 DISTRIBUTION AND CLASSIFICATION OF TERMITES

Insects of the order Isoptera are usually known as termites or "white ants". They are more closely related to cockroaches (Blattaria: Dictyoptera) than the true ants (Formicoidea: Hymenoptera). Approximately 1900 living and fossil species of termites have been described (Krishna, 1969) the vast majority being found within the tropics. The distribution of termites has been discussed by a number of authors in the second volume of "Biology of termites" (Krishna and Weesner, 1970).

The great majority of termites live in tropical and subtropical regions, but they extend into the temperate zone to about 45°N (Harris, 1970) or 48°N (Emerson, 1955) and about 45°S (Araujo, 1970). The greatest number of species is in the Afrotropical region where Bouillon (1970) recognised 570 species, of 89 genera. Within the tropics, many species in Africa and South America are found in rain forests.

Arid regions have few termites, but some are apparently confined to such regions (Paulian, 1970).

Krishna (1969) recognised the following families based largely on the work of Snyder, (1949) and Emerson (1955).

Mastotermitidae	}	Lower termites
Kalotermitidae		
Hodotermitidae		
Rhinotermitidae		
Serritermitidae		
Termitidae	}	Higher termites

The family Termitidae includes approximately 75% of the known termite species. The Termitidae are divided into four subfamilies: Termitinae, Macrotermitinae, Amitermitinae and Nasutitermitinae on the basis of their morphological characters. The subfamily Macrotermitinae includes such genera as Macrotermes, Odontotermes, Acanthotermes, Pseudocanthotermes, Synacanthotermes, Euscaiotermes. So far as is known, all species belonging to this subfamily have fungus combs in their nests, which may be subterranean, or in mounds sometimes of great size. They occur in Africa, India and the Malayan region.

Because of the economic importance of termites, the African termite fauna has received a lot of attention. Keys are available for identification of species within several important genera, notably Amitermes (Sands, 1957 and 1959); Coptotermes (Harris, 1966a); 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). Despite this attention, some genera are still in need of revision, notably Odontotermes, Microtermes and Microcerotermes all of which are poorly understood.

The genus Odontotermes is very widespread, of which more than half of the species occur in Africa. They have two worker castes and one soldier caste. They feed mainly on dead wood and litter but will also take green plants including seedlings. Their fungus combs are dispersed in separate chambers clustered together, either with no mound showing above ground or under a wide low mound, usually with open passages leading down to it. This genus includes a number of species whose feeding in wood and dead vegetation is of economic importance.

1.2 SOME BIOLOGICAL ASPECTS OF TERMITES

Termites are polymorphic, social insects which live in nests of their own construction. The nests serve to house and protect the colony, store food and maintain an optimum environment (Lee and Wood, 1971). Together with the social behaviour of the termites themselves, the nest (termitaria) tend to produce a condition of homeostasis by the self-regulation of optimal conditions for development, maintenance and reproduction of the society (Emerson, 1956). The functioning of the society is based on self-regulated behaviour of individuals and division of labour among the different groups (castes) within the colony.

The individuals comprising a colony of termites consist of several castes which are morphologically and functionally distinct. The reproductive castes; mainly consist of males (Kings) and females (Queens), also known as winged imagines or alates. Sterile castes; the most important are the workers and the soldiers which are apterous individuals in which the development of the sexual organs is suppressed or the organs are atrophied. The workers are by far the most numerous caste in the termite colony. The

function of the soldier is to defend the colony within the nest and also to defend workers when foraging away from the nest.

1.3 FEEDING ECOLOGY OF TERMITES

Food supplies for the termite colony are collected by the workers who feed themselves and the dependent castes namely larvae, nymphs, soldiers and reproductives. The range of food materials eaten by termites has been reviewed by Adamson (1943), Noirot and Noirot-Timothe'e (1969) and by Lee and Wood (1971b). Their basic food is plant material: Living, recently dead but in various stages of decomposition and soil rich in organic matter (humus). The trophic levels of termites are those of primary consumers (i.e. herbivores) and decomposers. As far as is known, termites are not predators (Wood, 1978). Although they occasionally attack vertebrate corpses, consuming skins, feathers, hairs, dried-out tissues and their own dead and exuviae (Wood and Sands, 1978).

Some of the Macrotermitinae consume, in addition to a wide variety of living plants (woody and non-woody), many forms of dead plant material but they do not seem to attack late stage of decomposing vegetation.

This may be related to their habit of cultivating specific fungi on their faecal material. The tree-trunks, shrubs, herbs, grasses, dung and plant litter are resources for a wide range of termites, which either forage in the open or under the protection of runways or sheets of soil constructed over the food source. The food and foraging habits of many termites can be observed in the field by direct observation of foraging parties, observation of removal of marked food, examination of food stored in nests and galleries and tracing of foraging galleries to the source of food (Wood, 1978). Studies of foraging activity are more readily made on species which construct covered runways above ground level than those which have an almost completely subterranean system of foraging galleries.

Many grass-harvesting species (e.g. Hodototermes) and litter-feeding species (e.g. Odontotermes) construct subterranean galleries which terminate in the foraging holes (Wood, 1978) from which the termites emerge to forage in the open or under soil cover. Extensive covered sheetings are constructed by certain species of Odontotermes and Macrotermes. In contrast to covered runways, which protect the termites moving between the nest and the source of food, sheeting covers the source of

food itself. Many scavenging termites feed under such protective sheetings. The genus Odontotermes often builds extensive sheetings to envelop their food supply, but the purpose of these sheetings is poorly understood. Probably it serves to protect the foraging termites at the same time creating a conducive foraging atmosphere.

There is no adequate information on the amount of food consumed by termites in the field. Measurement of consumption rates in the field is very difficult. The estimates of natural rates of consumption have in some cases relied on extrapolation from laboratory data while others have relied on direct measurement in the field (Wood, 1978). Direct estimates of consumption have relied on either measurement of removal of naturally available food or removal of food in the form of baits. The most widely used method of studying the feeding habits of subterranean termites, particularly the polyphagus and wood-feeding species is by the use of baits presented in varying situations on the soil surface or completely or partially buried (Williams, 1973; Haverty and Nutting, 1975).

There is little information on the quantities of soil transported above ground for the purpose of

packing the eaten-out portion of fallen branches, logs, grasses, standing trees, and tree stumps and for constructing runways and sheetings (Sands and Wood, 1978). However, Wood & Sands (1978) reported preliminary measurements of the amount of soil in the form of sheeting constructed by Macrotermitinae (largely Macrotermes bellicosus, and species of Odontotermes, Anacristotermes, and Microtermes) on trunks and branches of trees in southern Guinea Savannah woodland in Nigeria at 300 kg per hectare per year.

1.4 OBJECTIVES OF THIS STUDY

The effect of termites especially Odontotermes on vegetation, soil and litter decomposition has been scarcely documented and very little information is available. However, their foraging activity on wood, dead vegetation and litter can be of economic importance (Lee and Wood, 1971; Buxton, 1979). This study was directed at finding out the role of termites in an ecosystem. In addition, the current global concern over degradation of the semi-arid lands by man's activity prompted the initiation of termite study in northern parts of Kenya. The main objective

was to determine the amount of various types of vegetation removed and soil used in the form of sheetings by termites. Primarily, this information was to assess to what extent are termites responsible for the decomposition of plant materials in arid areas.

Other objectives included:

- a) Estimation of standing crop of grass litter, woody litter, standing grass (Live or dead) and standing shrub (Live or dead).
- b) Investigating forage preferences of termites by providing known quantities of plant materials.
- c) Relating foraging activity to environmental parameters e.g. rainfall, temperature, RH and available food.
- d) Relating the amount of Odontotermes soil sheeting covering the food materials to the amount of food material consumed.
- e) Estimating the density of the foraging termites.

- f) Ad hoc collection and identification of termites as a basis for a study of the termite fauna as a whole.

CHAPTER TWO

2. THE INTEGRATED PROJECT IN ARID LANDS (IPAL) STUDY AREA

2.1 BACKGROUND INFORMATION

From a geographical point of view, climatic regions in the drylands are subject to short term climatic fluctuations which are characterised by years of ample rainfall followed by Quasi-cyclic droughts (Edwards, 1979). The fluctuations cause semi-arid regions to experience arid conditions at one time, subhumid conditions at another. The progressive degradation of the arid and semi-arid regions of the world was recognised as a major environmental crisis (Anon, 1977) at the United Nations conference held in Nairobi in 1977. There is evidence that long-term climatic change, accentuated by man's activities in arid and semi-arid lands, i.e. agriculture, irrigation, grazing and fire has produced almost irreversible changes on the margins of the world's deserts.

For the last six years the UNESCO Integrated Project in Arid Lands of Northern Kenya, has been

carrying out research on components such as human activities, livestock, vegetation, geomorphology and soil, climate and hydrology. To broaden the scope of ecological studies in these arid areas, surveys of small mammals and insects e.g. grasshoppers and termites were also initiated. All these studies were carried out in order to understand the processes leading to desertification and to find solutions for restoration of stability and improved productivity.

2.1.1 STUDY AREA

The IPAL study area (see Figs. 2.1 and 2.2) covers approximately 23,000 km², which is 4% of Kenya. It is located in the west of Marsabit District in the Eastern province of Kenya. It lies between 1° 50' and 3° 30' N and 36° 64' and 38° 00' E. To the west lies the eastern shore of Lake Turkana while to the east is the Nairobi to Moyale road.

The bulk of the study area is made of a large central plain whose altitude is below 700m. Around this central plain lie a number of volcanic hill masses, the Hurri Hills (1310m) to the north and Mt. Marsabit (1836m) to the east, and Mt. Kulal

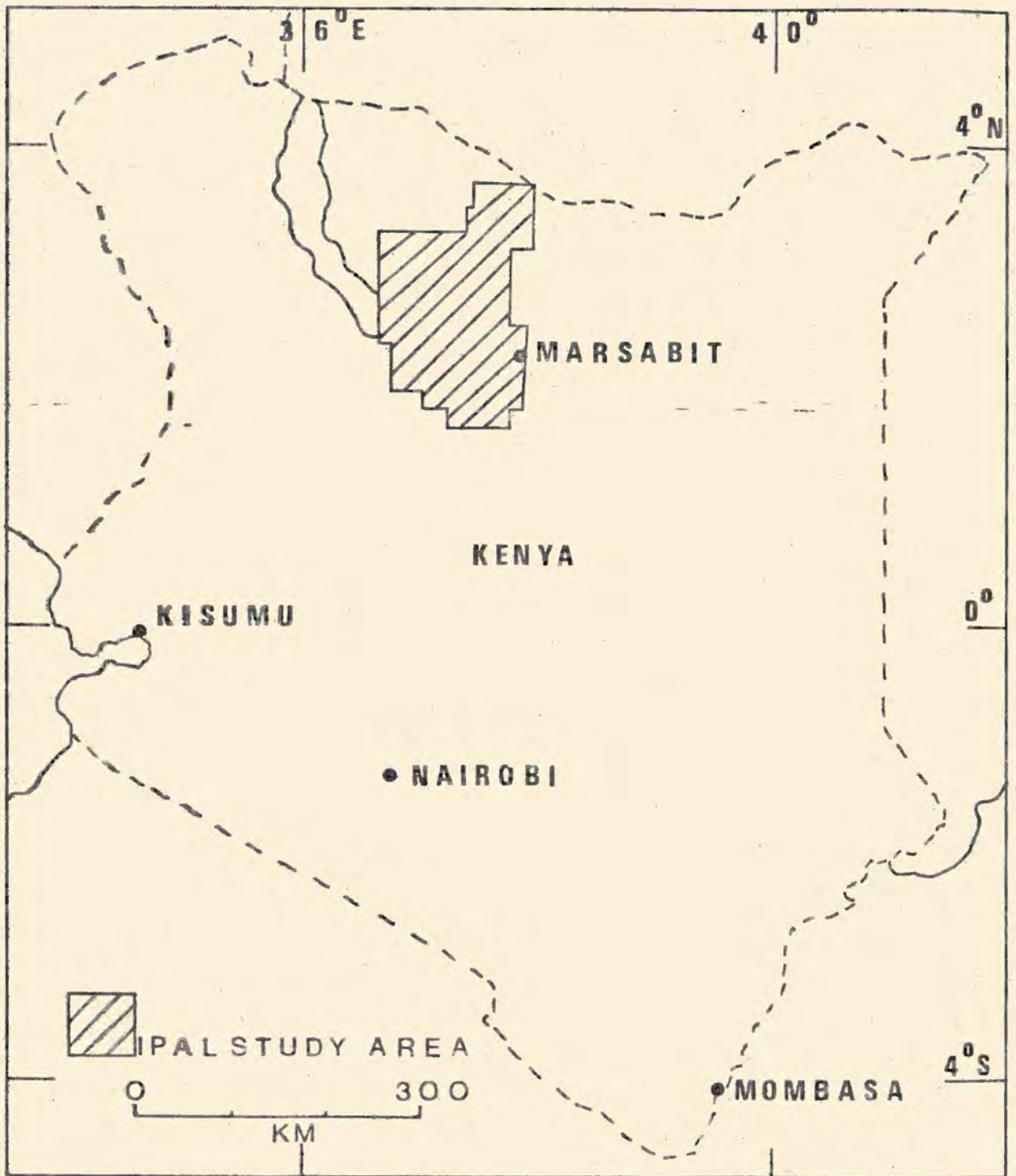
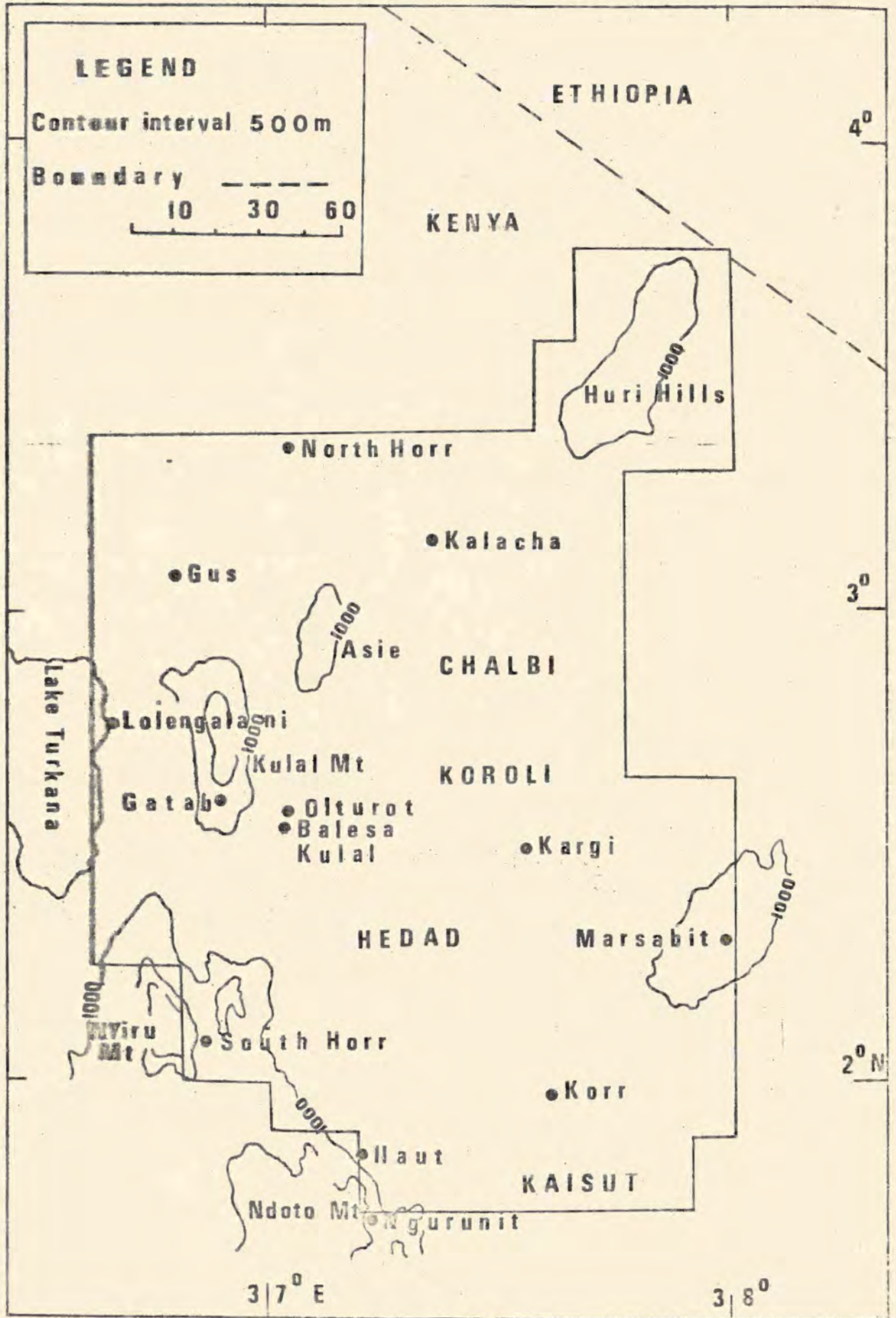


Fig 2.1 LOCATION OF IPAL STUDY AREA

Fig 2.2 IPAL STUDY AREA



(2,295m) to the West. Mt. Nyiru and Oldonyo Mara (over 2000m) to the south west are partly formed from basement material. The main drainage lines originate in the hill masses and are all in the form of seasonal sand rivers which dry out after a few days in the open plains. Most of the rivers in the study area drain into the Chalbi desert in the north of the area. The IPAL study area is on extensive plain which includes the Koroli, Hedad (Baiesha Kulal and Olturot lies here) and Kaisut areas (Fig. 2.2).

The climate of the study area has been discussed by Edwards et al. (1979). Because of the wide range of altitude, there is considerable variation in climate. According to the classification of eco-climatic zones of Pratt and Gwynne (1977), the highlands areas are represented by zone II (sub-humid) and as the altitude decreases the zones change to IV (semi-arid) V and VI (very arid). Most of the study area falls within zones V and VI. Apart from the highland masses, the rainfall is low and erratic. The main rainfall occurs in two seasons, March to May, during the S.E. Monsoon and October to December during the N.E. Monsoon. The rainfall in the lowland

areas is highly variable and has been calculated to have a coefficient of variation of greater than 50 percent (FAO, 1971). The potential evaporation is high and has been estimated at 2620 mm yr^{-1} in the lowland area (FAO, 1971).

Two major geological formations occur within the IPAL study area: Tertiary pliocene recent volcanic lavas around Kulal and Marsabit mountains, and around the Hurri Hills; and Quarternary pleistocene sediments derived from precambrian gneisses of the mountains to the south and south west (Fig. 2.2). These sediments also cover the Chalbi, Koroli, Hedad and Kaisut plains. Rainfall, in particular, controls the moisture status of the soils, the abundance and distribution and the availability of ground water. Because of lack of enough moisture, aridlands generally support only scanty amounts of plant and animal life. The soils are poor in organic matter and nutrients. The small essential reserve of fertility is concentrated in the upper few centimetres of the top soil, while the soil below is commonly salt-affected through lack of leaching and poorly structured in consequence, with adverse plant-water relations.

A detailed description and map of the vegetation of the study area prepared by Herlocker (1979) shows a marked relationship between vegetation type and altitude. The highlands are characterised by upland evergreen forests, and at the lower limits of the highlands, there is evergreen and semi-deciduous bushland, and upland perennial grassland. In lowlands, bushland and dwarf shrubland are the major vegetation types.

The bushland, which is found mainly on the sandy soils is dominated by a canopy of Acacia reficiens which is less than 10m in height, with Duosperma eremophilum growing underneath. The dwarf shrubland is dominated by Blepharis sp., which is found mainly on lava where the total percent cover of vegetation is often below 10% except along the occasional watercourses, and Indigofera spinosa which occurs principally on sandy soils. Along the larger drainage channels and on the old lake beds to the north of the Chalbi, there is Acacia tortilis woodland.

In the lowland areas of the IPAL study area, grasses become very much less frequent than the

highlands. The relative proportion of annual grasses increases but for much of the year there is virtually no grass cover at all. The annual grassland vegetation type has a scattered to open overstory of woody plants (2-20% canopy cover), primarily shrubs and dwarf shrubs. Trees are seldom associated with annual grassland (i.e., there is little wooded grassland). However annual grassland occurs primarily on shallow, poorly developed, stony, loam to clay-loam soils, often on water shedding sites overlying lava. Annual grasses such as Aristida adscensionis, A. mutabilis, Cenchrus ciliaris Chrysopogon plumulosus dominate. Lowland perennial grassland, usually with an open tree overstory, occurs in small isolated patches throughout the study area where ground water is available. It is dominated by Sporobolus spicatus, a salt tolerant species (Bogdan, 1958a).

2.2. TERMITE FAUNA OF THE STUDY AREA

Termites are an integral part of the extensive fauna of all the warmer countries of the world. They live almost exclusively in tropical and sub-tropical zones where they have a marked impact on vegetation

and soil (Lee and Wood, 1971). They are neither conspicuous as individuals, nor do they attract attention by any violent fluctuations in numbers, except when the alates fly. Because of their economic importance, the African termite fauna has received a lot of attention, but there are few details of their local distribution in Kenya. However J. Darlington from ICIPE, Kenya is currently gathering information to help survey the distribution of different types of termite in Kenya.

Preliminary field work carried out in connection with this present study on termites (Bagine, 1980 unpubl. report), surveyed the distribution of termite species by ad hoc collecting trips throughout the IPAL study area. This part was supplemented with more data collected during the main study period. The distribution of termite species recorded in relation to elevation, rainfall, soil and vegetation type is shown in table 2.1. The latter two factors probably influence the abundance and the distribution of termites in the IPAL study area strongly.

Table 2.1: The distribution of termites in IPAL study area Marsabit, Kenya

IPAL field stations (Fig. 2.1)	Qatab	Marsabit	Lugl	Ngurunit	Balesa/Olturot	Kargi	Korr	Kalacha	North Horr	Gus
Elevation (Approx. m)	1800	1500	1300	1100	850	530 200	500 200	500 200	500 150	500 100
Mean annual rainfall (est. mm)	700	900	600	500	250	Lava sandy Annual grassland and dwarf shrubland	Sandy bushland to shrubland	Alluvium sandy Annual grassland to shrubland	Sandy silt Annual grassland	Lava Annual grassland
Soil type	Volcanic cracking	Volcanic soil	Clay-loam	Volcanic	Lava sandy					
Vegetation type	Evergreen to semi-deciduous bushland	Evergreen to semi-deciduous bushland	Woodland	Wooded bushland	Annual grassland wooded shrubland					
Source: Herlocker (1979)	<u>Q. maroccanus</u>	<u>Q. maroccanus</u>				<u>Q. boranicus</u> sp.		<u>Ormitotermes</u> sp. <u>Ormitotermes</u> sp. <u>Ormitotermes</u> sp.		
Termite species	<u>Procastanotus</u> sp.									
	<u>Microtermes</u> sp.									
		<u>Macrotermes</u> sp.		<u>Q. medlocris</u>	<u>Q. boranicus</u>	<u>Q. boranicus</u>				
					<u>Macrotermes</u> sp.	<u>M. subhyalinus</u>				
				<u>Anditermes</u> sp.		<u>A. lönnbergianus</u> <u>A. trunculidens</u> (?) <u>Trinervitermes</u> sp. <u>Cubitermes</u> sp. <u>Synacanthotermes</u> sp. <u>Apicalotermes</u> sp. <u>Q. lateralis</u>	<u>A. lönnbergianus</u>			<u>Anditermes</u> sp.
			<u>Trinervitermes</u> sp.			<u>Trinervitermes</u> sp.				
			<u>Cubitermes</u> sp.							

2.2.1 IDENTIFICATION OF THE STUDY AREA TERMITES

All the termite species collected and preserved in alcohol were later identified with the use of a stereo-microscope in the field laboratory. The specimens were compared with those in the reference key texts. Webb's (1960) key to the genera of the African termites and other keys mentioned in Chapter One were used. In most cases identification was to generic level, and very few were identified to species level. For further identification, preserved specimens were taken to ICIPE, where Drs. M. Collins and J. Darlington identified a few of the species. Two species were identified by Drs. W.A. Sands and S. Bacchus at the British Museum (Natural History), London, through Dr. J. Darlington's request.

Generally, the identification was done on the basis of morphological characters, e.g. (i) general size, shape (ii) Mandible: size, shape, texture and colour (iii) Labrum: size, shape (iv) gulementum (v) fontanelle (vi) pronotum. However, some termite species were only identified down to generic name and all of them were later deposited at the Kenya National Museum Nairobi.

2.2.2 TERMITE SPECIES AND THEIR FEEDING HABITATS

Five sub-families of termites were found in the IPAL study area, namely Kalotermitinae, Nasutitermitinae, Termitinae, Amitermitinae and Macrotermitinae,

1. Kalotermitinae: These are dry wood termites represented by Epicalotermes sp. This species was found attacking dead trees such as Acacia tortilis and Salvadora persica. Colonies of this species are small and the nests are located within the food source. The species is a victim of fire wood collection and this threatens its habitat in these marginal areas. However, the species can be easily reared in captivity requiring little water. I reared some in Acacia tortilis wood and they did very well for 10 months.

2. Nasutitermitinae: Members of this sub-family are much more widespread in the semi-arid areas. The Trinervitermes sp. found in several of the IPAL stations (Table 2.1) is mainly a grass feeder and stores food in its nest. It forages in the open at night and sometimes until sunrise when the weather is mild and over cast. Workers and soldiers were

often seen emerging from small temporary openings and radiating to food sites nearby. Sometimes large columns guarded by soldiers were seen harvesting grass with no foraging hole in the vicinity. Much of the feeding activity was observed during April and May 1982. Grasses and small wood fragments are often their target.

3. Termitinae: These are humus feeders, many of them consuming large quantities of soil which after extracting the humus is excreted and used for building mounds. Procupitermes species was found at lower Gatab (Table 2.1) inside a small cone-shaped mound. Usually the mounds appeared scattered within the scanty vegetation of lower Gatab. When one of the mounds was opened, the nest was found to consist of several small chambers harbouring individuals of various developmental stages. No foraging activity was observed even around their nests. Cubitermes species were associated with decaying woody material and sometimes occurring at the bottom of dead shrubs in the soil. No nests were located but it probably exploits the humus content of the soil or decaying plant litter.

4. Amitermitinae: Most of these species are completely subterranean and form small to moderate

sized colonies which feed on wood, grass or vegetation debris. They confine their attention mainly to the decayed and weathered surface of wood. Microcerotermes species, the workers of this species were found as guest species in the Procubitermes mounds at Gatab. They were found inside rotting branches buried in the mound, suggesting that they feed on dead plant materials. Amitermes ¹¹lönbergianus is a fairly widespread termite of the IPAL study area. This species was often found consuming dead wood, and apparently preferred large logs and dead trees to small scattered fragments. The soil foraging covers were built similarly to those of Odontotermes but are distinguished by their black faecal lining. A. lönbergianus may be more important as a subterranean feeder than as a consumer of surface litter. Large populations consisting of all castes were occasionally encountered in decaying logs. No nests were located but large dead logs or trunks could probably have acted as temporary nests since nymphs, reproductives and other sterile castes were observed in such habitats.

5. Macrotermitinae: These are fungus growing termites which utilize a wide range of food sources which they often cover with a soil sheeting, and store their food in a diffuse subterranean nest. Their inability to penetrate extremely arid areas may be due to the high energy demands of their large colonies (Wood, 1977) and the unfavourable environments for the symbiotic fungus, Termitomyces. Synacanthotermes species is a tiny termite resembling Microtermes. This species was found inside small twigs and grass stem litter. It was noticeable during rainy periods and when ground litter decreased in abundance.

Odontotermes species were the commonest termites in many of the IPAL field stations. O. boranicus is tolerant of harsh conditions but avoids hilly masses. It is a small termite with no apparent centralised nest. Very intense foraging was observed, under extensive earth cover predominantly on the surface litter of grasses and herbs broken up by trampling, and on leaves and twigs fallen from bushes and trees. In general no termite species was recorded foraging on Acacia mellifera leaf litter. Probably it could be due to the nature or presence of repellent substances

in the leaves. In areas where there was very little or no litter, the bases of whole clumps of grasses and shrubs were surrounded with foraging cover and in the process of being consumed. During periods of low litter levels, termites were observed to forage on standing grass and intensively on tree barks. O. boranicus foraged on a wide range of food materials, it was also seen consuming decaying animal skeleton at Balesa Kulal. This species was most abundant in the main study sites at Balesa Kulal and Olturot and therefore selected for detailed studies in this present study.

Odontotermes latericius was also encountered in the same habitats with O. boranicus, but this species foraged mainly in dead wood and constructed earth tunnels up in small trees and dead shrubs. O. mediocris is a fairly widespread termite having no centralized nest structure. This species was found foraging on leaf, twig and grass litter and on herbivore dung under sheets of fine-textured earth cover. This same species was described by Buxton (1979) as the most common termite in Tsavo, Kenya. O. monodon exploits the locally moister areas of the IPAL study area. It was only found occurring above 1000 m elevation. Unlike its counterparts it

is a large termite living in centralised nests, and builds a low vegetated mound with conspicuous chimneys. It was often encountered foraging under earth cover on leaf, grass, wood and intensively on cattle dung at Gatab and Marsabit. At Gatab it was found feeding on the remains of a mammal skeleton.

Macrotermes species are widespread in most areas above 800 m elevation. They are common around Ngurunit and Loglog - Marsabit area. Their mounds are generally large, conspicuous and probably of ecological importance to the surrounding area. Two types of mounds were recognised and both had evidence of being live mounds i.e. fresh termite activity was associated with them. One type of mound was rounded and conical with no holes, and the other with open chimneys. Both types of mounds were occasionally associated with growing thickets. Macrotermes mounds were only present in certain types of soil and not others. For example no mounds were built in loose soil or sandy soil. On the other hand regular dispersion of mounds was observed which probably indicated a competition for foraging sites. M. subhyalinus was seen foraging on dead fallen wood and other surface litter at Ngurunit.

CHAPTER THREE

3. ECOLOGICAL COMPARISONS OF THE STUDY SITES: BALESA KULAL AND OLTUROT

3.1 CHOICE OF STUDY SITES

A general survey of the termite fauna as a whole was carried out at most of the IPAL Field Stations (Fig. 2.1), but the main experiments to assess the role of termites in arid areas were located near Balesa Kulal and Olturot camps (Fig. 3.1). The Balesa Kulal and Olturot stations lie on one of the Lowland plains called the Hedad. These sites were chosen because they were accessible and in use by IPAL scientists. At Balesa Kulal termite study experimental transects were laid out inside the existing IPAL fenced enclosures located on riverine vegetation. The enclosures (paddocks) were set up in 1977 for the purpose of measuring the impact of livestock upon plant communities. My Olturot experimental sites were situated in a dense bushland fringing annual grasslands on a lava floor. Experiments requiring daily inspection were all set up near Olturot Field camp due to ease of transport and contained more forage than at Balesa Kulal.

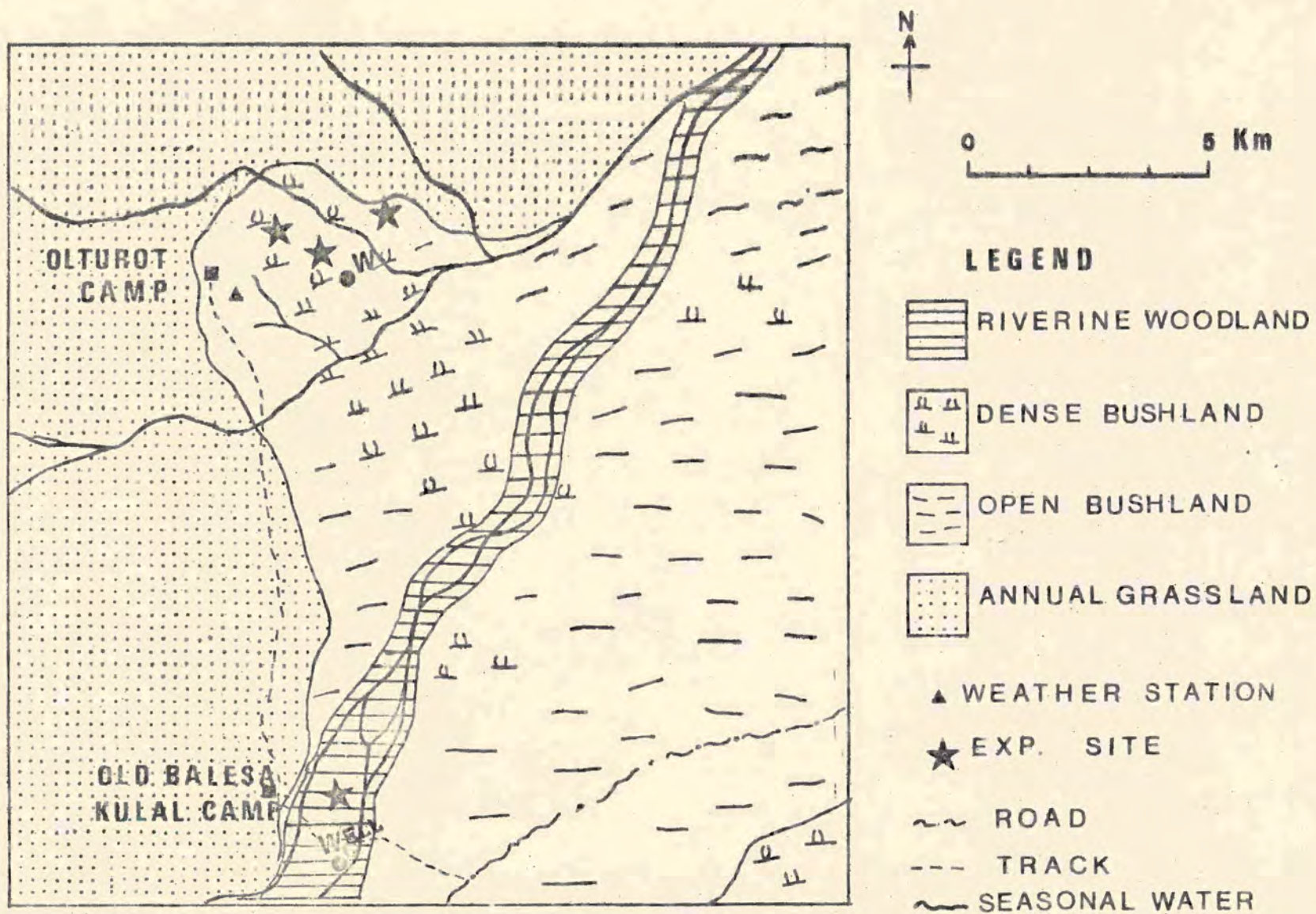


Fig 3-1 Vegetation types and exoerimental (Exp.) sites in the main study sites: Balesa Kulal and Olturot.

3.2 FLORA AND FAUNA OF THE STUDY SITE

Balesa Kulal is characterised by riverine vegetation dominated by Acacia tortilis trees some of which lead heights of approximately 15m and have canopies up to 10m across. The Balesa river which flows for only a few days in most years separates it from Acacia reficiens shrubland on its eastern limit. At an elevation of 650 m Balesa riverine woodland is bordered on its western side by an extensive lava flow which contains scattered vegetation along the gullies.

Olturot lies on the Eastern slopes of Mt. Kulal and is located at an elevation of about 630 m. Part of its Western and Eastern side embrace the lava floor. The vegetation is dominated by bush which is locally dense containing Acacia tortilis associated with Salvadora persica bush, and Salsola dendroides as understory dwarf shrub. The grass species are also common among the understory layer. Table 3.1 lists the most important plant species recorded in the two study sites. The flora of the two sites appear similar, but the occurrence of a few plant species e.g. a salt bush, Salsola dendroides, at Olturot only, suggest that the two sites have some

ecological differences which could affect termite activity. However, the purpose of setting up these two sites was to compare termite activity on disturbed and undisturbed areas.

The plant species listed in table 3.1 and together with others not recorded, provide substantial food requirements to grazing livestock, wild grazing herbivores, termites and other insects. The main species of wild grazing herbivores occurring within and around the study sites were Dik Dik (Rhynchotragus guentheri), Generuk (Litocranius walleri), Grant's gazelle (Gazella granti), Reticulated giraffe (Giraffa camelopardalis reticulata), Beisa oryx (Oryx baises baises) and Grevy's zebra (Equus grevyi) seen at Balesa Kulal. Rodents such as Tatera nigricauda, Gerbillus gerbillus, Xerus rutilans and Acomys subspinosus, and birds especially seed-eaters occur in the study sites and all remove a significant amount of primary production. Rabbits also occur around Olturot.

Because most of the plant species remain dry in most part of the year after short rainy periods (discussed later in this chapter), the grazing livestock rarely visit these areas for grazing.

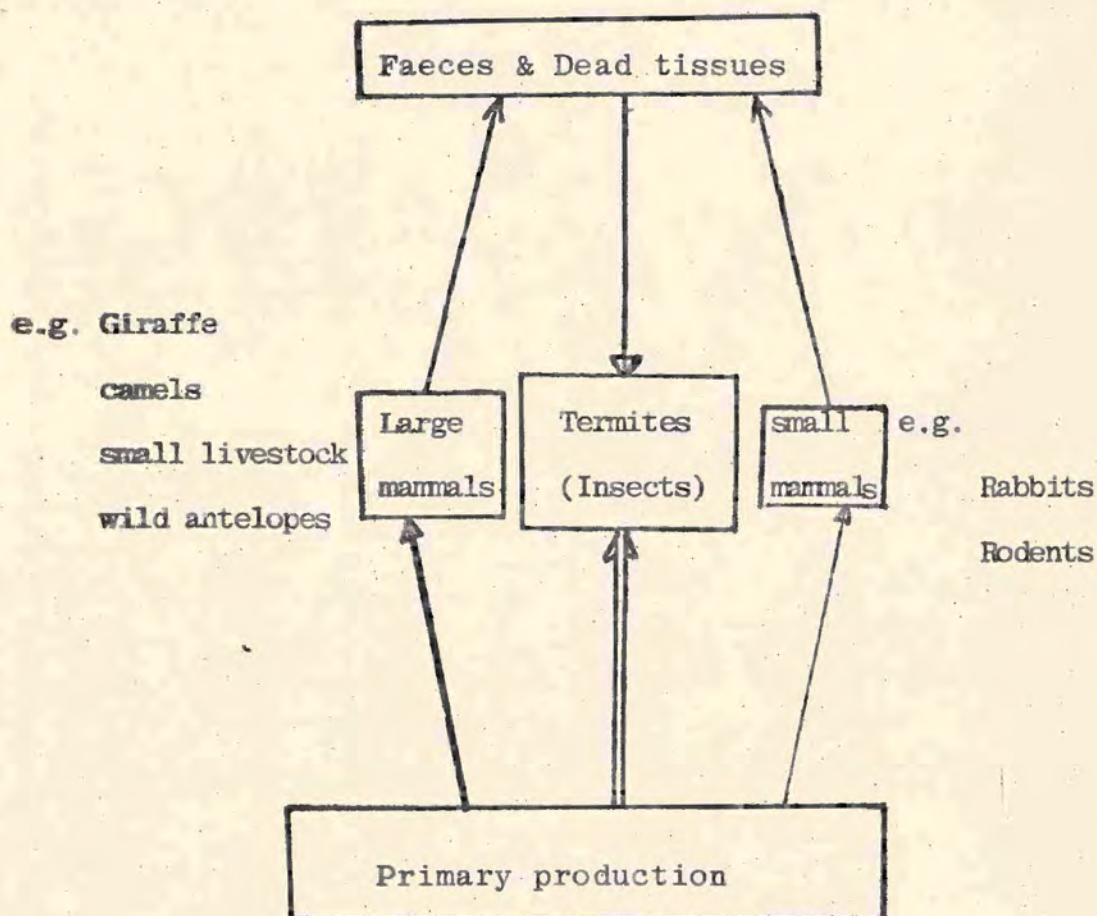
Table 3.1: Frequency of occurrence of plant species in two study sites.

Plant species	Balesa Kulal	Olturot
<u>TREES:</u>		
<u>Acacia tortilis</u>	*	*
<u>A. reficiens</u>	x	x
<u>A. mellifera</u>	x	0
<u>A. nubica</u>	x	0
<u>Grewia tenax</u>	0	x
<u>Salvadora persica</u>	x	*
<u>DWARF SHRUBS:</u>		
<u>Cyclocheilon eryanthemum</u>	0	x
<u>Duosperma eremophilum</u>	x	x
<u>Indigofera spinosa</u>	*	0
<u>Lycium sp.</u>	0	x
<u>Maerua sp.</u>	x	x
<u>Salsola dendroides</u>	0	*
<u>Sericocomopsis hildebrandti</u>	x	x
<u>Solanum sp.</u>	x	x
<u>GRASSES:</u>		
<u>Aristida mutabilis</u>	*	*
<u>Cenchrus ciliaris</u>	*	*
<u>Chloris virgata</u>	*	*
<u>Dactyloctenium aegyptium</u>	0	x
<u>Eragrostis cilianensis</u>	x	0
<u>Setaria sp.</u>	x	*
<u>Leptothrium senegalenses</u>	x	0

Note: * = common x = present 0 = none recorded.

Therefore a significant amount of primary production is not consumed by grazing herbivores, and ends up as plant litter consumed by termites. However, plant seeds and fruits are harvested by birds and rodents. Perhaps a model can be used in this case to demonstrate the flow of primary production to consumers (model 1).

Model 1.



3.3 SOILS OF THE STUDY SITES

Soil description and characteristics were studied by use of profile pits at Balesa Kulal and Olturot sites. In general the soils were found to have different characteristics but both had unconsolidated alluvial material as parent material. A. Van Kekem, a soil scientist, provided the description and sampled the profile pits for chemical and physical analysis. The Olturot soil was shown to be well drained, very deep, dark reedish brown, friable, strongly calcareous, moderately sodic and strongly saline, loam to clay loams overlying soft lime. Moderately heavy rill erosion and deflation occurs.

Balesa Kulal soils consist of unconsolidated alluvial sediments derived from Basement system rocks and from volcanic rocks. The soil is somewhat excessively drained, very deep, brown, loose, strongly calcareous, slightly gravel, sand. Slight sheet wash erosion and moderate deflation occurs.

Termites modify soils mainly through physical disturbances, especially the removal of fine materials from deep soil horizons to the surface, where they are used for the construction of mounds and surface

runways, galleries or sheetings. The chemical analysis of termite soil used for covering up eaten-food materials and soils from the profile pits are shown in the appendix. It was found that the percentage of clay at Olturot was higher than at Balesa Kula, while the reverse is true for sand percentage. Usually the most significant feature of soils for building soil structures is the proportion of sand, silt and clay and the distribution of these constituents throughout the profile.

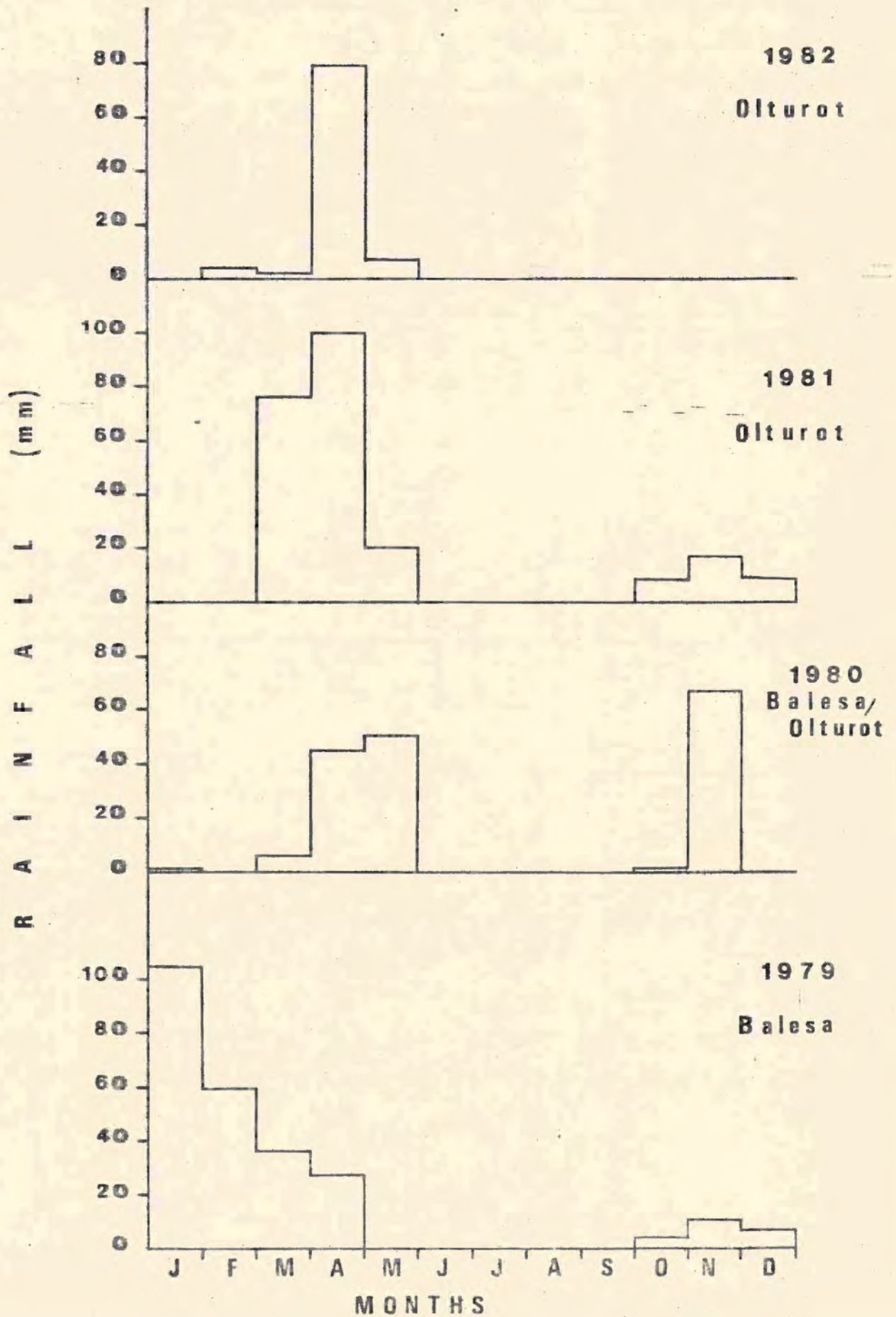
3.4 CLIMATE

A major environmental constraint in arid and semi-arid lands is the fluctuating and unreliable nature of the rainfall, which limits the growth of plants. The effectiveness of rainfall depends not only on the absolute amount that falls in any one year, but also on the monthly distributions throughout the year, the potential evapotranspiration rate, the soil moisture infiltration rate, and vegetation cover (Payne and Hutchinson, 1963). The rains in the lowland parts which include Balesa Kulal and Olturot are unreliable and occur in two seasons, mainly in April/May (Long rains) and November (short rains).

The climatological studies of Balesa Kulal were monitored by a Didcot Automatic weather station installed in June 1977 within the Balesa Kulal enclosures. In 1980 it was moved to Olturot. The present location of the weather station together with the daily standard rain gauge are shown in Fig.3.1. During this current study of termites, monthly rainfall records were kept from August 1981 to June 1982 at Olturot. On 8th December 1981 one storage rain gauge was installed inside the control enclosure at Balesa Kulal. This was to enable a comparison of rainfall season between Olturot and Balesa Kulal.

The rainfall records during the 11 months of study (August 1981 to June 1982) gave the total rainfall for Olturot as 129.2 mm. The months of April and May recorded a total of 86.1 mm at Olturot while Balesa Kulal a total of 114 mm was recorded. The total annual rainfall recorded at Olturot in 1981 was 232 mm which contributed to high standing crop at the start of this current study of termite ecology. The total monthly rainfall histograms for Balesa Kulal/Olturot are shown in Fig. 3.2. The histograms reveal a bimodal seasonal rainfall pattern with peaks in April and November.

Fig. 3.2 Monthly rainfall for Balesa Kulal and Olturot.



However, unpredictability of rainfall over the years and months, with monthly variability is evident from the histograms.

The annual range of mean monthly temperatures is small, being about 4.0°C at Balesa Kulal and Olturot. January and February are relatively warm months when dry north easterlies flow across northern Kenya. Clear skies allow high levels of insolation and mean daily maxima of 35°C and minima of 15°C are recorded. The relative humidities were recorded from wet bulb depression available at Olturot Field Stations. Although the depression is not an independent variable because of being moistened before use, it does provide a guide to the seasonal fluctuations of humidity. Records of RH during this study indicated that the humidity at Balesa Kulal and Olturot remained low throughout the year. For example, the lowest mean RH values of 38% were recorded in March, while the highest mean RH values of 59% recorded in April at both stations.

3.5 TERMITE ACTIVITY

In this study, termite activity on vegetation is described in terms of termite soil (protective sheetings) covering the eaten food portions on the ground surface or on the standing vegetation. This suggests that the more the surface area is covered with termite soil the more the termite activity. Apparently, termite activity can be compared from one place to another by assessing the area covered by the termite sheetings or by quantifying the amount moved per given area. Indirectly, such measurements can be used to estimate the amount of food eaten by termites. Again, through the assessment of the area covered with termite sheetings, a clue to the distribution and abundance of termites themselves can be obtained.

A general survey of termite activity indicated that Olturot had higher activity levels than Balesa Kulal. The difference in vegetation and soil characteristics discussed above may have contributed to comparatively low termite activity at Balesa Kulal. In addition, the degree of termite activity may strongly depend on the interaction of climate, vegetation and soil factors. A certain amount of clay or other colloidal material such as saliva or

faecal matter, is required to cement particles together, which accounts for the general absence of mounds and sheetings on pure sands.

The termite species recorded at Olturot and Balesa Kulal are listed in table 3.2. Because of their cryptic behaviour, some termite species might have passed unnoticed and therefore not appear in the list.

Table 3.2 List of termite species occurring at Balesa Kulal and Olturot study sites.

<u>Termite species</u>	<u>Balesa Kulal</u>	<u>Olturot</u>
<u>Odontotermes boranicus</u>	present	present
<u>O. latericius</u>	none	"
<u>Amitermes lönnerbergianus</u>	present	"
<u>Trinervitermes</u> sp.	"	"
<u>Cubitermes</u> sp.	none	"
<u>Synacanthotermes</u> sp.	present	"
<u>Epicalotermes</u> sp.	"	"

CHAPTER FOUR

4. STANDING CROP (LIVE AND DEAD VEGETATION)

Plant materials serve as the basic food for termites, and any long term changes in the amount of plant material available would affect the foraging behaviour and probably the consumption of termites. The seasonal changes in vegetation may help to explain and understand the role of termites in the exploitation of environmental resources. Investigations carried out in the Chihuahuan desert of Arizona (Johnson and Whitford, 1975) estimated that termites were the most important consumers, processing more than half of the estimated annual primary production. I hypothesized that the disappearance of all plant litter in the IPAL study area would be attributable to termite activity. To investigate this hypothesis, estimation of various plant material biomasses on a seasonal basis was carried out in the study sites.

4.1 MATERIALS AND METHODS

The study sites were situated at Balesa Kulal and Olturot (Fig. 3.1). The methods used to estimate monthly and bi-monthly standing grass, grass litter,

standing shrub/herb and woody litter weights were transect and quadrat methods. The quadrat method has been widely used for the assessment of primary production of grasses, shrubs and herbs, e.g. by Brown (1954); Mannelje (1978); Ohiagu and Wood (1979); Herlocker et al. (1981). This method was preferred because it could be used in drawing statistical inferences.

The experimental base-lines, which were permanently laid out for the purpose of establishing foraging strips for the soil collection (Chapter six) at Balesa Kulal and Olturot, were used for this study. The base-lines were laid out where the grass was common among the shrubs and herbs, and having an indication of termite activity. The experimental base-lines were measured 200m long at Olturot and in the cattle paddock at Balesa Kulal, and 100m long in the smaller ungrazed and sheep/goat paddocks at Balesa Kulal. They were marked at 20m intervals using fixed posts. At Olturot monthly and at Balesa bi-monthly transects, 100m long, were established perpendicular to the experimental base-line, passing through a randomly selected 20m interval post (Fig.6.1).

At the Olturot site, 30 quadrat frames each 50 x 50 cm (0.25m^2 or $\frac{1}{4}\text{m}^2$) were randomly located monthly on 100m long transects. Similarly, bi-monthly 20 quadrat frames of $\frac{1}{4}\text{m}^2$ each were randomly located on a 100m long transect in each paddock at Balesa Kulal. Less samples and longer intervals were allowed for Balesa Kulal because of other work demanding daily inspection. Standing grass and standing shrub/herb were sampled by clipping plants within the 0.25m^2 quadrat frames. The grass litter and woody litter were carefully collected and smaller fragments brushed up within the same quadrat frames. Clipped plants and plant litter were placed in paper bags in the field on the basis of standing grass (live and dead), standing shrub/herb (live and dead), grass litter and wood litter. All the samples were weighed using a standard beam balance at Olturot Field Station. A constant dry weight was obtained by air drying samples in sacks and polythene bags for six weeks. The samples were subjected only to air-dry weights and not to oven dry weights.

During this study, Balesa Kulal paddocks were twice used (September 1981 and May-June 1982) by the IPAL Livestock for feeding trails. The

IPAL cattle were not at Olturot during this time, although when the experiment started they had been expected. Consequently, the effect of termites on grazed paddocks was only studied in the sheep and goat paddock. The standing crop from each paddock was compared and related to termite activity.

4.2 RESULTS

The total standing crop of litter and standing vegetation varied considerably in time and space. The seasonal fluctuations of grass litter and standing grass weights were remarkable during dry and wet seasons. An average of 0.45 kg per m² per month of the total standing crop was estimated at Olturot.

In each month, results were tabulated as shown in Table 4.1. At Balesa Kulal paddocks 20 quadrat frames of 0.25m² each and at Olturot site 30 quadrat frames of 0.25m² each were sampled. Table 4.1 also indicates differences between vegetation or plant weights within each quadrat. Some quadrats recorded little or no standing crop. Also scanty vegetation which was thinly scattered contributed to such a varying statistical records. The monthly

Table 4.1: November, 1981 results showing variations in vegetation biomass within quadrats. note: 30 and 20 m^2 quadrats were samples at Olturot and Balesa Kulal paddocks respectively.

Units: g Air dry weight

Grass litter				Woody litter				Standing grass				Standing shrub/herb			
Olt.*	B*-C*/P*	B-U*/P	B-Sg*/P	Olt.	B-C/P	B-U/P	B-Sg/B	Olt.	B-C/P	B-U/P	B-Sg/P	Olt.	B-C/P	B-U/P	B-Sg/P
45.6	21.0	16.2	0.4	0.0	11.2	131.7	9.2	13.2	5.4	11.4	0.4	0.0	0.0	39.9	8.5
62.2	85.3	2.4	0.3	62.7	0.0	0.0	0.0	99.7	11.0	1.0	0.0	0.0	0.0	0.0	0.0
33.5	29.2	21.8	10.8	3.1	0.0	9.6	5.7	10.7	6.8	13.5	0.0	0.0	0.0	13.8	0.0
2.4	1.2	23.1	0.1	0.0	0.0	0.0	4.9	0.0	5.4	23.7	0.05	0.0	0.0	0.0	1.8
13.9	3.6	41.4	4.8	5.4	0.0	8.2	3.6	7.0	11.4	45.0	0.0	7.4	22.1	0.0	0.0
5.0	42.3	22.8	0.3	4.0	23.4	3.2	0.0	1.6	10.0	17.9	0.0	0.0	22.3	0.0	0.0
0.0	8.7	7.8	0.0	34.3	24.1	0.0	18.0	0.0	1.7	6.4	0.0	0.0	12.6	0.0	14.4
35.8	7.7	5.5	61.0	7.0	21.2	0.0	72.2	6.7	2.4	3.7	0.0	0.0	11.4	0.0	0.0
47.2	1.3	7.5	9.4	0.0	9.4	4.8	34.5	8.4	0.0	2.8	0.0	0.0	0.0	37.8	0.0
25.3	3.1	15.2	0.1	48.4	1.4	10.1	13.0	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0

Table 4.1 continues

Table 4.1 continued

3.5	6.2	10.4	1.9	0.0	16.2	15.6	7.9	0.0	2.9	4.9	0.0	0.0	0.0	8.9	0.0
26.7	85.2	40.0	0.9	4.2	46.5	0.0	0.0	19.0	4.6	16.0	0.0	0.0	10.9	0.0	0.0
27.9	4.2	17.4	3.6	1.8	0.0	0.0	23.9	15.9	0.0	2.8	0.0	0.0	0.0	0.0	1.0
5.6	6.5	20.7	1.0	0.0	2.5	6.9	0.7	0.0	0.0	10.2	0.0	0.0	39.5	0.0	0.0
30.0	22.0	20.3	14.4	5.8	0.0	0.0	2.6	16.8	2.4	17.1	0.0	0.0	0.0	0.0	0.0
73.0	11.4	9.9	31.2	0.0	32.8	0.0	190.4	81.2	0.0	4.6	0.0	4.6	0.0	0.0	300.0
9.9	20.0	24.3	0.6	25.3	0.0	0.0	6.7	12.3	0.0	11.6	0.0	263.4	0.0	0.0	0.0
0.0	48.3	6.1	0.0	35.9	10.2	7.0	23.8	0.0	4.9	4.1	0.0	0.0	0.0	0.0	16.0
1.7	35.6	21.4	0.4	0.0	0.0	53.8	9.6	0.0	5.2	15.5	0.0	0.0	0.0	0.0	9.0
22.1	1.9	12.2	7.8	6.1	8.2	0.0	94.5	20.5	0.0	15.3	0.0	0.0	0.0	0.0	0.0
3.5				239.0				6.2				626.7			
0.8				0.0				0.0				0.0			
37.1				0.0				14.3				4.2			
20.5				13.3				3.5				0.0			
33.2				9.9				21.6				0.0			
47.2				0.0				12.5				0.0			
2.8				0.0				0.9				0.0			

Table 4.1 continued

	7.5				7.0					0.3				0.0			
	73.5				93.6					65.3				38.9			
	10.2				22.4					0.0				1105.5			
n	30	20	20	20	30	20	20	20	30	20	20	20	30	20	20	20	
total	707.6	444.7	346.4	148.5	649.2	213.1	250.9	521.2	437.6	74.1	230.9	0.45	2136.1	118.8	100.4	353.0	
mean	23.6	22.2	17.3	7.4	21.6	10.7	12.5	26.1	14.6	3.7	11.5	0.02	71.2	5.9	5.0	17.7	
S.E.	+3.98	+5.76	+2.34	+3.29	+9.11	+3.03	+6.83	+10.26	+4.45	+0.85	+2.27	+0.02	+44.73	+1.33	+2.71	+14.9	

Olt. - Olturot; B-Balesa Kulal; C-cattle; p.-paddock; u-ungrazed and Sg - Sheep/Goat

means and standard errors of all the vegetation (grass litter, woody litter, standing grass and standing shrub/herb) weights at Olturot and Balesa Kulal are indicated in tables 4.2 and 4.3. The sheep and goat feeding trials were carried out after sampling the vegetation in September 1981 and May 1982.

The monthly frequency distribution of grass litter and wood litter (less than 4cm in diameter) which are the main food sources of termites show a characteristic of skewness (Figs. 4.1 (a) and 4.2 (a)). Because of this skewness, the monthly raw data collected from Olturot site were transformed using logarithms. The choice of logarithmic transformation was because of their simplicity and partly the large amount of data collected for analysis. Figures 4.1 (b) and 4.2 (b) show transformed frequency histograms. The frequency distribution of only grass and woody litter weights have been shown for September 1981 and April 1982. These months were chosen because September was the driest month, with no rain while April was the wettest month during this study period, with rainfall of 79 mm. The distribution

Table 4.2: Monthly mean vegetation weights (g per $\frac{1}{4}m^2$ d.wt) and calculated standard errors. Olturot site.
The number of samples were 30 in each case.

Month	Grass litter g/ $\frac{1}{4}m^2$ dry wt.	Wood/Twig litter g/ $\frac{1}{4}m^2$ dry wt.	Standing grass g/ $\frac{1}{4}m^2$ dry wt.	Standing shrub/herb g/ $\frac{1}{4}m^2$ dry wt.
	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)
August 1981	38.6 (7.9)	99.6 (14.8)	29.2 (12.7)	26.2 (12.9)
September "	37.6 (5.7)	45.2 (14.7)	14.1 (3.5)	21.6 (12.1)
October "	28.6 (5.1)	23.8 (13.7)	9.5 (3.3)	11.2 (7.3)
November "	23.6 (3.9)	21.6 (9.1)	14.6 (4.5)	71.2 (44.7)
December "	28.9 (5.7)	41.8 (11.7)	18.1 (4.3)	43.6 (27.9)
January 1982	26.9 (3.5)	44.9 (25.3)	16.9 (3.4)	33.5 (26.9)
February "	17.2 (2.8)	26.3 (7.2)	16.3 (3.5)	56.7 (23.6)
March "	18.5 (4.3)	73.9 (26.8)	15.6 (5.4)	24.8 (9.9)
April "	15.2 (2.8)	16.4 (6.3)	15.7 (4.0)	10.7 (7.6)
May "	6.4 (1.1)	24.3 (8.8)	18.4 (4.5)	31.8 (11.4)
June "	6.9 (1.6)	9.9 (2.3)	23.6 (7.7)	32.8 (11.7)

Table 4.3: Monthly mean vegetation weights (g per $\frac{1}{4}$ m² dry wt.) and standard errors drawn from samples at Balesa, Kulal paddocks. Sheep and goats were grazed from 21st to 29th September 1981 and from 23rd May to 15th June 1982.

The number of samples were 20 in each case.

Month	Balesa Kulal paddock	Grass litter	Wood/twig litter	Standing grass	Standing shrub/herb
		g/ $\frac{1}{4}$ m ² dry wt.	g/ $\frac{1}{4}$ m ² dry wt.	g/ $\frac{1}{4}$ m ² dry wt.	g/ $\frac{1}{4}$ m ² dry wt.
		Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)
September 1981	Cattle	13.1 (3.5)	12.6 (3.3)	4.4 (2.1)	12.9 (5.4)
	Ungrazed	20.7 (4.5)	15.1 (5.8)	14.1 (3.1)	20.8 (6.8)
	Sheep/goat	15.4 (5.7)	57.1 (20.6)	4.3 (1.3)	33.8 (9.5)
November	Cattle	22.2 (5.8)	10.7 (3.0)	3.7 (0.9)	5.9 (1.3)
	Ungrazed	17.3 (2.3)	12.5 (6.8)	11.5 (2.3)	5.0 (2.7)
	Sheep/goat	7.4 (3.3)	26.1 (10.3)	0.02 (0.02)	17.7 (14.9)

Table 4.3 continues

Table 4.3 continued

January 1982	Cattle	19.6 (4.9)	33.2 (10.4)	10.8 (7.9)	27.8 (15.9)
	Ungrazed	13.4 (2.2)	11.4 (3.6)	8.2 (2.1)	7.9 (3.3)
	Sheep/goat	11.9 (2.7)	37.1 (14.2)	1.0 (0.6)	26.9 (11.2)
March 1982	Cattle	8.2 (1.4)	18.7 (5.8)	2.4 (1.2)	24.4 (2.6)
	Ungrazed	8.9 (1.7)	29.9 (20.9)	4.6 (1.1)	16.2 (7.1)
	Sheep/goat	3.9 (1.4)	71.0 (32.1)	0.8 (0.6)	6.9 (2.5)
May 1982	Cattle	6.2 (1.3)	12.4 (3.2)	12.3 (2.6)	39.0 (12.9)
	Ungrazed	11.9 (3.6)	21.3 (11.9)	14.5 (3.2)	47.3 (32.9)
	Sheep/goat	1.5 (0.4)	18.5 (8.2)	7.7 (1.9)	20.9 (5.1)

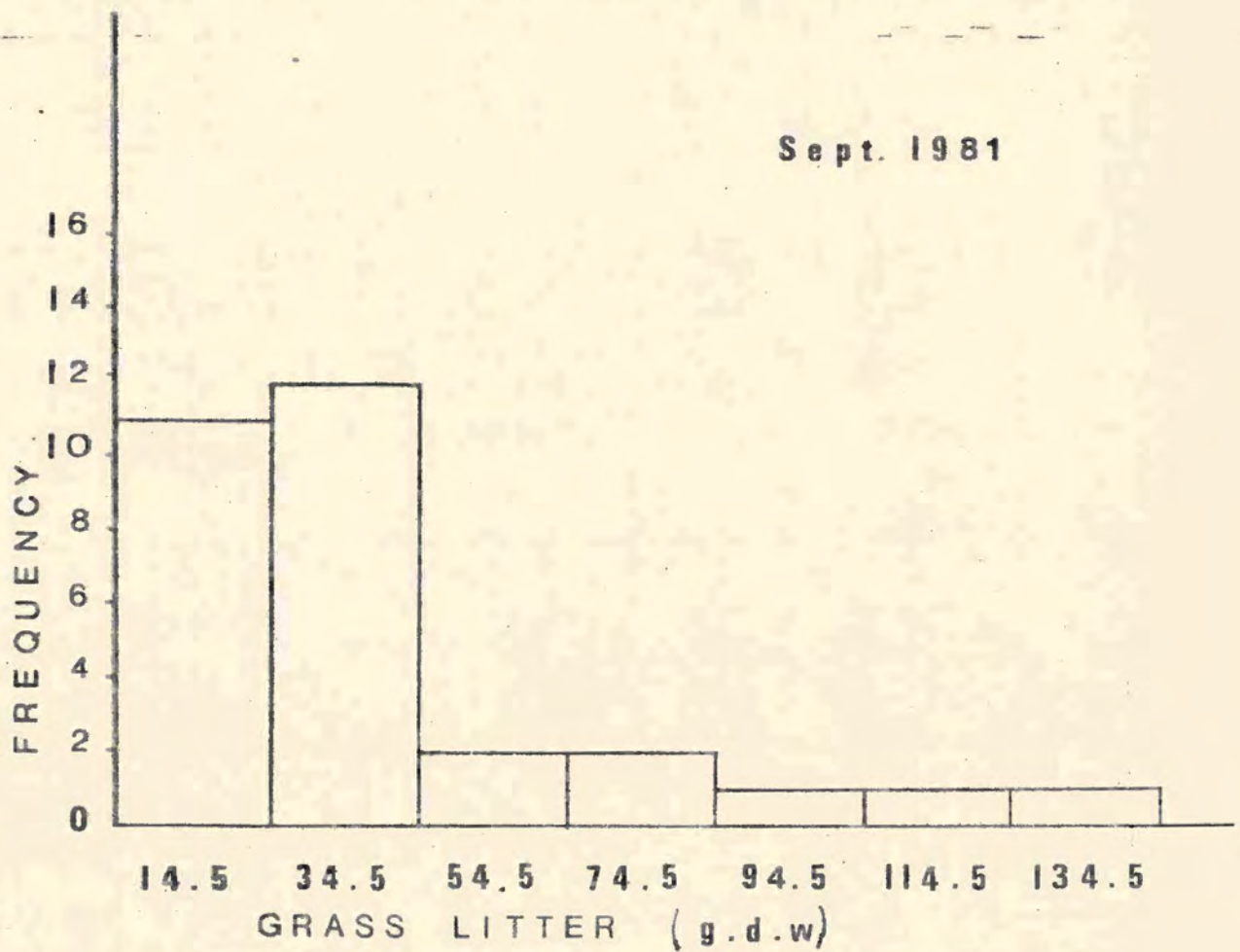


Fig-4-1a The frequency of standing crop of grass litter in 30 - 1 m² quadrats laid in one of the eleven transects at Olturot September 1981.

Sept. 1961

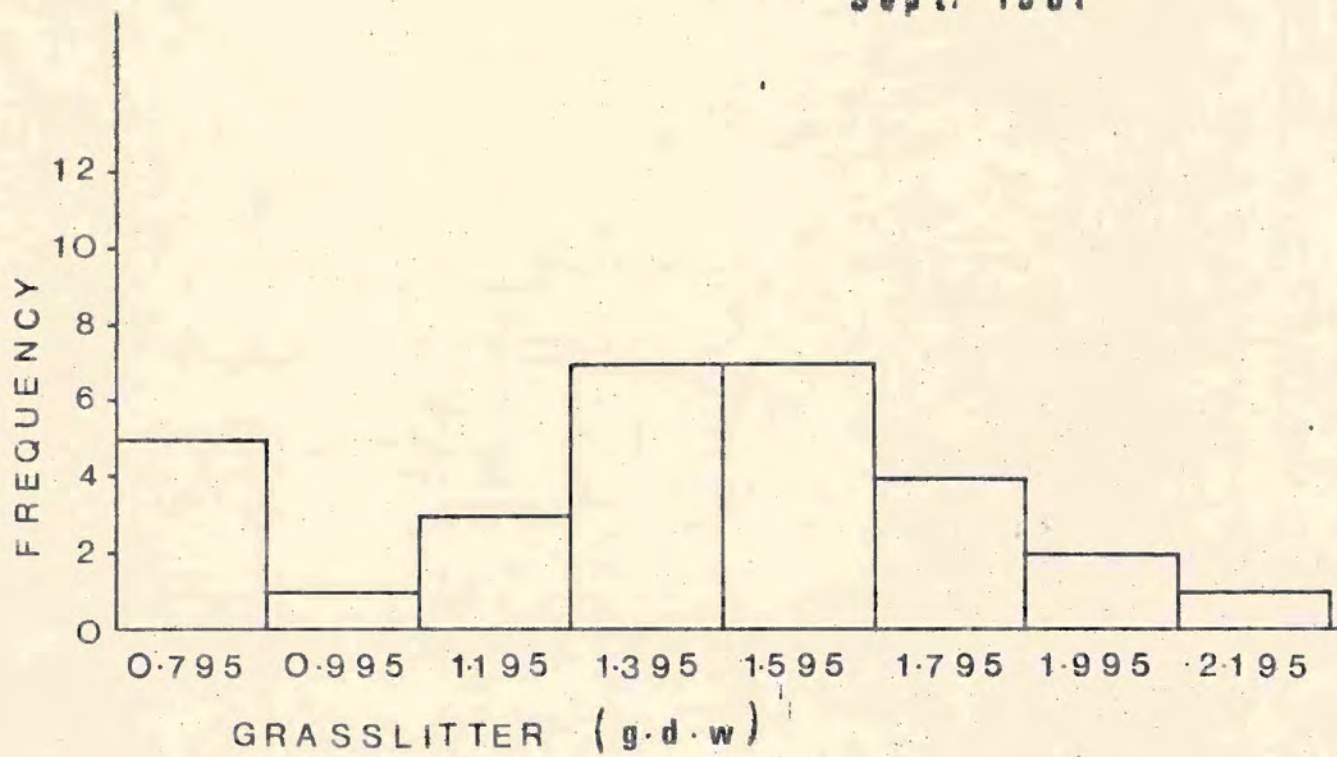


Fig 4.1b Log. transformation of frequency histograms in Fig. 4.1a.

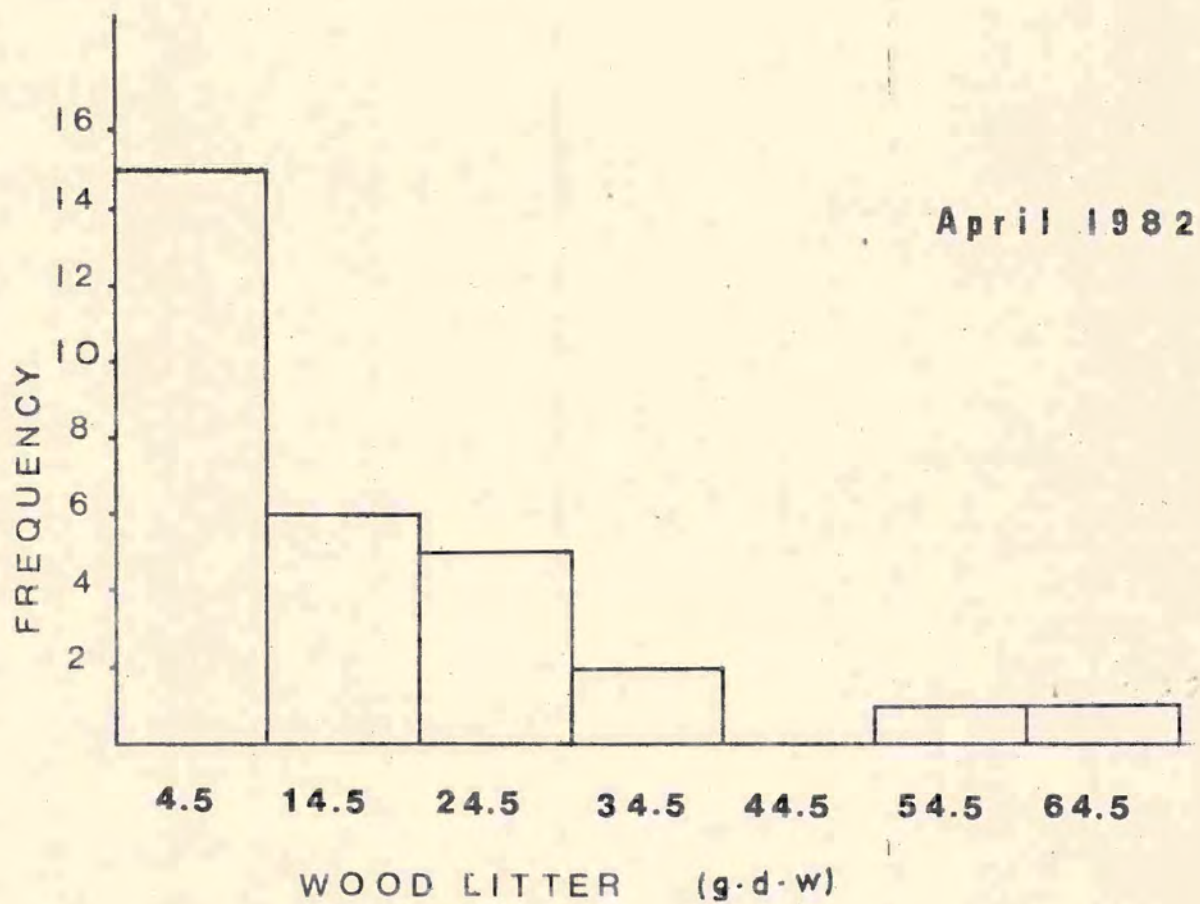


Fig 4.2 a The frequency of standing crop of woody litter (< 4 cm in diameter) in 30 - 1 m² quadrats laid in one of the eleven transects of Olturot April 1982.

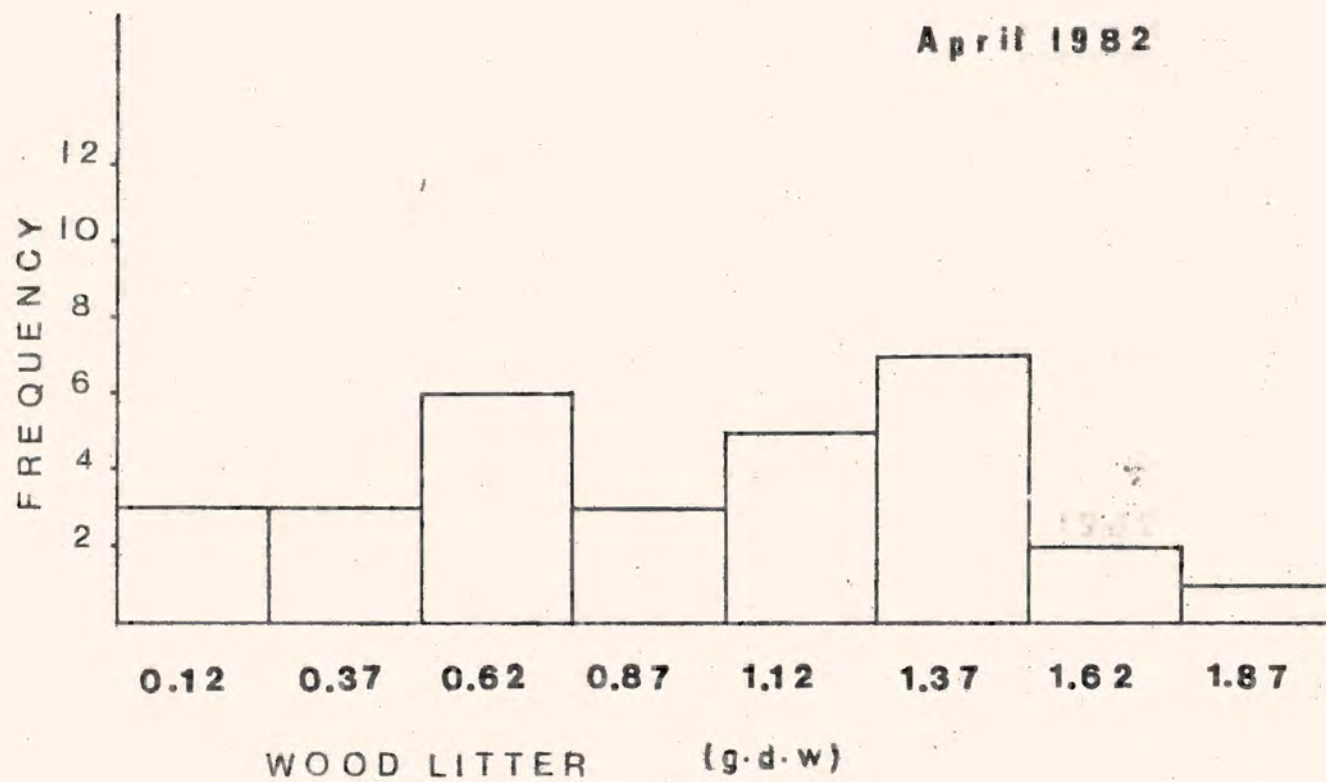


Fig. 4.2b Log. transformation of frequency histograms in Fig. 4.2a.

of the standing crop in other months at both sites was similar to that in Figs. 4.1 and 4.2.

The examples of the relationships between logarithmes of monthly rainfall data and logarithmes of monthly grass and woody litter weights at Olturot are shown in Figs. 4.3 and 4.4. There were no correlations established, probably due to the irregular pattern of rainfall which occurred in the study area. And for this reason, monthly rainfall data are unlikely to give any correlation with monthly standing crop. Vegetation weights are again compared with termite activity in chapter six.

4.3 DISCUSSION

Increases in grass litter weights during dry periods especially August and September (Table 4.2) can be attributed to the growth of grass induced by earlier rainfall. However, there were no close relationships established between vegetation biomasses and monthly rainfall data. This could be due to the short period for data collection compared to highly variable monthly rainfall. Perhaps to produce any significance relationship would be to

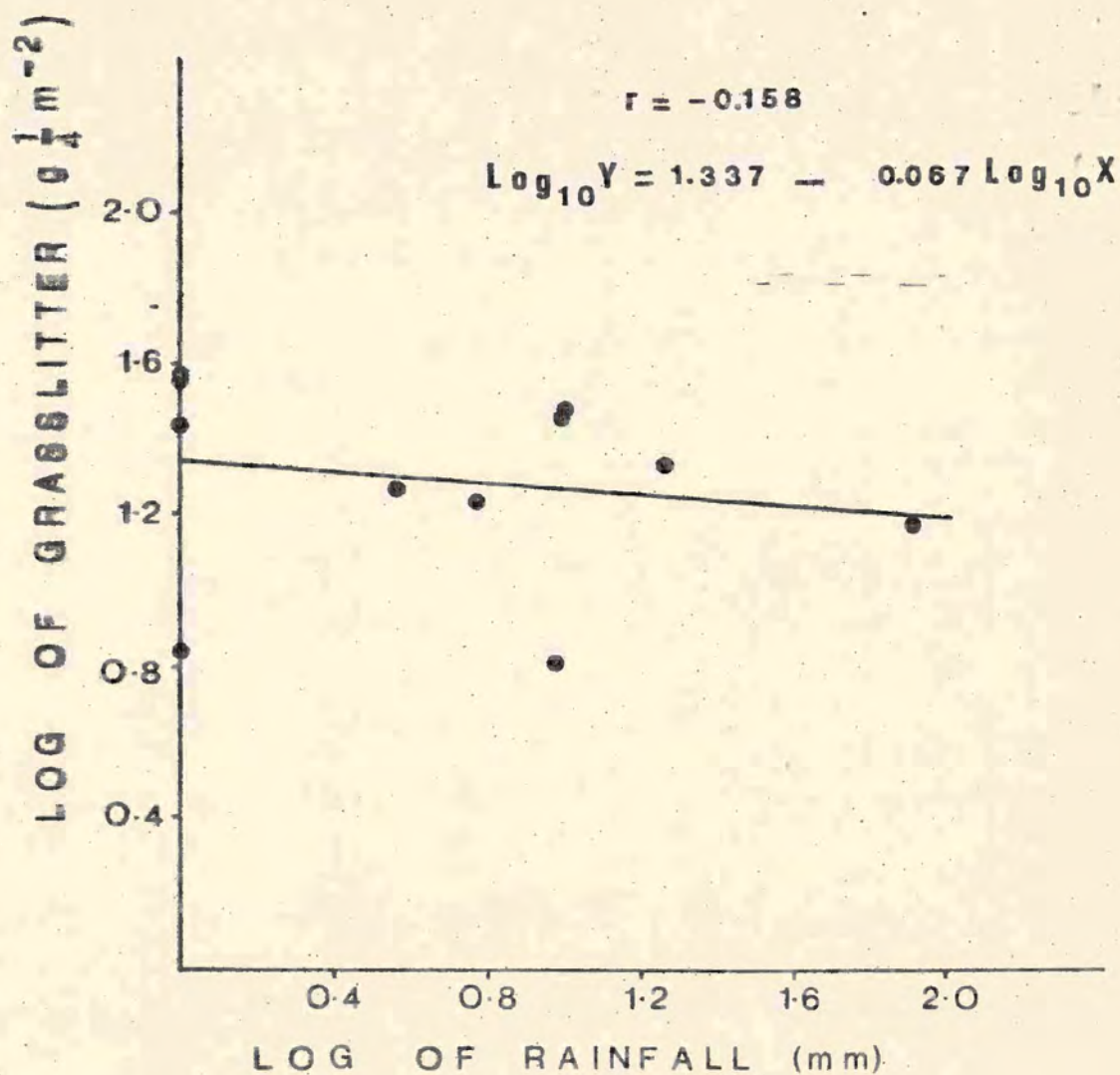


Fig-4-3 Monthly relationship between logarithms of the amount of grass litter (g) to rainfall (mm).

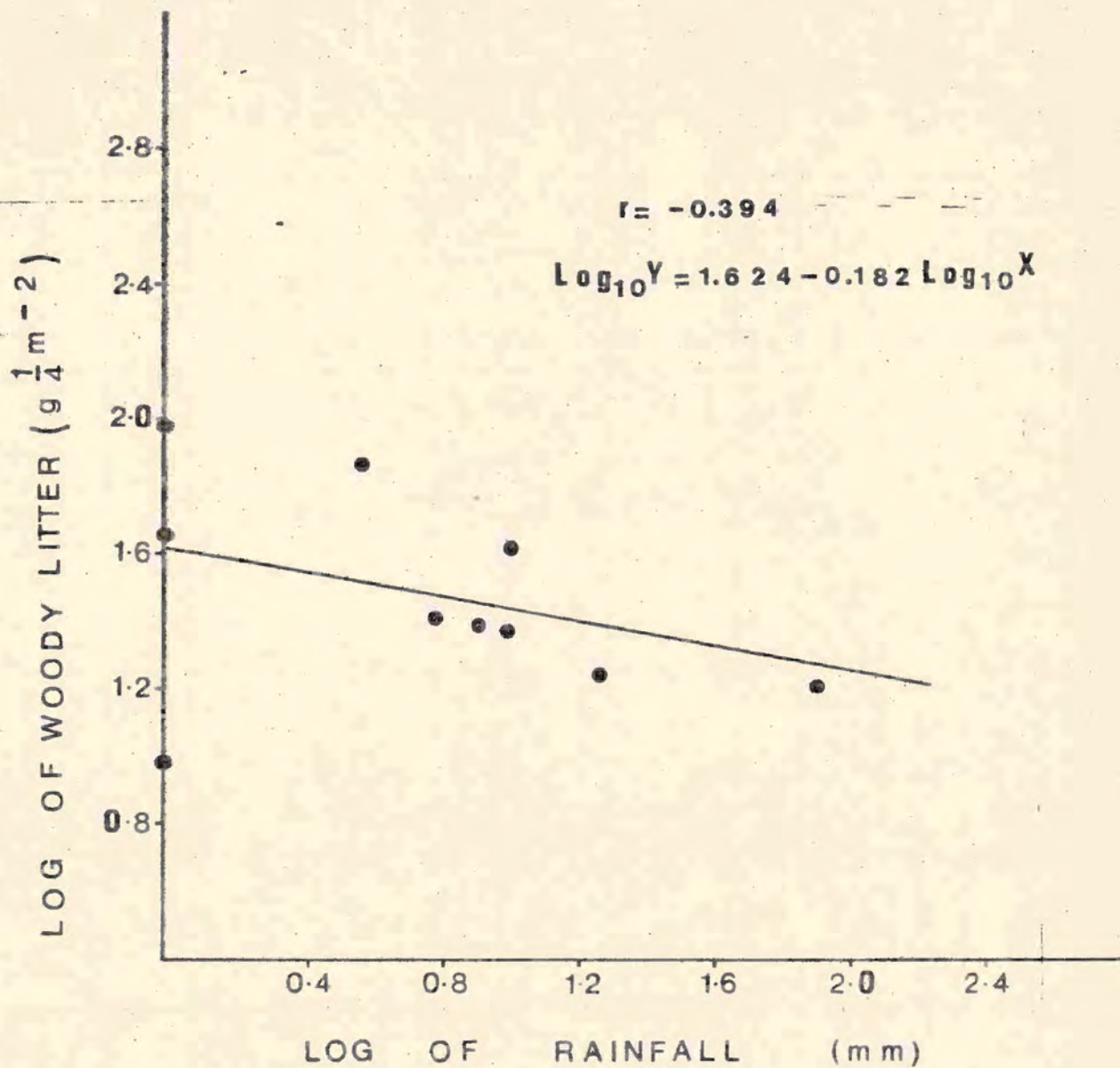


Fig.4-4 Monthly relationship between logarithms of the amount of woody litter (g) to rainfall (mm).

to monitor the rainfall records and standing crop over a period of more than a year. The rainfall which could have contributed significantly to the production of more vegetation during the present study (August 1981 to June 1982) was exceptionally low and only 129.2mm were recorded at Olturot.

The plant litter disappeared more rapidly during rainy season than in dry seasons (Tables 4.2 and 4.3). Studies carried out elsewhere, have demonstrated relationships between rainfall and primary production (Walter, 1954; Whittaker, 1970; Herlocker et al 1981) and rainfall and total litter fall (Collins 1977a).

The breakdown or decomposition of plant litter involves two major processes: a biotic process involving the detritus chain (Ovington 1962, Macfadyen 1963; Wiegart et al, 1975) and abiotic processes which include fire and leaching. Adequate moisture and temperature enhance the rate of decomposition (Minderman, 1968). Looking at the results reported in this study, increases in litter fall could be a result of climatic changes affecting the plant growth and trampling of vegetation by

animals. On the other hand, the decreases in litter can be accounted for by the detritus chain because fire and probably leaching are uncommon agents in the lowland parts of the IPAL study area. Termites are part of the detritus chain and indeed contribute to the breakdown of plant litter in the study sites. However, the removal of a whole standing crop involves several other consumers including grazing mammals, insects, birds and rodents.

The decline of vegetation biomass recorded in the sheep/goat paddock after the feeding trials, reveals the effect of grazing mammals on vegetation. The grass litter among the other vegetation categories decreased remarkably and apparently affected the termite activity (Chapter six).

CHAPTER FIVE

5. REMOVAL OF PLANT MATERIALS BY TERMITES

The fungus cultivating Macrotermitinae have a very broad diet of fresh litter and avoid decomposing materials (Buxton, 1981). In general, they forage within their feeding territories under favourable conditions of earth cover. The plant components used by termites would probably depend on their abundance and predictability. This implies that the most abundant plant component is likely to be removed at a higher rate than the least abundant. There have been no adequate investigation so far to assess their role in the removal of plant materials in an arid ecosystem. In the present study three different approaches were used to demonstrate their importance in litter consumption. These approaches are described in section 5.1.1; 5.2.1 and 5.3.1 of this chapter.

5.1 REMOVAL OF GRASS AND GRASS LITTER BY ODONTOTERMES

5.1.1 SAMPLING TECHNIQUE

A representative site of the open grassland within the woodland area was selected 2.5 km N.E. of Olturot Field Camp (Fig. 3.1). Plant materials, particularly grass litter serve as a potential food source for Odontotermes in the study area. The field observations carried out on termite activity revealed that roughly 0.5% of the ground surface was covered with Odontotermes soil sheetings. Because of this, the present study was directed into finding out the quantities of grass litter removed by Odontotermes. Lee and Wood (1971b) pointed out that direct assessment of the consumption of food by natural populations of termites in the field was difficult. This is probably due to the foraging behaviour of termites in their localised habitats. Because direct assessment of the consumption of grass litter by termites in the field is rather difficult, I hypothesized that the amount of grass litter removed would be correlated with the amount of soil used for covering eaten grass litter by Odontotermes in the field.

A method was developed in association with Dr. M. Collins whereby paired samples of foraged and unforaged grass were collected simultaneously and compared. The sampling apparatus consisted of two open-ended tins, each 10 cm in diameter. The two tins were held in a rigid frame which separated them by 4 cm. A short handle was fixed vertically between the two tins to help hold them firmly (Plate 1). I assumed that before sampling the areas beneath the two tins would have had (on average) the same amount of grass litter as each other. I tested this assumption by sampling 20 randomly located paired samples that had not been foraged and compared their differences statistically. This technique, developed for the purpose of comparing adjacent samples is limited to areas with a reasonably uniform spread of grass or grass litter on the ground surface.

During each month, 100 to 117 paired samples were collected. To avoid collecting biased samples, the apparatus was placed at a pre-decided orientation (North-south or East-west) depending on the direction of the line transect chosen) with one tin over an area of foraging gallery and the other outside it.



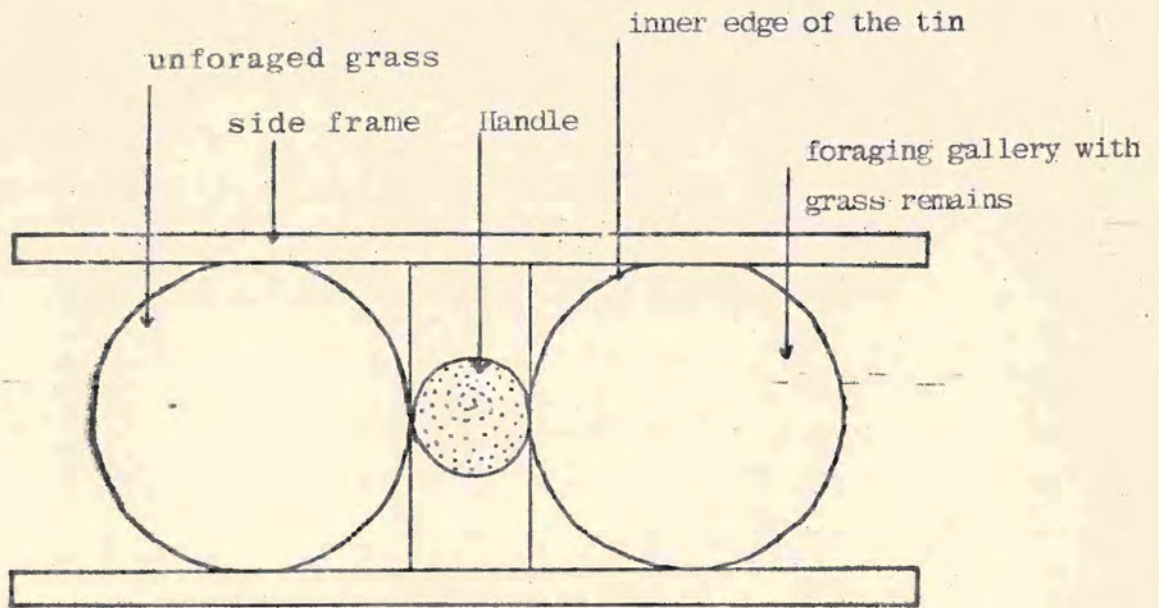
Plate 1: A photograph of the apparatus (two open-ended tins) used for sampling un-foraged grass litter (arrow 1) and foraged grass litter (arrow 2) and foraging soil of Odontotermes.

Any grass remains within the tin over the area of foraging gallery was carefully cut around the inner sides of the tin using a sharp scalped or knife (Fig. 5.1). Soil used by Odontotermes for constructing foraging galleries or sheetings, and any remaining grass litter, were brushed up into empty containers and then placed in a labelled paper bag. Similarly, unforaged grass within the other tin was collected and placed in a separate paper bag. At the field camp Odontotermes soil was separated from grass remains by sieving before weighing. The soil weight and the two grass weights were recorded and compared.

5.1.2 RESULTS

A test of significance made to compare 20 randomly placed paired samples showed no difference between the two adjacent samples of grass. The calculated value of t was found to be 0.0118 with 38 degrees of freedom. Therefore it was concluded that no real differences existed between the two adjacent samples of grass.

Fig. 5.1 A diagrammatic representation of the apparatus used for estimating off take of grass and grass litter by Odontotermes boranicus (Chidini).



Scale : 0 10 cm

Odontotermes foraging galleries or sheeting were conspicuous in the places where grass litter was abundant. Their foraging galleries differed from the other termite (Amitermes, Trinervitermes and Syracanthotermes) in colour, size, structure and texture. Lee and wood (1971) described subterranean galleries to be often lined with excreta which may have a characteristic appearance peculiar to the species. Odontotermes foraging galleries are lined with uniformly thin brown sheetings which are perforated and do not last more than a month on the ground surface.

The paired tins gave an estimate of the difference between the amounts of un-foraged grass litter and foraged grass litter that was removed by Odontotermes. The ground area occupied by one tin was 78.5 cm^2 . A total of 1189 paired samples was collected for 11 months. From this an average of 1.08 g per 78.5 cm^2 (i.e. 137.6 g per m^2) of grass litter was removed while an average of 9.73 g per 78.5 cm^2 (i.e. 1239.5 g per m^2) of soil was used. Table 5.1 lists the monthly mean weights of un-foraged grass litter, foraged (removed) grass litter and soil

Table 5.1: Monthly mean weights and standard errors of un-foraged grass, foraged grass and Odontotermes soil at Olturot.

Month	Sample size	Un-foraged		Foraged		<u>Odontotermes</u>	
		Grass litter		Grass litter		soil	
		(g m ⁻²)		(g m ⁻²)		(g m ⁻²)	
		Mean	(S.E.)	Mean	(S.E.)	Mean	(S.E.)
August 1981	110	299.4	(11.2)	194.9	(8.4)	2235.7	(79.9)
September "	108	207.0	(12.9)	201.3	(7.2)	2234.4	(151.1)
October "	108	310.8	(11.2)	202.5	(8.5)	2029.3	(175.4)
November "	110	225.5	(11.4)	149.0	(6.4)	1606.4	(49.6)
December "	108	173.2	(5.9)	128.7	(5.4)	1585.9	(47.7)
January 1982	102	164.3	(7.1)	132.5	(4.9)	1461.1	(47.7)
February "	111	154.1	(17.8)	109.6	(7.5)	894.3	(40.3)
March "	112	229.3	(10.2)	143.9	(6.9)	745.2	(41.9)
April "	117	132.5	(6.7)	85.4	(4.4)	304.5	(17.4)
May "	100	91.7	(4.5)	68.8	(3.3)	230.6	(12.9)
June "	103	123.6	(5.6)	86.6	(4.5)	284.1	(16.6)

used for covering foraged grass litter. The sample size varied from month to month because of other experiments on termites.

The monthly mean weights (g per 78.5 cm^2) of Odontotermes soil, grass removed and un-foraged grass are compared in Fig. 5.2. There was a possibility that grass litter could have persisted on the ground for more than a month, and for this reason, continual sampling of grass litter each month may have included last month's litter. The un-foraged grass weights did not account for the increases and decreases shown in Fig. 5.2 although sampling only involved grass and grass litter lying on the ground surface. However increases could have been due to the addition of more grass litter from the adjacent standing grass. There was a remarkable, regular drop in soil brought up from month to month in Fig. 5.2. It may be argued that building activity of termites depends on the amount of grass available on the ground surface. Thus Odontotermes covered large patches of grass litter with more soil than small scattered fragments which are sometimes consumed from the foraging holes only. Also the amount of grass foraged declined similarly.

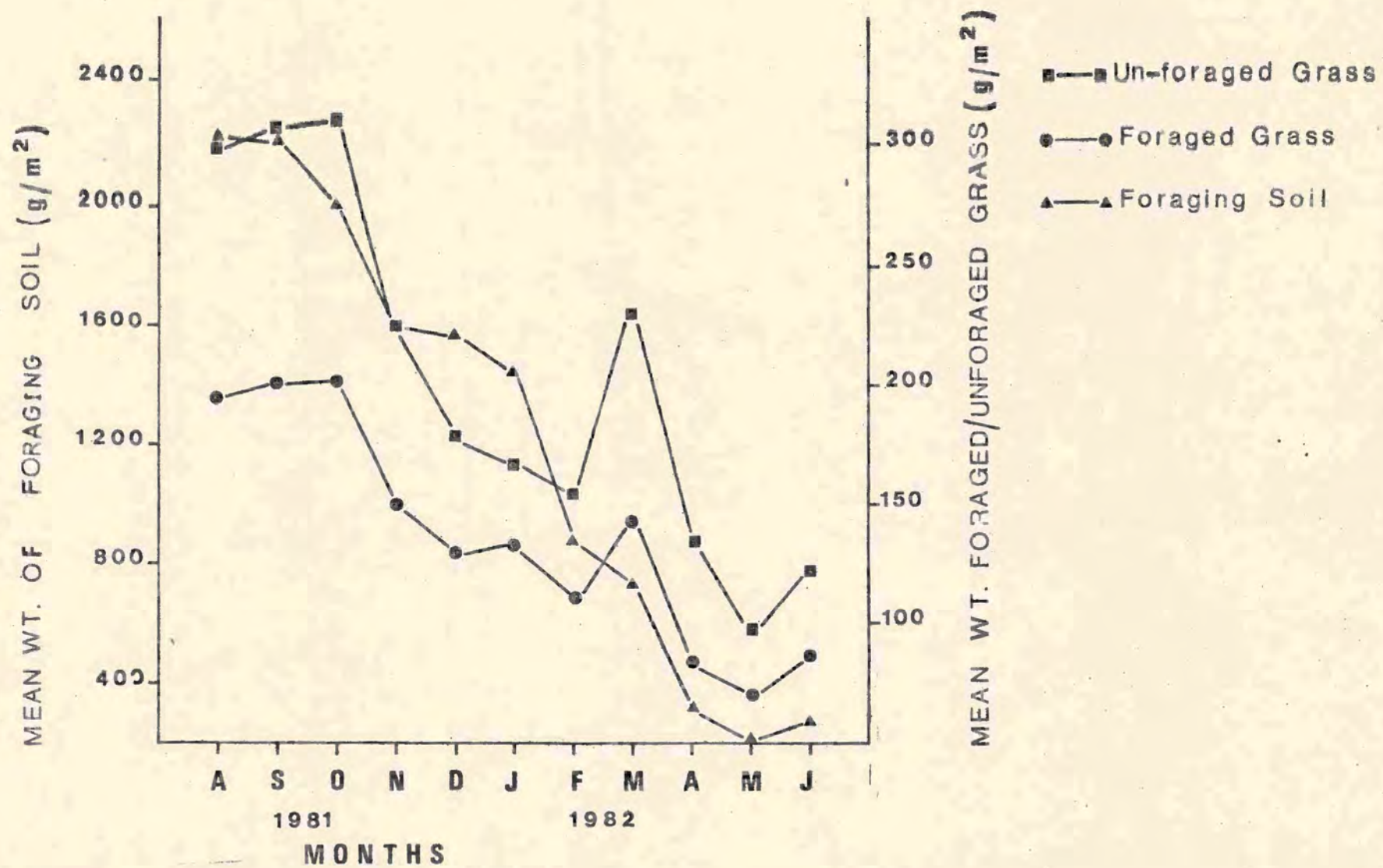


Fig 5.2 Monthly mean weights of soil brought up, un-foraged grass and grass removed by *Odontotermes* at Olturot.

The calculated monthly coefficients (r) values between the amount of grass or grasslitter moved and soil used for covering eaten grass are shown in Table 5.2. The coefficient (r) value for all the eleven months was calculated to be 0.921 with nine degrees of freedom. Therefore $P = < 0.001$ gave a very highly significant relationship between the amounts of grass litter removed and soil used up. Figure 5.3 shows the regression line and the equation as $y = -653.14 + 14.65x$. Single months values were assumed to show a similar trend of relationship to that in Fig. 5.3. However, the regression suggests that when less than about 40 g grass removed, no soil was used. The same point is demonstrated by the decline of soil and foraged grass in Fig. 5.2.

5.2 FOOD PREFERENCE

5.2.1 THE BAIT SAMPLING TECHNIQUE

The site for this study was located near Olturot Field camp (Fig. 3.1). A modification of the bait sampling technique (Sands 1972) was used to study food materials eaten by termites. Three representative places were selected and from each, 2 x 20 m plots

Table 5.2: Monthly product-moment correlation coefficient (r) values between the amounts of grass litter removed and soil used for cover by Odontotermes at Olturot.

Month	n	r	t
August	110	0.276*	32.266*
September	108	0.074*	7.887*
October	108	0.116*	12.454*
November	110	0.646*	119.736*
December	108	0.673*	130.399*
January	102	0.146*	14.918*
February	111	0.168*	18.844*
March	112	0.190*	21.683*
April	117	0.282*	35.232*
May	100	0.013	1.274
June	103	0.264*	28.662*

*Highly significant relationship at $p = 0.05$ level

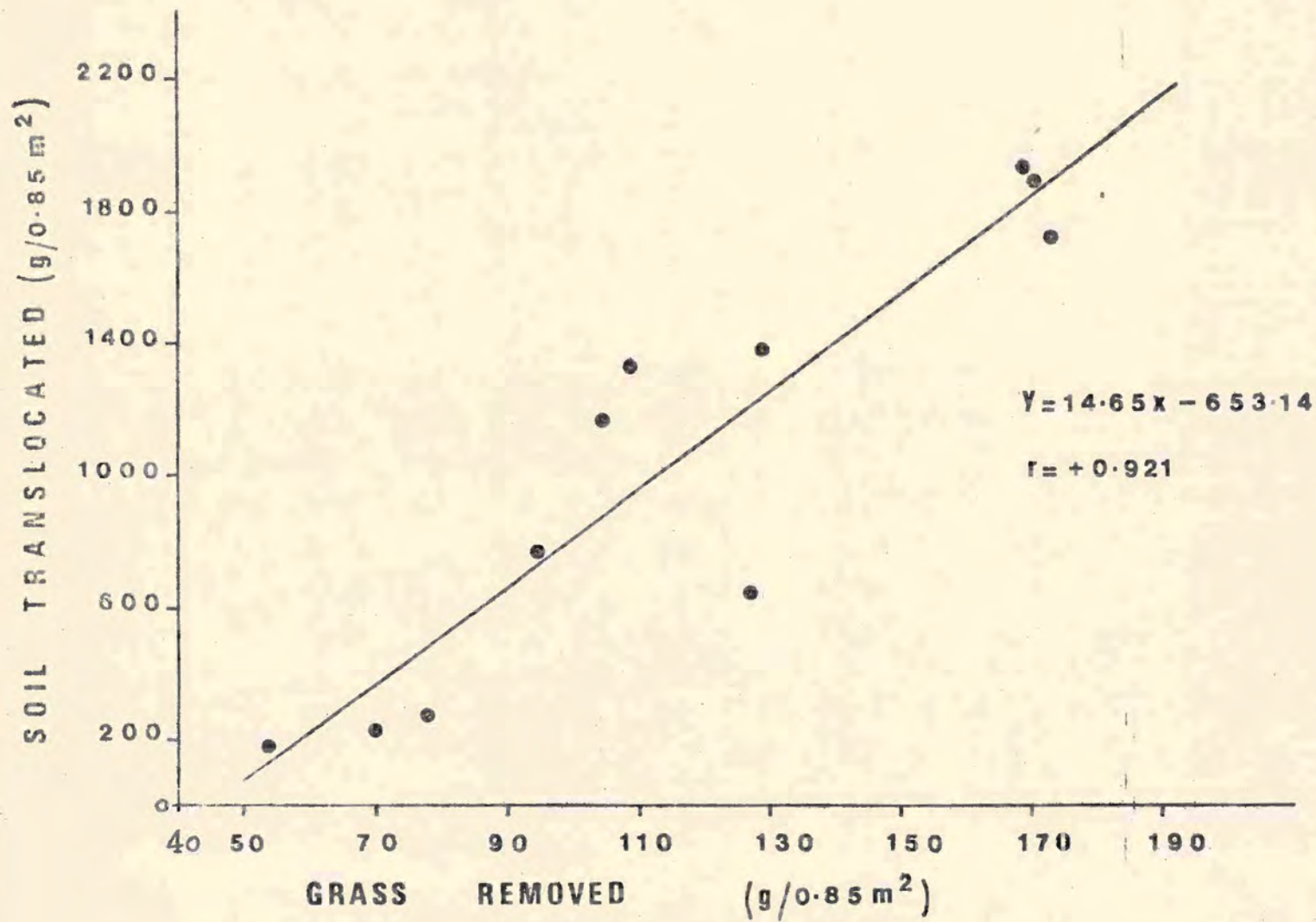


Fig. 5.3 The correlation between the total weights of grass removed and soil translocated by *Odontotermes* at Olturot.

were marked out. Small standing shrubs, grasses and dead plants on these plots were cleared a few days prior to setting out the experimental baits or substrates. This was to eliminate any possible competition between naturally occurring litter and artificial baits. Although some very small pieces remained, little potential food was present which might have drawn termites away from the baits. The substrates used were composed of common grasses and trees from nearby sites.

In the 2 x 20 m plots, three contiguous grids, each containing 20 bait substrates at 1m interval were set up (Plate 2). In the first 2 x 20 m plot, bait substrates consisted of 20 grass substrates (mainly comprised of Digitaria sp., Sporobolus sp., Eragrostis sp., Setaria sp., Dactyloctenium sp., Cenchrus sp.), 20 twig substrates (Less 2 cm in diameter) and 20 wood baits from Acacia tortilis, Salvadora persica, Salsola dendroides, Lycium sp., Cyclocheilon eryanthemum. All the substrates or baits were air dried, weighed, and placed in a randomized order at fixed 1 m interval on the grids.

Daily inspection for termite attack on the experimental substrates was carried out for 113 days.

The substrates discovered to have been attacked were noted, the date and the termite species involved was recorded. Little disturbance when checking termite species was incurred. However, the foraging galleries appearance (colour) were distinct from one termite species to another (See section 5.1.2) and so this assisted in the identification of the termite species involved. The genus Odontotermes was the most common and therefore responsible for more than 90% attacks on the bait substrates.

The remaining two 2 x 20 m plots were set up to determine plant species preferred by termites in dry and wet periods. Field identification of the commonest plant species used in these two plots was done with the help of IPAL research workers. Where necessary, samples were compared with sample specimens at the IPAL Herbarium. In February, 1982 (dry period) and April 1982 (rainy period), 13 different plant species occurring near the site were collected, air dried, and weighed. Each plant species was divided into smaller baits (substrates) ranging from about 7 to 85 g for grass species and 24 to 290 g for twig and wood species. As in the first plot, the baits were randomly placed at 1 m interval on

2 x 20 m plots. Daily inspection to check termite attack on the experimental substrates were made for wet and dry months. The plant species attacked and termite species involved were recorded. The weights consumed were calculated and the rate of consumption per day by termites was determined.

The experimental substrates suffered disturbances from birds such as Crested francolin, Yellow-necked spurfowl, Crowned plover, Yellow-billed hornbill etc. which scattered the substrates in search of grass seeds or the termites themselves. To avoid these disturbances, circular pieces of iron sheets and wire mesh were placed around loose plant substrates, they also acted as wind breaks (plate 2). This kind of situation might have affected the foraging activity of termites by creating a different micro-climate. To eliminate this, circular pieces of iron sheets were shifted from one substrate to another and replaced by a wire mesh after one to two days. The rate of substrate consumption was calculated from the first day of attack until the experiment ended.



Plate 2: A photograph of the bait sampling technique showing the arrangement of the substrates on the experimental plot and circular pieces of metal.

5.2.2 RESULTS

Most of the food substrates on the first 2 x 20 m plot were not attacked by termites. These unattacked substrates were collected at the end of the experiment and used as controls to estimate weight loss due to agencies other than termites. Unattacked grass substrates, twig baits and woodbaits, lost a mean weight of 1.9 g (S.E. 0.157, N = 9), 1.8 g (S.E. 0.223, N = 14) and 2.9 g (S.E. 0.265, N = 16) respectively. Average loss per day was found to be 0.017 g for grass substrates and 0.016 g for twig baits. These figures: 0.017 g and 0.016 have been subtracted from attacked grass substrates and twig baits not attributable to termites^{attack} in tables 5.3 and 5.6. The original weights in both cases were about the same. The amount of grass, twig and wood baits consumed mainly by Odontotermes in the first 2 x 20 m plot are shown in Table 5.3. To determine whether termites showed any preference for grass, twig or wood baits, an analysis of variance was performed based on all the baits provided from the three groups regardless of whether attacked or not. Non-attacked baits had no record of consumption but since termites were free to forage according to their own choice, and from

Table 5.3: The amount of bait substrates consumed from those substrates that were attacked by termites on the first 2 x 20 m plot placed for 113 days, at Olturot.
All weights in grams

No. of substrates consumed	Grass substrates		Twig baits		Wood baits	
	Initial weight	weight consumed	Initial weight	weight consumed	Initial weight	weight consumed
1	10	3.7	55	1.1	290	2.9
2	10	1.2	55	1.7	255	1.6
3	11	7.0	58	1.4	203	0.9
4	9	0.9	57	3.9	248	1.1
5	11	0.9	57	0.6	340	2.9
6	10	1.5	57	5.2		
7	10	1.2				
8	10	1.2				
9	11	1.0				
10	6	0.9				
11	9	0.7				
Σ		20.2		13.8		9.3
\bar{x}		1.84		4.30		1.86
S.E.		0.57		0.75		0.42

randomly placed baits, all the records were included in the analysis. Table 5.4 gives an analysis of variance summary for the three groups of substrates (grass, twig and wood) consumed. There was no significant difference between treatment means, therefore the null hypothesis ($H_0: u_1 = u_2 = u_3$) was accepted, that is, termites did not show any preference for grass, twig or wood baits.

The food choice trials carried out in dry and wet periods did not show any statistical preference for any particular plant species provided on the two plots when analysis of variance was made. However, preference could be drawn from field records by ranking the time (date) at which each substrate was attacked by termites. The hypothesis is that the first plant species to be attacked was most preferred. Table 5.5 lists the plant species ranked (from top to bottom) from the first to the last to be attacked. Every plant species provided was attacked and partly consumed in the process. The order of attack was used as a criterion to explain the termite preference because all the substrates were assumed to have equal chances of being attacked and all within the foraging sites of termites. Almost all the plant species occurring in the study area were observed to be palatable to termites except for Acacia mellifera leaf litter.

Table 5.4: Analysis of variance summary

Source of variation	Sums of squares	d.f.	Mean squares	F
	SST	K-1	$\frac{SST}{K-1}$	
Among substrates	2.999	2	1.499	0.789
	SSE	K(n-1)	$\frac{SSE}{K(n-1)}$	
Within substrates	108.36	57	1.901	
Total	111.36	59		

P > 0.05 no significant difference between treatment means.

Table 5.5 Plant species arranged according to the time of attack by termites; the first plant species to be attacked at the top and the last to be attacked at the bottom of the list, in dry and rainy periods at Olturot.

Order in dry period		Order in rainy period	
<u>Chloris virgata</u>	Grass	<u>Digitaria macroblephara</u>	Grass
<u>Digitaria macroblephara</u>	"	<u>Aristida mutabilis</u>	"
<u>Salsola dendroides</u>	Shrub	<u>Eleusine sp.</u>	"
<u>Eleusine sp.</u>	Grass	<u>Chloris virgata</u>	"
<u>Aristida mutabilis</u>	"	<u>Sporobolus sp.</u>	"
<u>Lycium sp.</u>	Shrub	<u>Salvadora persica</u>	Tree
<u>Sporobolus sp.</u>	Grass	<u>Setaria verticillata</u>	Grass
<u>Acacia tortilis</u>	Tree	<u>Solanum dubium</u>	Shrub
<u>Cordia sp.</u>	Shrub	<u>Acacia tortilis</u>	Tree
<u>Setaria verticillata</u>	Grass	<u>Salsola dendroides</u>	Shrub
<u>Salvadora persica</u>	Tree	<u>Diosperma eremophilum</u>	"
<u>Diosperma eremophilum</u>	Shrub	<u>Cordia sp.</u>	"
<u>Solanum dubium</u>	"	<u>Lycium sp.</u>	"

The mean rates of consumption per day of plant species in dry and rainy periods are shown together with total weights consumed from each plant species (Table 5.6). Unlike the previous experiment, it seems here that grasses are more favoured by termites than shrubs and trees. Overall total difference between wet and dry periods was made using t-test. The calculated t-value (1.139) is lower than the critical tabular value of t for $P > 0.05$ (2.064) with 24 degrees of freedom. So it was concluded that there was no significant difference between the amount of plant material consumed in wet and dry periods.

The dry and wet period total consumption of each plant species (i.e. grasses, shrubs and trees Table 5.6), were lumped together, and analysis of variance was made to determine statistical differences between grasses, shrubs and trees. Analysis of variance summary showed significant difference between treatment means at $P = 0.05$ (Table 5.7). Therefore it was concluded that termites show food preference to grasses,

Table 5.8: Rate of consumption of plant species by termites in dry and rainy seasons at Olturot.

Plant species	Dry season (February - March 1982)			Rainy season (April - May 1982)		
	Total g. wt. Provided	Total g. wt. consumed	g. day ⁻¹ consumed	Total g. wt. provided	Total g. wt. consumed	g. day ⁻¹ consumed
	<u>Grasses:</u>					
<u>Aristida mutabilis</u>	65.8	57.7	0.63	90.2	78.5	0.82
<u>Chloris virgata</u>	65.8	31.3	0.32	81.6	50.1	0.53
<u>Digitaria macroblephara</u>	60.0	47.3	0.65	78.3	69.5	0.85
<u>Eleusine sp.</u>	60.0	8.3	0.09	98.7	28.0	0.61
<u>Setaria verticillata</u>	60.0	5.8	0.18	51.7	32.8	0.20
<u>Sporobolus sp.</u>	60.0	35.5	0.55	99.9	45.0	0.29
Σ			2.4			3.3
\bar{x}			0.4			0.55

Table 5.6 continues

Table 5.6 continued

<u>Shrubs</u>						
<u>Cordia</u> sp.	100.0	1.9	0.05	52.3	2.3	0.07
<u>Duosperma eremophilum</u>	150.0	0.2	0.07	71.7	4.4	0.10
<u>Salsola dendroides</u>	150.0	3.2	0.02	102.9	6.9	0.11
<u>Solanum dubium</u>	150.0	2.1	0.04	57.4	6.2	0.10
<u>Lycium</u> sp.	164.5	5.9	0.10	164.3	3.2	0.07
			Σ			0.32
			\bar{x}			0.06
						0.45
						0.09
<u>Trees:</u>						
<u>Acacia tortilis</u>	210.1	9.7	0.16	643.4	2.2	0.03
<u>Salvadora persica</u>	150.0	3.0	0.09	452.4	14.0	0.17
			Σ			0.25
			\bar{x}			0.06
						0.2
						0.1
Overall total		211.9	2.99		343.1	3.95
Mean		16.3	0.23		26.4	0.30

Table 5.7: Analysis of variance summary

Source of Variation	Sums of squares	d. f.	Mean squares	F
Among plant substrates	SST 16924.3	K-1 2	$\frac{SST}{K-1}$ 8462.15	10.477**
Within plant substrates	SSE 8076.8	n-K 10	$\frac{SSE}{n-K}$ 807.68	
Total	25001.1	12		

** Highly significant difference at $P < 0.01$

5.3 RATE OF LITTER CONSUMPTION

5.3.1 THE QUADRAT METHOD

This study was situated near the bait sampling experiment at Olturot. 25 quadrat frames each 50 x 50 cm ($\frac{1}{4}$ m²) were randomly dispersed in a shrub invaded grassland to determine the consumption of naturally occurring litter. The purpose of this experiment was to investigate the time taken to remove a known quantity of naturally occurring plant litter.

From each $\frac{1}{4}$ m² quadrat frame, grass and woody litter (less than 4 cm in diameter) were carefully removed and immediately weighed in the field. After the standing vegetation within or suspended above the quadrat were marked with a water proof mark pen, the litter was replaced in its original position within the quadrat. Any new growths occurring in the course of this experiment were also marked. Small white painted stones were lined along the quadrat frame edges to mark the boundary. A few more stones were placed on top of the litter to prevent it from being blown out by strong winds. These stones were moved often from one position to another to limit any possibility of creating another micro-climate.

After every 2 to 3 days the litter within the quadrats was inspected for termite activity and animal disturbances. This experiment was carried out for 176 days from November 1981 to May 1982. Because of the high temperatures, sprouting vegetation during rainy periods wilted and dried quickly increasing the litter fall. Efforts were made to remove fresh litter within the quadrats, although it was not always satisfactorily accomplished, and could have led to my under estimating consumption of litter by termites.

Plant litter from two extra $\frac{1}{4}$ m² quadrats was removed and weighed like in the other 25 $\frac{1}{4}$ m² quadrat. However, the litter was not replaced on the ground instead it was placed on 2 mm wire mesh, measuring about 50 x 50 cm each. The wire meshes containing the litter were placed on small stones on the same site. This was to prevent any possible contact of litter with termites but still being accessible to micro-organisms and environmental parameters. When the experiment ended, mean percentage weight loss of litter from these two controls was then used in the calculation of the amount lost due to termites from the 25 $\frac{1}{4}$ m² quadrats (Table 5.8).

5.3.2 RESULTS

The grass and woody litter in each quadrat were attacked by termites and some were removed. In the control quadrats, grass litter lost about 26% of the original weight while woody litter lost about 14%. These percentages were due to other agencies other than termites. The plant litter especially grass appeared normally distributed from the data shown in Table 5.8. Although their original weights differed, the percent loss attributable to other agencies was subtracted from the overall loss of each $\frac{1}{4}$ m² quadrat to obtain weight loss due to termites (Table 5.8).

The mean rate of grass litter consumption in situ by termites was found to be $1.08 \text{ g m}^{-2} \text{ day}^{-1}$ while woody litter was $0.09 \text{ g m}^{-2} \text{ day}^{-1}$. The loss of grass litter due to other agencies especially micro-organisms and probably leaching was $0.38 \text{ g m}^{-2} \text{ day}^{-1}$ for grass litter and $0.02 \text{ g m}^{-2} \text{ day}^{-1}$ for woody litter. Converted into yearly figures termite consumption was $394 \text{ g m}^{-2} \text{ year}^{-1}$ for grass litter and $32.8 \text{ g m}^{-2} \text{ year}^{-1}$ for woody litter. Mean percentage consumption in yearly basis were 56% for grass litter and 15% for woody litter.

Table 5.8: The estimated plant litter weights attributable to termite attack on 25 $\frac{1}{4}$ m² quadrats randomly placed for 176 days, at Oiturot.

No. of quadrat	Grass litter (g per $\frac{1}{4}$ m ²)				Woody litter (g per $\frac{1}{4}$ m ²)			
	Initial wt.	Overall wt. loss	Loss due to other agencies	Loss due to termites	Initial wt.	Overall wt. loss	Loss due to other agencies	Loss due to termites
1	64.8	58	15	43	7.8	6	0.8	5
2	39.3	35	9	26	26.2	4	0.6	3
3	110.5	93	24	69	0	0	0	0
4	67.6	54	14	40	228.2	48	7.0	41
5	98.6	90	23	67	0	0	0	0
6	52.0	29	7	22	4.9	1	0.1	1
7	80.3	75	19	56	60.2	10	1	9
8	51.1	41	11	30	60.2	0	0	0
9	108.6	86	22	64	7.8	0	0	0
10	75.8	53	14	39	102.9	15	2	13
11	109.6	79	21	58	0			
12	65.7	57	15	42	0	0	0	0

Table 5.8 continues

13	71.2	52	14	38	37.9	2	0.3	2
14	94.0	87	23	64	30.1	3	0.4	3
15	105.9	65	17	48	6.0	6	0.8	5
16	119.6	101	26	75	5.0	5	0.7	4
17	73.9	56	15	41	0	0	0	0
18	71.2	34	9	25	0	0	0	0
19	71.2	60	16	44	0	0	0	0
20	120.5	57	15	42	11.7	7	1	6
21	75.8	46	10	36	0	0	0	0
22	167.1	123	32	91	55.3	13	2	11
23	66.6	41	11	30	0	0	0	0
24	83.1	61	16	45	19.4	0	0	0
25	89.5	77	20	57	0	0	0	0
<hr/>								
Total	2138		418.6	1192	663.3		16.8	103.3
Mean	85.5		16.7	47.7	26.5		0.7	4.1
S.E.			1.2	3.4			0.3	1.7

A succession of foraging activity was observed within the quadrats. Odontotermes species was the most common surface feeder in all seasons. As the wet season approached, Amitermes species increased its feeding activity on woody materials and at the same time Odontotermes appeared to switch from grass litter which was becoming less abundant to woody litter and standing vegetation. The foraging activity of Synacanthotermes became conspicuous during the wet season and concentrated more on small litter fragments than large twigs. Part of the litter loss may be attributed to Trinervitermes species and harvester ants (Messor spp.) which occurred in the study area.

5.4 DISCUSSION

Estimates of natural rates of consumption have in some cases relied on extrapolation from laboratory data while others have relied on direct measurement in the field (Lee and Wood, 1971; Lepage, 1974b; Haverty and Nutting, 1975). Direct estimates of consumption have relied on either measurement of removal of naturally available food or removal of food in the form of baits.

The results reported in this study indicate that over a six month period about 56% of the grass litter available in the study sites was removed by termites, mainly of the genus Odontotermes. It is likely that due to high rainfall (a total of 196.3 mm) in March to May, 1981, followed by high temperatures in August to October, more litter accumulated on the surface. This could have led to the high rate of consumption reported here for Olturot. Again this may suggest that termites continue foraging on litter all the time provided the environmental conditions are favourable for them. Micro-organisms could also be decomposing a significant amount of litter but only in humid conditions, and termites are obviously more important litter feeders in dry conditions than micro-organisms (Fig. 5.2). Many grazing mammals avoid arid areas during dry seasons (e.g. Sumburu and Rendille herds come to graze around Balesa and Olturot only in rainy seasons), as a result there is more of litter available for decomposers. One can suggest that due to lack of many competitors on food resources, termite populations are high and in turn remove more surface litter to a level controlled by the existing colonies.

The estimates of plant litter removed by termites at the study sites are summarised in Tables 5.1, 5.3, 5.6 and 5.8. These results showed that more grass litter was consumed than twig or wood litter. Although one experiment (section 5.2 Table 5.4) showed that there was no statistically significant differences of food preference by termites, perhaps due to limited resources in arid ecosystem or due to termite behaviour on experimental baits, the results of another (Table 5.7) indicated that grasses were more favoured than woody materials. It seems more likely to me that the termites may choose grass for its availability and nature while woody materials may be more difficult to exploit.

The study area typically receives rain in two seasons: April and November, but during the study period a total of only 26.5 mm was recorded in November to December. This accounts for a general decline of the amount of grass and grass litter indicated in Fig. 5.2. Hence the amount of grass removed by Odontotermes subsequently decreased. The amount of soil used for constructing surface sheetings or galleries depended on the availability of plant litter, as this declined, so the rate of

soil used also declined (Fig. 5.2). The decline of Odontotermes activity was probably regulated by the grass litter present on the ground and on the other hand grass litter fall was controlled by the environmental variables such as rainfall and temperature. The two processes namely termite activity on soil and on plant litter are important aspects in arid or semi-arid ecosystems because degradation of either of the two or both could contribute in desert encroachment. However termites unlike livestock are a natural part of the ecosystem and at most they might be a contributory factor.

The correlation between grass litter consumed by Odontotermes and soil used for constructing foraging galleries (Fig. 5.3) could be a useful tool for assessing food consumed indirectly. These results can also be used to predict the level of feeding activity of termites by the assessment of surface sheetings.

CHAPTER SIX

6. SOIL TRANSLOCATION BY ODONTOTERMES

6.1 METHODS

Nearly all termites construct a system of galleries or covered runways which they use when searching for food. Many members of the subfamily Macrotermitinae construct galleries in the soil or make covered runways or sheetings on the soil surface, on low-growing plants and on fallen logs or on the outside of standing trees. In contrast to covered runways, which protect the termites moving between the nest and the source of food, sheetings cover the source of food itself.

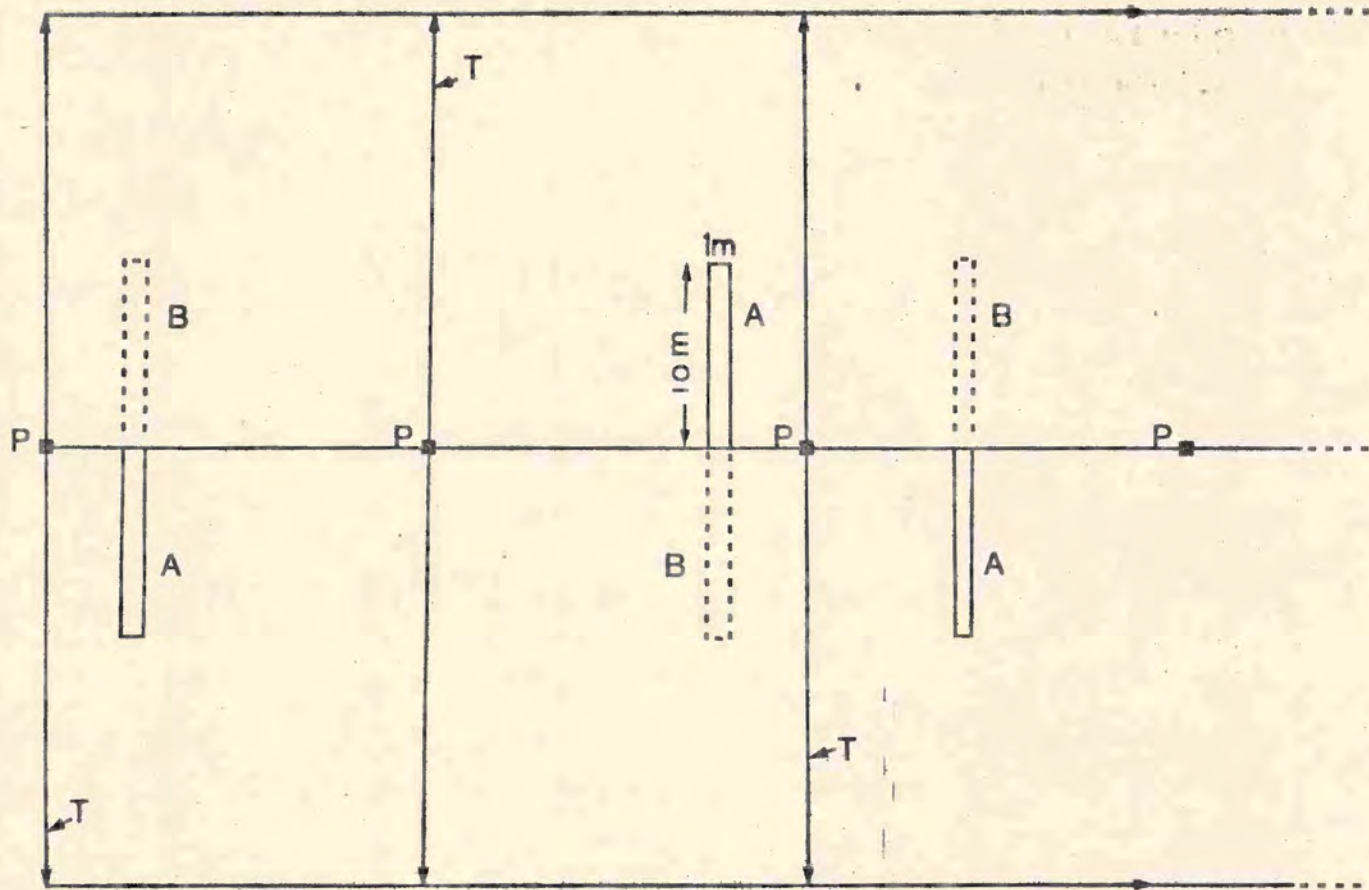
Some species of the genus Odontotermes construct extensive covered sheetings. Several other surface feeding termites feed under such protective sheetings. There is little information on the quantities of soil transported above ground for the purpose of packing the eaten-out portions of fallen branches, logs, standing tree stumps and grasses (Lee and Wood, 1971). The aim of this study was to measure the quantities of soil translocated for the purpose

of covering food materials consumed by Odontotermes in an arid area. Such measurement may help to explain the activity of termites on the vegetation and soil in general.

A method was developed to measure the quantities of soil translocated or moved on to the surface by Odontotermes. Four permanent transect lines were laid out at the study sites: one at the Olturot site and the others inside the cattle, the ungrazed and the sheep and goat paddocks at Balesa Kulal (Fig. 3.1). Each transect line was used as an experimental base-line and was marked at 20 m intervals by fixed posts. At the Olturot site and in the cattle paddock the base-lines were 200 m long while those laid out inside the smaller ungrazed and sheep/goat paddocks were 100 m long.

Randomly selected one metre wide and ten metre long strips were marked out in one within each 20 m interval along the experimental base-line, using a stratified random method (Fig. 6.1). These foraging strips once established, were kept permanently for weekly collections of Odontotermes soil. An

Fig. 6.1: A diagrammatic representation of sampling plan laid on the ground showing some of the foraging strips and transects used for termite soil collection and estimation of standing crop of plants respectively.



- A** foraging strips
- B** side of foraging strip unsampled
- P** 20m interval Posts on base-line
- T** 100m transects

Odontotermes foraging gallery or sheeting was recognised by its appearance (colour, homogeneity, hardness etc) and once identified within the foraging strips, it was carefully brushed into collecting containers. Three categories of Odontotermes soil were recognised i.e. soil covering grass, soil covering wood and soil covering dung. Each soil category was placed in a separate paper bag. At the Field camp, collected soil was separated from small plant debris by a 2 mm sieve mesh before weighing.

I assumed that removal of termite soil does not inhibit or enhance further soil translocation. I tested this assumption by randomly locating 15 pairs of 50 x 50 cm ($\frac{1}{4}m^2$) quadrat frames over an area containing Odontotermes foraging soil. This soil was removed from one of each pair while the soil on the other pair was lightly marked with a white powder "polyfilla". After one week, fresh Odontotermes soil was collected from each pair and weighed. The weights on treated and untreated quadrats were compared using a t-test. Their variances were similar and the data approximately normal. The test was repeated in two areas and

gave t-values of 0.027, n = 15 and 0.156, n = 15 respectively. Therefore no significant difference was found between the amount of fresh soil on the two paired quadrats.

The decomposition of foraging galleries or sheetings to unrecognisable (and therefore uncollectable) state during the weekly intervals was negligible especially in dry seasons and where disturbances were minimal. Nevertheless, frequent collection was desirable during rainy periods. The Odontotermes soil data which was taken as a measure of termite activity was compared to rainfall, relative humidity and temperature data recorded at Olturot and Balesa Kulal (see Chapter Three).

6.2 RESULTS

In their endeavour to exploit the primary production, termites bring up soil from the lower layers to the surface in order to cover themselves and the food they consume. However, the erosive factors such as wind, water and animals act on the termites soil structures and erode them from their

original position. Therefore the loss of foraging galleries is at its highest level when these factors are operating.

Odontotermes were found to translocate large quantities of soil during their feeding activity. The total soil (i.e. soil on grass, on wood and on dung) translocated at the main experimental site at Olturot was found to be 119.3 kg per 100 m² per eleven months. An average of 3.6 g per m² per day was translocated. This figure is equivalent to 13 metric tons per hectare per year. The quantity of soil used for building foraging galleries varied considerably from week to week and month to month (Tables 6.1, 6.2 and 6.3).

A comparison of the amount of soil translocated at the various sites, together with monthly rainfall records are plotted in Figures 6.2 and 6.3. There was no rainfall in the months of June and July before setting up this study in August 1981. The results shown in Figures 6.2 and 6.3 do not include soil on dung pats because it was very little and again the dung pats were not uniformly distributed within the foraging strips. This was due to the

Table 6.1 Monthly mean variation of the amount of soil translocated by Odontotermes on various food components at Olturot.

	No. of foraging strip	Soil on grass g/10m ² Mean (S.E.)	Soil on wood g/10m ² Mean (S.E.)	Soil on Dung g/10m ² Mean (S.E.)
August 1981	30	114.8 (24.1)	7.3 (2.4)	3.5 (1.9)
September 1981	40	364.4 (49.2)	33.5 (10.2)	6.0 (4.2)
October "	50	283.5 (59.2)	31.2 (7.2)	7.1 (3.5)
November "	40	98.5 (23.3)	13.4 (5.8)	3.5 (2.2)
December "	40	300.1 (75.9)	31.3 (16.6)	0.9 (0.8)
January 1982	50	98.3 (34.1)	11.3 (3.3)	2.6 (1.7)
February "	40	95.2 (21.1)	40.7 (15.6)	1.7 (0.7)
March "	40	47.4 (13.1)	23.5 (16.7)	0.7 (0.6)
April "	50	122.3 (20.9)	27.3 (5.0)	0.9 (0.4)
May "	40	242.4 (68.8)	39.3 (16.9)	0.4 (0.3)
June "	40	261.3 (59.4)	34.6 (8.7)	0.4 (0.2)
Overall means		184.4 (40.8)	26.7 (9.9)	2.5 (1.5)

Table 6.2 Monthly mean variation of the amount of soil translocated by Odontotermes on various food components at Balesa Kulal: cattle paddock

Month	No. of foraging strip	Soil on grass g/10m ²	Soil on wood g/10m ²	Soil on Dung g/10m ²
		Mean (S.E.)	Mean (S.E.)	Mean (S.E.)
September 1981	20	233.7 (81.4)	11.8 (4.6)	4.3 (3.3)
October "	40	85.0 (16.0)	4.9 (2.9)	7.9 (7.6)
November "	40	81.3 (28.4)	9.3 (4.0)	7.6 (7.2)
December "	50	74.0 (16.0)	5.9 (3.8)	0.2 (0.2)
January 1982	40	65.9 (13.5)	16.4 (4.3)	4.2 (3.1)
February "	40	34.8 (6.7)	10.5 (3.0)	0.8 (0.6)
March "	50	47.9 (12.6)	22.8 (10.6)	0.0 (0.0)
April "	40	224.0 (45.5)	61.7 (15.4)	6 (2.2)
May "	40	116.9 (28.9)	25.5 (10.4)	3.7 (2.5)
June "	50	72.6 (20.7)	11.6 (5.6)	0.8 (0.5)
Overall means		103.6 (26.9)	18.0 (6.5)	3.6 (2.7)

Table 6.3: Monthly mean variation of the amount of soil translocated by Odontotermes on various food components at Balesa Kulal; Ungrazed and sheep/goat paddock.

Month	Number of foraging strip	SOIL ON GRASS g/10m ²		SOIL ON WOOD g/10m ²		SOIL ON DUNG g/10m ²
		Ungrazed paddock Mean (S.E.)	Sheep/goat paddock Mean (S.E.)	Ungrazed paddocks Mean (S.E.)	Sheep/goat paddock Mean (S.E.)	Sheep/goat paddock Mean (S.E.)
September 1981	10	748.7 (275.9)	331.0 (120.3)	185.6 (75.3)	39.1 (39.1)	4.5 (3.0)
October "	20	288.6 (86.4)	771.1 (23.7)	87.0 (40.1)	11.8 (9.3)	1.2 (0.9)
November "	20	122.4 (35.8)	64.1 (21.9)	39.8 (14.0)	11.4 (5.8)	1.0 (0.5)
December "	25	151.7 (43.2)	88.2 (41.5)	34.0 (16.5)	6.5 (5.6)	3.3 (2.6)
January 1982	20	178.5 (45.6)	36.0 (8.4)	154.5 (60.5)	10.8 (5.8)	0.0 (0.0)
February "	20	104.4 (46.6)	32.6 (16.7)	86.6 (32.0)	22.3 (13.2)	0.7 (0.5)
March "	25	32.0 (9.6)	19.8 (11.3)	39.0 (11.9)	8.1 (5.2)	1.8 (1.7)
April "	20	109.5 (41.7)	53.7 (19.4)	36.6 (14.2)	16.1 (6.8)	2.8 (2.2)
May "	20	101.1 (35.5)	43.6 (21.3)	39.7 (4.5)	28.1 (18.1)	0.9 (0.5)
June "	25	198.3 (97.3)	9.1 (4.1)	84.8 (39.8)	0.8 (0.5)	0.0 (0.0)
Overall means		203.5 (71.8)	75.5 (28.9)	78.8 (30.9)	15.5 (10.9)	1.6 (1.2)

Note: Offtake trials with small stock were carried out from September 21st to 29th 1981 and 23rd May to 15th June 1982. Soil samples were collected on 22nd and 27th September 1981 and, 25th, 29th May and 1st, 8th and 15th June 1982.

litter in three experimental sites. Total monthly rainfall is also shown for Balesa Kulal and Olturot.

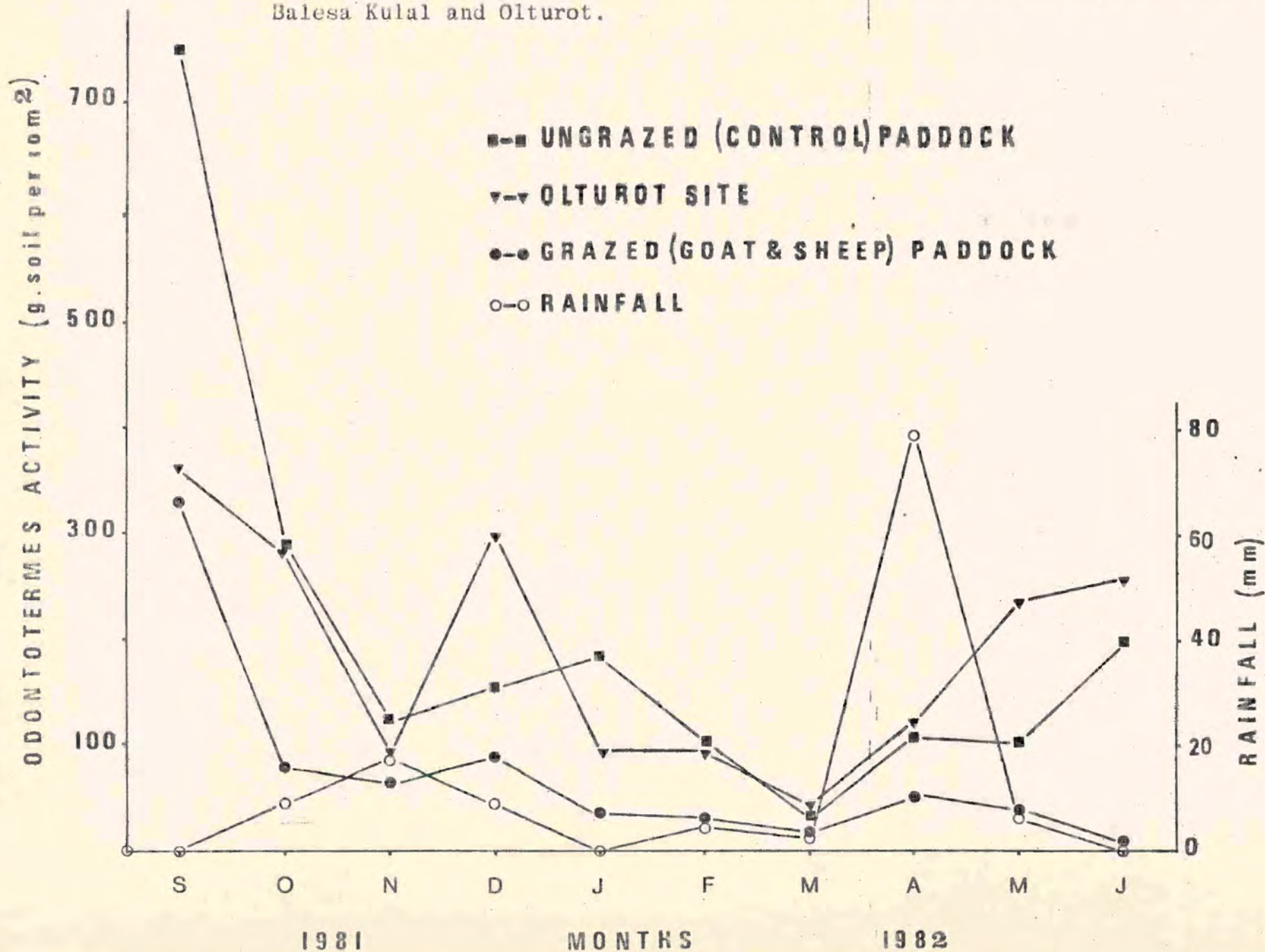
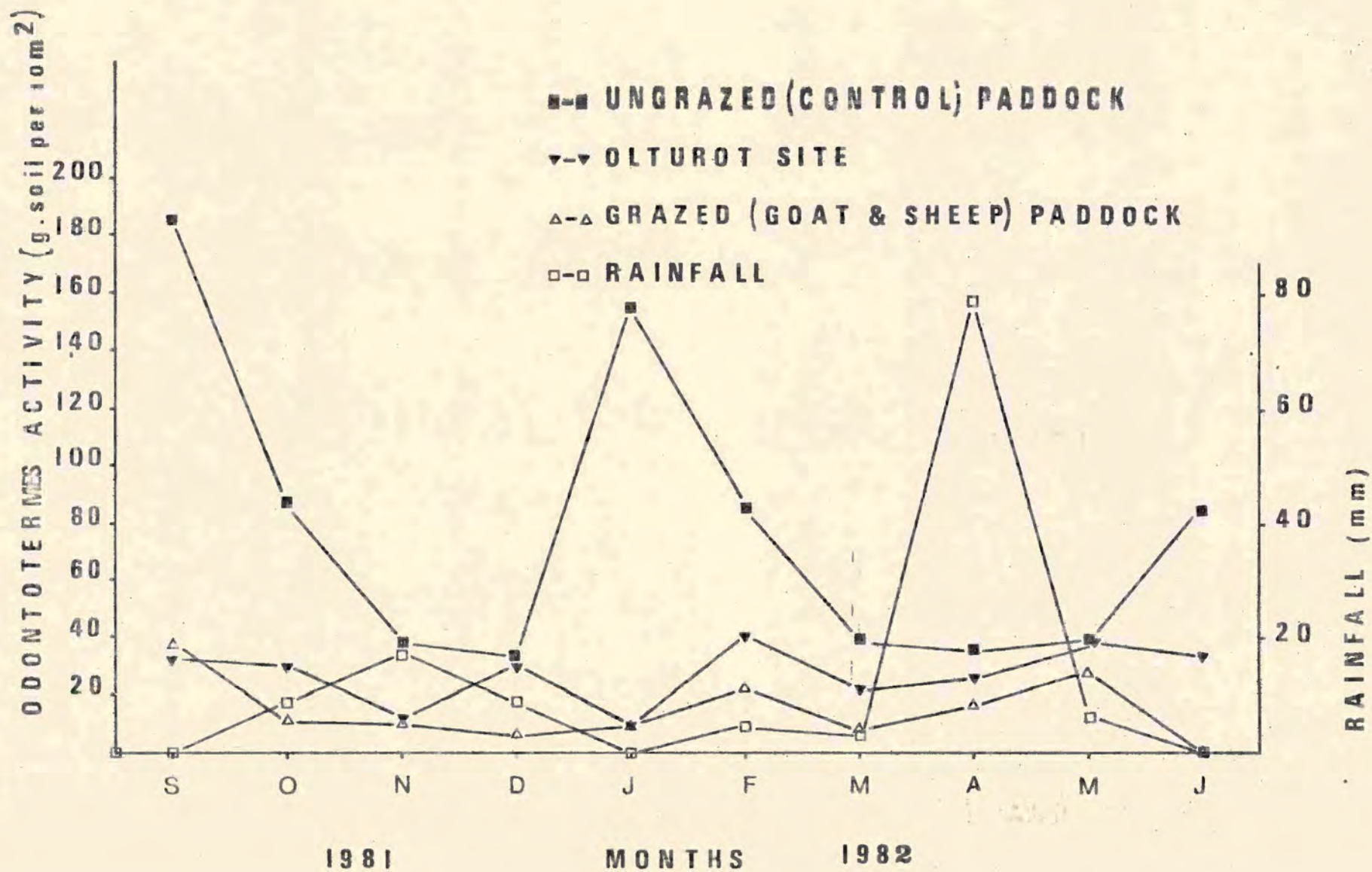


Fig. 6.3: Comparison of *Odontotermes* activity (g. of soil translocated per 10 m²) on woody litter in three experimental sites. Total monthly rainfall is also shown for Balesa Kulal and Olturot.



absence of grazing herbivores especially in dry periods. On the other hand data from the cattle paddock were not included in the graphs (Fig. 6.2 and 6.3), because the paddock was not subjected to any feeding trial as had been expected.

All the monthly quantities of soil translocated on the plant litter per m^2 by Odontotermes and the monthly standing crop of plant litter (grass and wood) per m^2 sampled at all the study sites (Chapter Four) were compared (Fig. 6.4). Their statistical relationship was found to be significant at $P = < 0.1$ with a correlation coefficient (r) value of 0.575, and the regression line equation as $\log_{10} y = 0.877 \log_{10} x - 0.721$. Therefore it was concluded that quantity of soil translocated by Odontotermes related to the amount of plant litter available.

There was no significant correlation established between the environmental variables listed in Table 6.4 and the quantities of soil translocated on the surface per m^2 per month by Odontotermes at all the study sites. As noted earlier, temperatures and relative humidity were not recorded from the soil surface or food-soil interface, but only from the surrounding air.

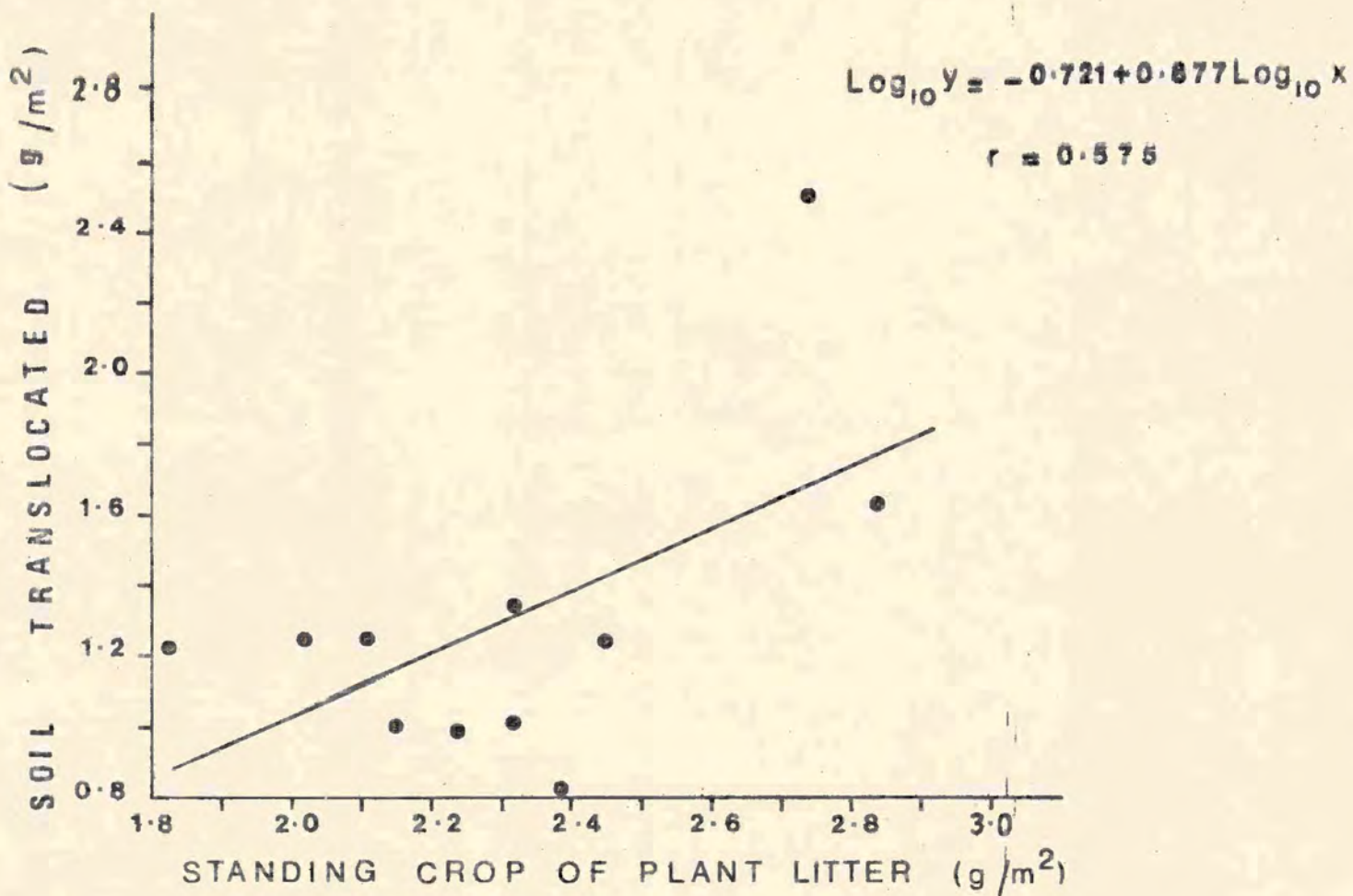


Fig. 6.4: The relationship of the amount of soil translocated by Odontotermes on plant litter' at Balesa Kulal and Olturot. Lumped monthly data.

Table 6.4 A comparison of Odontotermes activity on soil and environmental variables. Mean monthly readings at Balesa and Olturot.

Month		Odontotermes activity (Soil translocated)		Total monthly rainfall (mm)	Mean R.H %	Mean Air Temperature °C
		n	g/m ²			
August	1981	30	324.6	0	41.0	30.6
September	"	80	42.3	0	47.0	32.6
October	"	130	22.0	8.9	48.5	32.8
November	"	120	10.7	17.2	47.0	31.2
December	"	140	17.3	9.3	44.8	31.3
January	1982	130	12.6	0	49.5	31.5
February	"	120	9.8	4.9	39.3	32.2
March	"	140	6.3	2.8	38.5	32.8
April	"	130	17.9	79.3	59.0	29.1
May	"	120	17.7	6.8	49.5	31.2
June	"	140	16.7	0	46.5	30.6

6.3 DISCUSSION

In general, the Odontotermes activity was mainly on surface litter, but it was shown that there was more soil covering the grass litter than woody litter (Table 6.1, 6.2 and 6.3). This suggests that Odontotermes prefer foraging on grass litter to woody litter if it is available on the ground surface. The large quantities of Odontotermes soil sheetings reported here were not necessarily for protecting themselves against predators but probably for creating more favourable atmosphere within their food source. The soil sheetings seemed to prolong the feeding activity on the food during unfavourable weather conditions. The sheetings or galleries could also be beneficial in guiding other termite workers to the food sources.

It appeared from the result shown in Fig. 6.3 that the presence of food sources influenced the amount of soil brought on to their surfaces by Odontotermes. Subsequently, this soil is washed away by rain leading to soil degradation.

The pattern in Figures 6.2 and 6.3 is very similar. Thus foraging was generally high in September - October, December - January and again in May - June and low in between. As the same pattern is found in both sites (Olturot and Balesa Kulal), it seems that some external cause is responsible. The rainfall data plotted in Figures 6.2 and 6.3 suggests that rainfall stimulates foraging activity. That is, high peaks of foraging activity come after rains. However, the soil moisture and temperature within the feeding territories of termites probably influence the foraging intensity in the study sites, although no records of relative humidity and temperatures were taken below the soil surface or at the food - soil interface due to lack of suitable thermometers. In addition the process of leaching in rainy periods may help dissolve plant chemicals repellent to termites and subsequently enhance feeding activity. Although data shown in Table 6.4 do not give big differences in the monthly air temperatures or RH, they probably indicate that together with monthly rainfall do control the foraging activity of termites. Haverty, Lafage and Nutting (1974) working in Arizona on the subterranean termite, Heterotermes aureus. indicated

that temperature and rainfall were the primary controlling factors of foraging activity.

The effect of grazing by small stock in the paddock did not reveal much on the activity of Odontotermes. This was probably due to the short periods of feeding trials with small-stock, which could have incurred disturbances on termite feeding territories. Before grazing in September 1981, the standing crop of plant litter was estimated at 290 g per m² and after grazing, November 1981 the plant litter was estimated at 134 g per m² (Chapter Four). Using the consumption data in Chapter Five, Odontotermes would only have removed about 50 g per m² of the initial weight (290 g). Therefore this suggest that small stock removed significant quantities of fallen litter and apparently coming into competition with termites. However, weekly collections of Odontotermes soil indicated that their activity declined in the first week of the feeding trial with small stock, and recorded 0.12 g of soil per m² in May, 1982. As the feeding trials continued for 3 weeks, Odontotermes activity appeared to increase and in the last week in June 1982, 1.2 g

of soil per m² were recorded. Perhaps the termite activity would have become more conspicuous if grazing had been continued.

CHAPTER SEVEN

7. DENSITY ESTIMATE OF FORAGING TERMITES

7.1 MATERIALS AND METHODS

This study was carried out in the same area used for the sampling of grass and grass litter removed by Odontotermes using the two tin technique discussed in Chapter Five (Fig. 3.1). The densities of surface foraging termites were determined by quadrats. Relative density or intensity of foraging can be measured with baits, pits and quadrats (Bodot, 1967; Lee and Wood, 1971; Sands, 1972; Haverty et al. 1974). Soils cores have been used to estimate the numbers of termites in the upper 15 or 30 cm of soil (Sands, 1972). However, soil core - sampling poses problems because subterranean termites tend to be clumped, with their distribution best described by a negative binomial (Sands, 1972). So this method was not chosen for my study.

Haverty et al. (1976) developed two techniques to measure relative densities of surface foraging populations (not absolute densities). The first technique outlined in detail by Haverty et al. (1974),

employed toilet paper rolls as bait. In the second technique (Harvety and Nutting, 1975 a, b) all superficial and partially buried wood on the ground within a series of 50 m² circular quadrats was examined for termites. Similarly I developed a method whereby temporary 2 by 20 metre plots (quadrats) were examined for foraging termites.

Before an attempt is made to sample a foraging termite population, perhaps an important first step would involve a knowledge of their feeding time. A survey done in the IPAL study area (Bagine, 1980 unpubl. report) indicated that Odontotermes species foraged mainly during daylight hours. More observations carried out during this present study, revealed that Odontotermes were active between 0700 hours to 0930 hours and 1700 hours to 1830 hours. However, these foraging peak periods depended on the prevailing weather conditions at that particular place. Diurnal feeding activity was assessed by checking for termite activity at different hours. By assessing the frequency of encountering actively feeding termites in several habitats, hours of high activity could be gauged. Pomeroy, (1981) pointed out that Odontotermes sometimes continue foraging during the

day beneath earth covers and they attract diurnal predators.

The night observations carried out near Olturot Field Camp, showed very little activity by Odontotermes. However, Trinervitermes species were often encountered foraging on grass at night especially in cool conditions or after rain. Amitermes species were found in decaying wood both at night and day. It can be argued that because termites are poikilothermic creatures, the fluctuating environmental factors stimulate or retard their feeding periods. I concluded that in order to estimate the foraging population, time at which maximum number of foragers are out foraging would be an important factor for determining with some precision the density of foraging termites.

After pacing out random 2 x 20 m plots at times of high foraging activity, a search was made for surface foraging termites. It involved turning all surface and partially buried litter covered with termite soil. Once foraging termites were discovered within 40 m² plot, I immediately attempted to block their runways holes. Then quick visual

counts were made using a tally counter. After counting all the foragers, I placed them in specimen bottles for determining fresh and dry biomass.

There were no particular intervals set for sampling surface foraging termites, but this depended on other work on termites. Because of this, only four months were sampled, and between these four months, the sample size varied considerably. The foraging Odontotermes collected in specimen bottles were divided into major and minor workers, no soldiers were collected although an account of them was made. Fresh weights of each group were taken and specimen samples were taken for oven dry estimates. The temperature was kept constant at 60°C for 48 hours.

Signs of predation on foraging termites were noted and all predators seen attacking, carrying or eating termites were recorded.

7.2 RESULTS

7.2.1 TERMITE DENSITIES

The technique used for estimating surface foraging termites assumes that the maximum number of workers are out foraging during the sampling period. However, absolute counts are difficult to make especially with foraging termites which spend much of their time moving from their nests to the feeding sites and vice versa. It is also difficult to count moving and running termites without errors especially when the foraging group is large. Some foragers may disappear into foraging holes nearby while others take refuge beneath soil particles or buried litter.

The number of termites counted and the plant litter weight estimates for each month are shown in Table 7.1. A large food patch attracted more workers than small plant litter debris. Odontotermes boranicus was the most abundant surface grass-feeder and appeared to increase its feeding intensity in April and May. In the same months Amitermes lönnbergianus became common and was found foraging on woody litter.

Table 7.1 The estimated density of termites and the monthly standing crop of plant litter. Olturot.

Month	Density of <u>Odontotermes</u> per m ²		Density of <u>Amitermes</u> per m ²		Density of <u>Synacanthotermes</u> per m ²		Standing crop (g m ⁻²) (Plant litter)
	Workers	Soldiers	Workers	Soldiers	Workers	Soldiers	
November 1981 (10)*	1.59	0.02	0	0	0	0	181
February 1982 (4)	11.29	0.15	0.29	0.04	0	0	174
April 1982 (4)	17.76	0.14	0.43	0.04	0.10	0.01	127
May 1982 (2)	145.84	0.45	1.24	0.09	0	0	123
Highest density estimate	145.84	0.45	1.24	0.09	0.10	0.10	

* Figures in parentheses represent the number of plots which were sampled.

The Synacanthotermes species was only encountered in April, the wettest month during this study (Fig. 3.2). Since Odontotermes was the most important surface feeder, more emphasis was put on it, and specimens were taken for biomass estimate. Fresh and oven dry weights of Odontotermes workers are shown in Table 7.2. The mean biomass of Odontotermes workers per hectare was calculated using the oven dry weights of 1280 workers.

7.2.2 PREDATION

Many termite predators such as ants and spiders were found invading and carrying termites away as soon as the galleries or sheetings were disturbed. Additional field observations indicated that large numbers of foraging termites provided rich food sources for predators, that even some are largely dependent upon termites for food. Table 7.3 lists some of the predators of the foraging termites. There are probably more predators in the study area than those recorded. Aardwolf and Elephant shrew occur in the study area, an examination of their stomachs, showed that they contained foraging termites. The Aardwolf stomach was collected by Dr. C. Field from a dead Aardwolf found in the study per hectare was calculated.

Table 7.2 Fresh and oven dry weights of Odontotermes workers collected at Olturot.

CASTE	No. of Individ. weighed	Fresh weight(g)	Mean Fresh weight(mg)	Oven-dry weight(g)	Mean oven-dry weight(mg)
Major workers	600	2.700	4.500	0.430	0.717
Minor workers	780	1.600	2.353	0.325	0.478

0.590

Table 7.3: A list of predators of foraging termites recorded in the IPAL study area.

Ants of the genera	<u>Dorylus</u> spp
	<u>Pachycondyla</u> spp.
	<u>Megaponera</u> spp.
Spiders	
Birds	Yellow-necked spurfowl (<u>Francolinus leucoscepus</u>)
	Crested Francolin (<u>F. sephaena</u>)
	Yellow-billed Hornbill (<u>Tockus flavirostis</u>)
	Red-billed Hornbill (<u>T. erythrorhynchus</u>)
Mammals	Aardwolf (<u>Proteles cristatus</u>)
	Elephant shrew (<u>Elephantulus rufescens</u>)

area. The stomach contained mainly Trinervitermes spp. The Elephant shrew was trapped during a short survey study of small mammals at Balesa Kulal. The stomach contained some broken parts of foraging termites and termite species were not identified, but probably could have been Odontotermes which occurred in the same habitat.

7.3 DISCUSSION

Lee and Wood (1971) presented a summary of data from tropical Africa, South and Central America, and arid and semi-arid regions of Australia. Total termite numbers per m² for all species in each area, ranged from 12 in a desert grassland steppe and a rain forest in Panama to 4450 in a Trinidad rain forest. The foraging activity (and probably populations) of termites are presumably related to the amount of food available on the surface. The number of termites recruited for foraging activity would therefore depend on the amount of food available and the distance it is from the nest. Probably more food would be harvested from nearer sites requiring few foragers than from far sites.

Apart from the food resources, the other probable external factors which may inter-act to regulate the number of foragers at a particular place are the rainfall, temperature and soil moisture. Foraging also depends on internal activity of the colony (Lepage, 1981b). Although, there were no adequate data gathered to support this, the number of foragers increased during rainy periods (April and May) which coincided with the swarming of alates. The *Odontotermes* workers were accompanied by a relatively few soldiers during the feeding time. Thus the foraging groups of *O. boranicus* consisted mainly of workers and only 0.5% soldiers. Nutting et al. (1973) reported foraging groups of *Gnathamitermes perplexus* to contain mainly workers and only about 0.4% soldiers, a figure close to that of *O. boranicus*.

The density estimates (Table 7.1) indicated that *Odontotermes* had the highest number of workers feeding on the surface litter while *Synacanthotermes* had the lowest record. The reason for these differences could be that different species differ in their method, time and place of feeding.

Termites suffer most from opportunistic predation and this could reasonably cause fluctuations in foraging termite populations. It should be emphasised here that density estimates of termites and termite biomass per hectare are based on foraging groups. Therefore, the mean surface foraging biomass figure 125 g per hectare over dry - weight, represents only one caste (workers) out of the entire total nest colony biomass. The foraging groups present an instantaneous sample of only a fraction of the total foraging force (Bodine, 1973).

The field observations suggested that many foraging termites end up being eaten by predators. Many ants and spiders were often seen associated with foraging termites. Mainly large Dorylus species and spiders attacked foraging termites by opening a small part of their foraging galleries. Perhaps some of the Dorylus species specialise on foraging termites unlike game birds which are opportunistic feeders. Birds and other animals destroyed termite sheetings on the plant materials in search of foraging termites. Swank (1977) working near Selengei, in Kajiado District, discovered that Odontotermes and Hodotermes formed

a major part of the food of the Yellow-necked spurfowl, Francolinus leucoscepus and Crested Francolin, F. sephaena. Pomeroy, (1981) estimated a consumption by birds as 180,000 termites per hectare per year. While Lapage (1981) estimated that ants took 350,000 Odontotermes per hectare per year from a similar habitat north west of Selengei.

Although there were no data collected as regards the number of termites consumed by ants, spiders and birds in the IPAL study area, one can speculate that since food selection in arid areas is limited, a predator would probably tend to specialise on one or a few predictable preys than many unpredictable ones. Thus the predators may be consuming more termites than those quoted for Selengei due to lack of large choice in food resources. Surface-foraging termites, such as the harvester termites (Trinervitermes spp.) which feed in the open, or certain Macrotermitinae, e.g. Macrotermes spp. or Odontotermes spp. which feed in the open, suffer most from opportunistic predation whether this is by ants, birds or mammals.

CHAPTER EIGHT

8. GENERAL DISCUSSION

8.1 THE IMPORTANCE OF SOME ENVIRONMENTAL FACTORS TO THE FORAGING ACTIVITY OF TERMITES.

Bodot (1967) studied the seasonal foraging patterns of three African termites (Trinervitermes trinervius; Amitermes evuncifer and Cubitermes severus) in a tropical savannah, Ivory Coast, and concluded that foraging occurred at any time of the year when climatic conditions permitted, that rainfall increased foraging intensity and that foraging activity declined during the dry season. In an arid area of Northern Kenya the foraging activity of Odontotermes boranicus increased its activity after rainfall. Thus in December - January and May - June the soil brought on to the surface increased (Figures 6.1 and 6.2). Among the specific climatic factors which Bodot found to influence foraging were soil temperatures, relative humidity and rainfall.

Lepage (1981c) and Collins (1982) reported that the level of foraging varied considerably throughout the year, with main peak during the long dry season (June - October) and a minor peak in the short dry season (February - March) in semi-arid grassland in Kajiado Kenya. However, apart from external factors (e.g. rainfall, relative humidity) influencing foraging activity, termites themselves may modify their surroundings by building soil sheetings over the food source. Indeed this condition may create a suitable micro-environment and subsequently prolong the foraging period.

The termites of the genus Odontotermes were found to forage all the year round (Figs. 6.1 and 6.2) with a maximum foraging activity appearing after periods of heavy rainfall (long rains) preceded by high plant litter fall (Table 4.2). The Amitermes; Synacanthotermes and Trinervitermes increased their foraging activity after and during rainy periods.

Whereas temperatures affect the time which is spent foraging and to some extent foraging intensity (number of individuals at the surface), periodic

risers in soil moisture following rain also increase foraging intensity (LaFage et al. 1973). My field observation support the findings of LaFage et al. and indicate that foraging intensity increased in the morning and evening periods when environmental temperatures were between 25-30°C. Probably the combination of temperatures, rainfall and humidity allowed more feeding activity, although internal factors might have contributed to feeding time.

8.2 RECYCLING OF NUTRIENTS BY TERMITES

In a natural environment, termites function as detritivores, which are a group of decomposers. The plant material in whatever form it is consumed (wood, grass, dung etc.), once collected by foraging termites is largely utilized in the region of the central nest system housing the queen and young termites. The mound-building termites (Macrotermitinae) retard nutrient turnover by concentrating and retaining nutrients in the mound by using faeces as a food source, and as a structural material and by cannibalism (Lee and Wood 1971b; Matsumoto, 1976). Schaefer and Whitford (1981) concluded that termites played a key role in the nitrogen cycle in the Chihuahuan

desert ecosystem providing rapid turnover and redistribution through termite predation. Much of the Macrotermitinae nutrients in the IPAL study area is returned to the ecosystem through predation and accession of the bodies of alates and other termite castes.

On the other hand, in arid ecosystems where temperatures are high ($>35^{\circ}\text{C}$) and rainfall very low, erratic and unreliable, the nutrients locked up in the termite soil structures i.e. galleries, runways, sheetings and mounds, are not immediately redistributed to the surrounding area. However due to the nature of arid region, vegetation cover is thinly spread, and during rainy periods, nutrients from these termite structures are eroded. Therefore soil erosion in arid regions can be viewed as deleterious rather than beneficial in terms of plant nutrient re-distribution.

8.3 THE EFFECT OF TERMITES ON SOIL

Many termites construct extensive and often massive nest systems in response to their need for food, environment control and social homeostasis. As a result they have a marked impact on redistribution

of soil particles, on physical and chemical properties of soils. The modification of the soil profile as a result of termite activity depends on the fact that termites remove soil from various depths and bring it to the surface in the form of runways, sheetings or mounds from which it is redistributed by water, wind and animals. Termites also excavate cavities for nests and have underground passages which have their effects on soil aeration and percolation.

Information on the amount of soil in runways, surface sheetings and in-filling of vegetation is scarce except for certain unpublished information (Wood and Sands, 1978). Lepage (1974b) estimated that the soil surface runways and sheetings of Macrotermes subhyalinus in Sahel Savannah in Senegal amounted to 675-950 kg. per hectare per year. In northern Kenya in an arid open bushland, I estimated 13000 kg of soil per hectare per year on surface runways and sheetings of Odontotermes boranicus and Odontotermes latericius covering the grasses, woody materials and dung pats. Field observation indicated that these fragile structures were rapidly eroded by wind and rain and were just as rapidly re-constructed on the same food material or on

different material. Intensive foraging often left some areas almost denuded of litter.

The principal processes by which termite activity could contribute to accelerated soil erosion are considered by Lee and Wood (1971b) to be the removal of vegetation and litter with resultant exposure of the surface soil to erosive forces, and the deposition of soil above ground during foraging in the form of runways and sheetings. The only measurements of these process have been made by Bodine and Ueckert (1975) and Spear, Ueckert and Whigham (1975) in a semi-arid short-grass prairie in Texas. They demonstrated that termites reduced the protective cover of living and dead vegetation and contributed to increased erosion. Similarly, Arshad (1980) working in Kajiado, Kenya, showed that vegetation reduced run-off and soil loss in the semi-arid grassland ecosystem. However, the effect of termites on the removal of vegetation and therefore contributing to soil erosion would need to be balanced against their positive effect on infiltration in pastoral management practices, and it is likely that the same principles apply in arid ecosystems.

In arid ecosystems where much of the vegetation cover is removed by grazing mammals and termites, termite soil structures become vulnerable to running-water during rain periods. This leads to soil loss, and poor plant growth accompanied by soil nutrient loss.

8.4 THE EFFECT OF TERMITES ON VEGETATION

The impact of invertebrates such as termites and grasshoppers on the process of desertification has received scant attention, but Johnson and Wood (1980) indicated that the removal of herbaceous vegetation by termites is unlikely to have a major impact unless preceded by factors such overgrazing and droughts, which reduces the availability of food for all herbivores to abnormally low levels.

The activity of termites on vegetation in the grazed paddock reported in this work indicated that termite activity continued despite the litter production being curtailed by grazing livestock. This suggested that termites were adaptable, and if litter production fell below the levels required by termites, they climbed on standing grasses, shrubs

and herbs, and foraged on drying parts of these plants. The tree barks and fixed fence posts were also consumed. This is because termites unlike other primary consumers are not limited by their accessibility to the aerial parts of the plants.

The termites of the subfamily Macrotermitinae cultivate fungus gardens, and the digestive properties of the fungus combs assists in the breakdown of intractable organic compounds such as polyphenols and cellulose (Abu-khatwa, 1978; Martin and Martin, 1978). The fungi permit the termite to process larger amounts of food than non-fungus growing termites. I estimated that fungus-growing termites removed about 56% of grass litter and 15% of woody (< 4 cm in diameter) litter from a known stock of naturally occurring litter annually. Termites are responsible for removing a high proportion of primary production probably due to lack of competitors in the exploitation of food resources. Because arid regions are water-limited ecosystems, the IPAL Lowland plains, the Hedad, Chalbi etc. are avoided by water-dependent herbivores during dry seasons. In turn, these areas are left for the termites to exploit.

Usually, whenever termites are abundant, they become one of the more important groups of organisms in an ecosystem. Wood and Sands (1978) pointed out that the importance of any organism in its ecosystem depends partly on its ability to use the energy available in the ecosystem for its own production. Finally, the removal of surface litter cover by termites in arid ecosystems may give an insight into the depletion of soil moisture inputs and probably plant nutrients resulting in the degradation of the environment.

Several workers have estimated consumption of wood by termites and have related this to annual rainfall. Wood (1978) reviewed the field estimates of food consumption by termites. The studies of dead wood consumption made in various places in the world used a variety of methods. In two investigations out of six previous studies, only one of the several wood eating species in a habitat was studied (Lee and Wood, 1971; Harverty and Nutting, 1975a). In both these studies laboratory estimates of consumption were used to convert field estimates of population to estimates of field consumption.

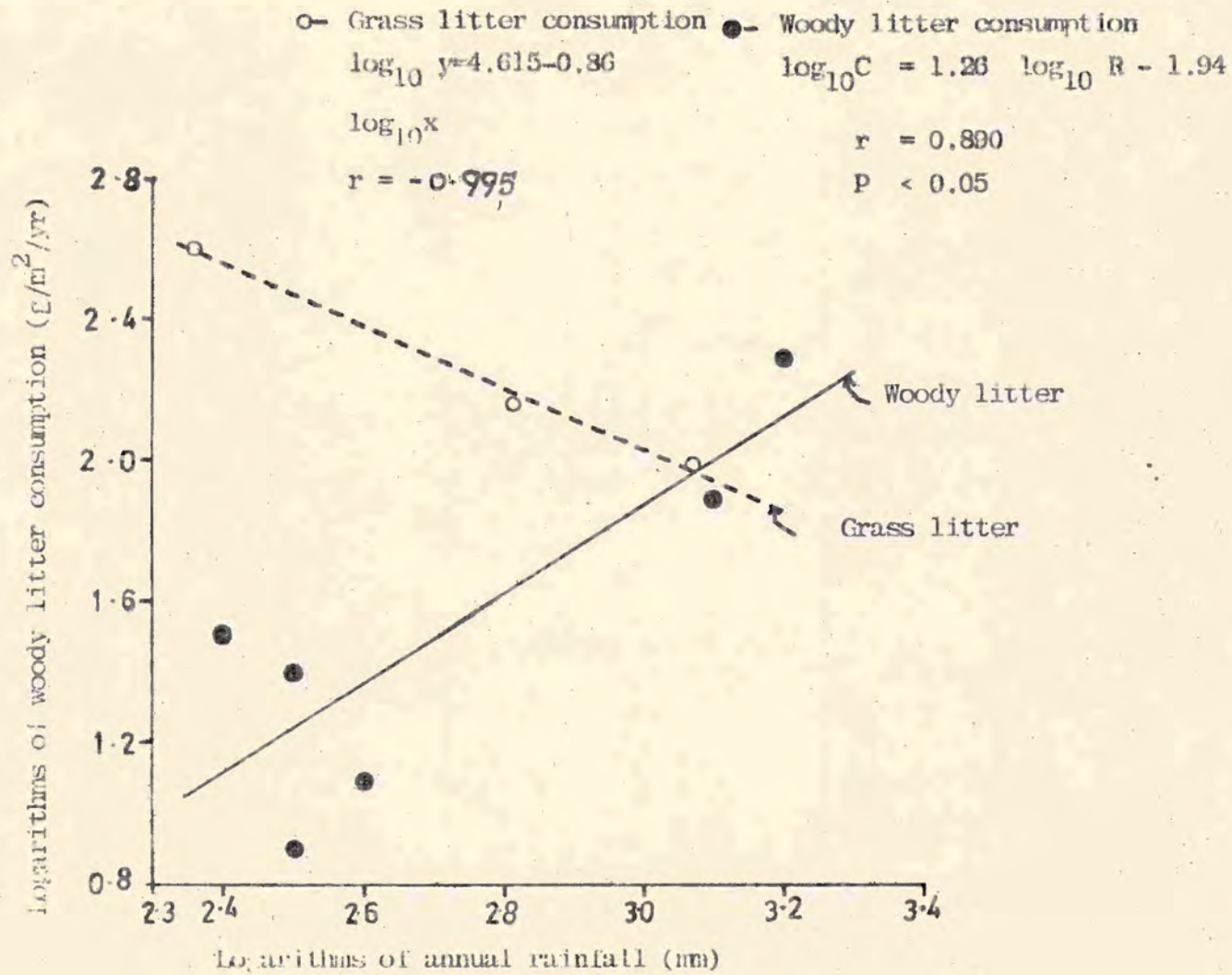
Williams (1973) and Usher (1975) employed identical methods, the graveyard method with wooden blocks set in the ground. Williams estimated a consumption of wood by termites at 540 to 1508 $\text{g m}^{-2} \text{yr}^{-1}$ whereas Usher's estimate was 210 $\text{g m}^{-2} \text{yr}^{-1}$. Collins (1977) made direct measurements of consumption of naturally occurring dead wood. He estimated consumption of wood litter by termites as 83.5 $\text{g m}^{-2} \text{yr}^{-1}$. Buxton (1979), working in Tsavo, Kenya used thirty discs of wood laid out at 5 m intervals along a transect. He found wood litter consumption to be 28.1 $\text{g m}^{-2} \text{yr}^{-1}$. These figures are compared with the present study (Table 8.1). A regression of consumption (C, $\text{g m}^{-2} \text{yr}^{-1}$) against rainfall (R, mm yr^{-1}) gave the equation $\log_{10} C = 1.26 \log_{10} R - 1.94$. The value of the correlation coefficient was found to be 0.890 ($n = 6$) (Figure 8.1). The correlation was found to be significant.

Very few field estimates of quantities of grass litter consumed by surface feedings termites are in the literature (e.g. Lepage, 1974b, 1981; Ohiagu and Wood, 1979; Collins, 1982). Ohiagu and Wood measured grass litter consumption by termites by placing 10 samples of grass each weighing 5 g

Table 8.1: Independent estimates of wood litter consumption by termites in various places of the world.

Author and date	Locality	Rainfall mm yr ⁻¹	Consumption g m ⁻² yr ⁻¹
Lee and Wood (1971b)	South Australia	300-400	11.6
Hawerty and Nutting (1975b)	Arizona	330	7.9
Usher (1975)	Ghana	1499	210.0
Collins (1977b)	Nigeria	1175	83.5
Buxton (1979)	Tsavo East Kenya	453	28.1
Present study	Marsabit Northern Kenya	232	32.8

Fig. 8.1: The relationship between the consumption of woody litter and annual rainfall based on the published data from different parts of the world.



on the ground in wire cages. Both Lepage and Collins utilized the litter bags technique to correlate food offtake with the number of holes opened during a certain time. Lepage (1981) showed that yearly food offtake by Macrotermes michaelseni ranged between 1250 and 1600 kg per ha in 1977 receiving 647 rainfall. The consumption estimates of grass litter are summarised in Table 8.2 together with annual rainfall at each site.

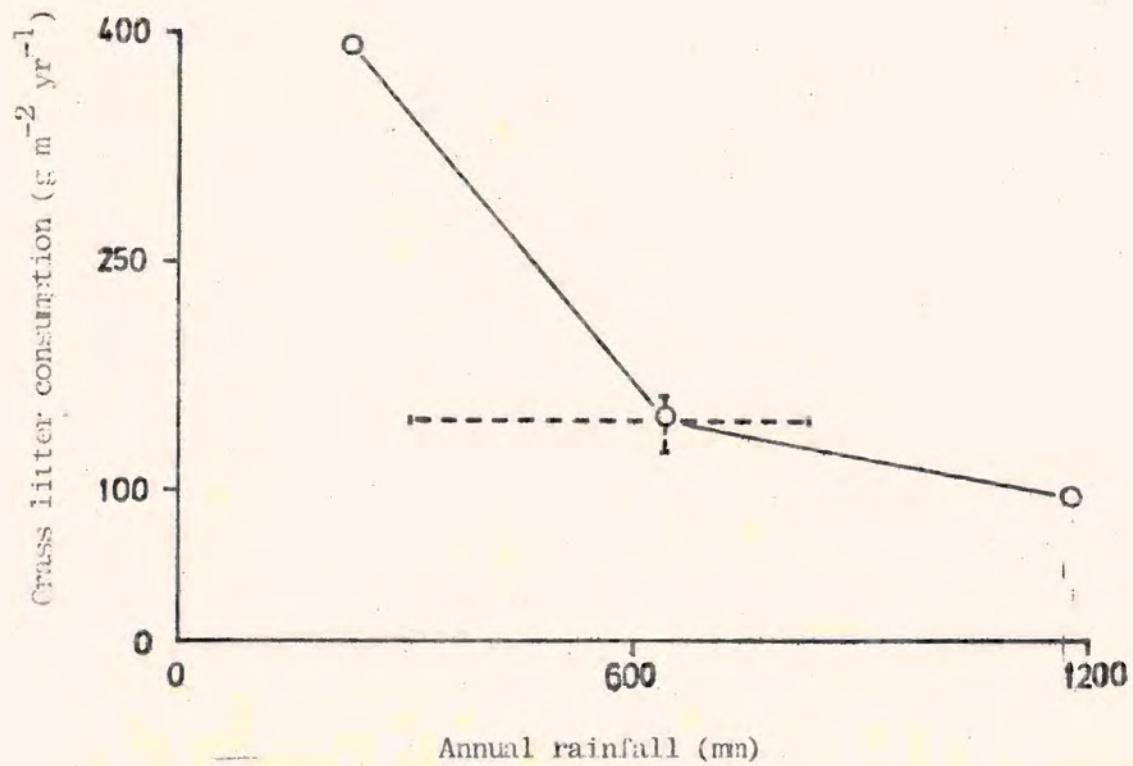
Further data will probably show a negative relationship between annual rainfall and grass litter consumption by termites. Unlike woody litter it seems that the importance of termites as consumers of surface grass litter declines as rainfall increases (Figs. 8.1 and 8.2). Probably grasses are more common and do not decay faster in low rainfall areas than in high rainfall areas. Therefore termites have longer periods of foraging in dry areas than in wetter areas. Lepage's (1981) data for consumption and annual rainfall are given in the form of ranges, therefore the means of these ranges were used in Fig. 8.2 together with other raw data shown in Table 8.2.

Table 8.2: Independent estimates of grass and grass litter consumption by termites in various places in Africa.

Author and date	Locality	Rainfall mm yr ⁻¹	Consumption g m ⁻² yr ⁻¹
Oniagu and Wood (1979)	Nigeria	1175	98
Lepage (1981)	Kajiado, Kenya	306-839 (647)	125-160 (143)*
Present study	Marsabit, Kenya	232	394

* Figures in the parentheses were used in the calculation of regression in Fig. 8.1.

Fig. 8.2: Grass litter consumption drawn against annual rainfall for three places in Africa.



8.5 TERMITES AND THE ECOSYSTEM

The present study has demonstrated that termites play a key role in the arid ecosystem through the removal of available plant materials, soil movement and to some extent the recycling of nutrients via predation. The plant material in whatever form is removed by termites, it is part of net primary production either accumulated over the previous years or produced during last rainy season. Thus vegetation production follows the distribution of rainfall.

Herlocker and Dolan, (1981) estimated primary production at Balesa Kulal paddocks by clipping plants within 0.5 m^2 quadrats at the peak of the growing season in order to obtain net standing crops. They measured primary production after $133 \text{ mm}^{\text{of}}$ rainfall in the month of April 1977 (Table 8.3) They estimated a mean of 658.4 kg per hectare. Assuming this production represented only one rainy season, then one year's production would have been represented by two rainy seasons. The primary production available during this current study on termites is presumably accounted for by the previous years' rainfall of 232 mm. Using 232 mm rainfall

Table 8.3: Primary production of the herb and dwarf shrub layers at the Balesa Kulal experimental site measured after 133mm of rainfall in the month of April 1977. Estimates in kg/ha dry matter.

Source: IPAL data

Paddock and livestock species and stocking rates	All dwarf shrubs	All herb species	Total production
Control: Ungrazed	54.5	309	363
S.W. sheep and goat heavy	189.2	296	458
N.W. sheep and goat medium	35.5	360	395
S.E. sheep and goat light	54.7	1229*	1284
N.W. camel heavy	23.6	761	785
S.E. camel medium	18.3	390	471
N.E. camel light	52.4	555	853
		Mean	658.4

* high productivity probably due to ground water in drainage line.

together with the estimates of Herlocker et al., I estimated net primary production as 114.9 g per m^2 per year at Olturot.

So far, there have been very little primary production estimates made at Olturot, although it receives similar amounts of rainfall to Balesa Kulal (Fig. 3.2). However Olturot is situated in a more densely wooded vegetation than Balesa Kulal except along the drainage lines. Since the woodland vegetation covers a small fraction of the entire IPAL study area, it cannot be taken as a typical vegetation type of the whole study area. The net primary production of woodland vegetation may be much higher than for open grassland. According to Dr. H.F. Lamprey (pers. comm.) primary production of Balesa Kulal and perhaps Olturot may range from 80 to 200 g per m^2 per yr.

In the present study carried out at Olturot, I estimated the primary production of grasses, herbs and shrubs by extrapolating the monthly standing crop data from transect and quadrat methods given in detail in Chapter Four. The experiment was conducted in a shrub invaded woodland near Olturot well, and

500 m S.E. of the bait sampling experiments (Fig. 3.1). I assumed that the increments of standing vegetation shown in Fig. 8.3 are due to new production attributable to rainfall. By deducting the lowest level from the highest peak level, and adding them together (a+b+c), an approximation of annual net primary production of $488 \text{ g m}^{-2} \text{ yr}^{-1}$ was obtained. Termites were found to consume about $427 \text{ g m}^{-2} \text{ yr}^{-1}$ i.e. about 87% of net primary production.

Ian K. Deshmukh (pers. comm.) estimated net primary production of grasses and herbs in an African Savannah by collecting published data on rainfall and primary production. He derived the least squares regression line, $\text{NPP} = 8.817 \text{ AP} - 366$ where $\text{NPP} =$ Net primary production ($\text{kg ha}^{-1} \text{ yr}^{-1}$) and $\text{AP} =$ rainfall (mm). Applying this equation to 232 mm, rainfall, the net primary production was estimated to be $168 \text{ g m}^{-2} \text{ yr}^{-1}$. Rosenzweig (1968) showed that net primary productivity of terrestrial communities could be predicted from climatological data. His productivity prediction equation, including 5% confidence intervals for the slope and intercept is $\log_{10} \text{NAAP} = \log_{10} \text{AE} (1.66 \pm 0.27) - (1.66 \pm 0.07)$.

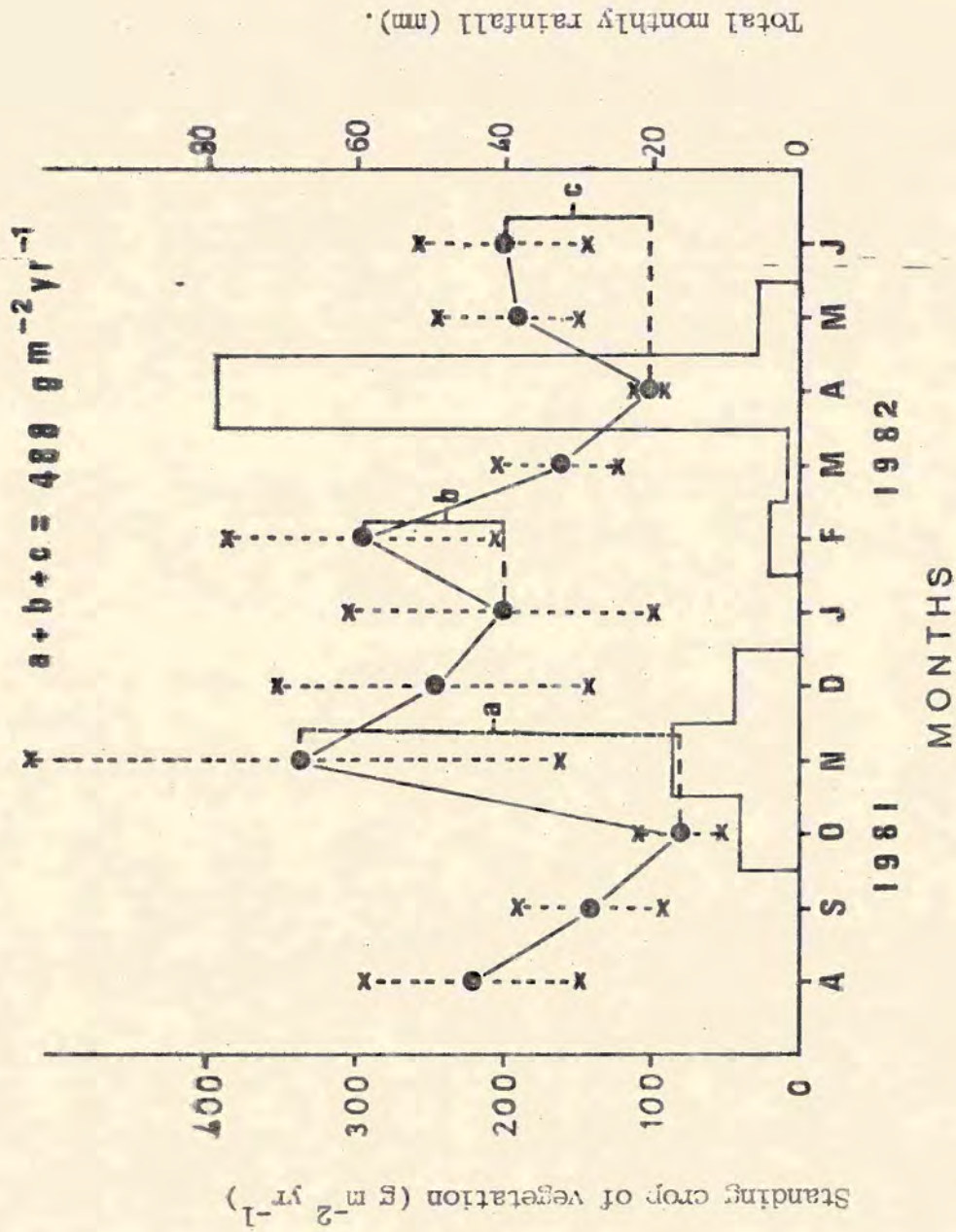


Fig. 3.3: Estimation of net primary production and standard errors, using monthly changes in standing crop of standing vegetation. Bar-graphs represent monthly rainfall (mm) at Olturot.

Where AE = Actual evapotranspiration which is approximately equal to rainfall in dry areas, and NAAP = Net primary production above ground ($\text{g m}^{-2} \text{yr}^{-1}$), Coe et al (1976) and Phillipson (1975) have suggested that this relationship is applicable to African Savannas with less than 700 mm annual rainfall. Using the same amount of rainfall 232 mm, Rosenzweig's equation gave net primary production above ground for Olturot as $185 \text{ g m}^{-2} \text{yr}^{-1}$, with an upper limit of $685 \text{ g m}^{-2} \text{yr}^{-1}$ and a lower limit of $50 \text{ g m}^{-2} \text{yr}^{-1}$.

LeHou rou, (1980) estimated productivity of browse (mainly woody plants) for broad ecological zones as $1 \text{ kg dry matter ha}^{-1} \text{yr}^{-1}$ per mm of rainfall. Therefore 232 mm rainfall would give $232 \text{ kg ha}^{-1} \text{yr}^{-1}$ (i.e. $23 \text{ g m}^{-2} \text{yr}^{-1}$). All predicted and estimated net primary production of Olturot are summarised in Table 8.4.

Net primary production vary from time to time and from one place to another. Methods used vary in their application and predicting net primary production from evapotranspiration or rainfall have some disadvantages

Table 8.4 Net primary production estimates calculated from various productivity prediction equations, using 232 mm rainfall in 1981 at Olturot.

Authors	Net primary production estimates ($\text{g m}^{-2} \text{yr}^{-1}$)	Annual Rainfall (mm) 1981
Deshmukh (pers. comm.)	168 (herbs)*	232
IPAL DATA (Herlocker & Dolan, 1981)	115 (herbs + shrubs)	"
Rosenzweig (1968)	184 (Total above ground)	"
Le Hove'rou (1980)	23 (browse)	"
Present study	488 (grasses + herbs + shrubs)	"

* Category of vegetation in parentheses represent the primary production estimated.

that other external factors such as soil nutrients affect the growth of vegetation. The results shown in Table 8.4 vary a lot and my estimate is considerably higher than others. This may have been due to the method used and the location of the site. The study site was in a dense wooded bush associated with a very common salt shrub, Salsola dendroides, which was often sampled during this period. For these reasons, there is a possibility of overestimation of net primary production. However, due to high rainfall in March to May 1982, there was high primary production in the study site. On the other hand, Herlocker's et al. could have underestimated primary production because the samples were only taken after the April 1977 rains.

In arid conditions ephemeral plants disperse their fruits and seeds, and die before the end of rains. Also perennials including grasses drop leaves during growing season. Therefore it can be argued that sampling such plants after rain excludes part of their production. In addition results of Herlocker et al includes only three common shrubs: Indigofera spinosa, Dousperma and Sericocomopsis at Balesa Kulal paddocks. Unlike my results which

included all shrubs and herbs at Olturot site. Another possible error which could have resulted in underestimation of primary production is the level at which plants are harvested. In conclusion, my figure of 488 is possible because of above-average rainfall, and the fact that the methods almost certainly underestimate NPP.

Whatever the actual percent taken by termites (presumably not 87) it is clearly very high, more than any other group, for example, 7% consumed by camels, sheep and goats (Field, 1979) and 2.5% consumed by acridids (Okelo, 1981). Although, where the termite study was located is not typical of the whole IPAL study area, personal observations carried out elsewhere within the study area, showed that termites are an important element of the ecosystem removing a considerable amount of primary production mainly plant litter.

In man-modified habitats termites have long been of more than academic interest to man because of their attacks directly on his crops as well as on his structures and possessions which are commonly made of plant materials. Conversely, when it comes to natural ecosystems termites become more of ecological concern to scientists than a human-pest.

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A P P E N D I C E S

Appendix 1. Physical and chemical analysis of soil profile and Odontotermes soil at Olturot 42 - 17.

Depth (cm)	0 - 20	20 - 32	32 - 55	55 - 85	85 - 120	<u>Odontotermes</u>	Soil fertility
						soil sheetings	me/100g
Sand %	43	60	42	40	34	66	
Silt %	40	22	24	30	16	14	
Clay %	12	18	34	30	48	20	
Texture class	loam	sand loam	clay loam	clay	clay	sand loam/ sand clay loam	
pH - H ₂ O (1: 2.5)	8.6	8.6	8.2	8.5	8.0	7.9	
pH, Kcl (1:2.5)	7.0	7.1	7.0	7.1	7.2	7.0	
CaCO ₃ %	12.48	12.44	10.90	9.45	35.0	-	
C.E.C. (me/100g)	29.6	21.8	34.6	36.0	29.4	25.1	
Exchangeable cations:							
Ca (me/100g)	56.0	45.0	42.0	37.0	37.0	58.7	37.0
Mg "	8.8	6.6	9.6	6.4	4.0	7.1	7.6

Appendix 1 continued

K (^{me} /100g)	2.6	2.0	1.9	0.4	0.5	3.9	0.57
Na "	1.9	1.3	4.9	6.7	4.0	1.5	1.63
Base saturation	100%	100%	100%	100%	100%	100%	
E.S.P.		5	14	19	14	-	
Saturation extract:							
Ece (^{mmbo} /cm)	-	-	7.0	25.5	26.0	-	
C%	-	-	-	-	-	0.52	
Mn							trace
P ppm							23

Appendix 2. Physical and chemical analysis of soil profile and
Odontotermes soil at Balesa Kulal 42 - 18.

Depth (cm)	0 - 15	15 - 45	50 - 100	<u>Odontotermes</u> soil sheetings	Soil fertility
Sand %	78	88	96	72	
Silt %	12	8	2	16	
Clay %	10	4	2	12	
Textures class	Sandy loam	Sand	Sand	sand, loam	
pH - KCl	7.5	7.8	7.3	7.9	
pH - KCl	6.8	7.2	6.2	7.2	
C.E.C.	9.7	5.3	2.1	11.7	
Exchangeable cations					
Ca ^(me) /100g)	11.6	9.4	3.6	11.4	9.8
Mg "	2.3	1.9	0.8	4.0	4.8
K "	0.70	0.30	0.13	0.42	0.62
Na "	0.18	0.33	0.10	0.80	0.26
Mn					0.66
P. ppm					16
Base Saturation	100%	100%	100%	100%	
ESP				7	
% C.	0.07			0.30	0.05
% N					0.20

Appendix 3: Scientific names of the termite
species referred to and the authorities
for species.

<u>Amitermes</u>	<u>evuncifer</u>	(Silvestri)
<u>Amitermes</u>	<u>lönningbergianus</u>	(Sjöstedt)
<u>Cubitermes</u>	<u>severus</u>	(Silvestri)
<u>Gnathamitermes</u>	<u>perplexus</u>	(Banks)
<u>Gnathamitermes</u>	<u>tubiformans</u>	(Buckley)
<u>Heterotermes</u>	<u>aureus</u>	(Snyder)
<u>Macrotermes</u>	<u>bellicosus</u>	(Smeathman)
<u>Macrotermes</u>	<u>michaelseni</u>	(Sjöstedt)
<u>Macrotermes</u>	<u>natalensis</u>	(Haviland)
<u>Macrotermes</u>	<u>subhyalinus</u>	(Rambur)
<u>Odontotermes</u>	<u>boranicus</u>	(Chidin)
<u>Odontotermes</u>	<u>latericius</u>	(Haviland)
<u>Odontotermes</u>	<u>medriocris</u>	(Sjöstedt)
<u>Odontotermes</u>	<u>monodon</u>	(Gerst)
<u>Trinervitermes</u>	<u>geminatus</u>	(Wasmann)
<u>Trinervitermes</u>	<u>trinervius</u>	(Rambur)