ABUNDANCE AND DISTRIBUTION OF *MICROTERMES* (ISOPTERA; TERMITIDAE; MACROTERMITINAE) IN CULTIVATED AND UNCULTIVATED AREAS AT MOKWA IN THE SOUTHERN GUINEA SAVANNA VEGETATION ZONE OF NIGERIA

by

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Corrigenda

Chapter Six: Foraging activity of *Microtermes* on surface-laid baits.
Pages 140 and 147 referring to analysis and interpretation of data.

ABSTRACT

Population dynamics of *Microtermes* (Isoptera; Macrotermitinae) are investigated in the Southern Guinea savanna vegetation zone of Nigeria. Study sites were primary woodland, long-term maize and a randomised block experiment established from secondary woodland with woodland, pasture, sweet potato, groundnuts, yam and maize. The species assemblage was comprised of *Microtermes aluco*, *Microtermes n.sp. C.*, *Microtermes grassei*, *Microtermes lepidus*, *Microtermes subhyalinus*.

Microtermes abundance and distribution (n/m^2) to a soil depth of 1 metre are examined in Chapter Four. Community structure differed with vegetation cover. Abundance was generally higher in the wet compared to the dry season and abundance was greatest in long-term maize and higher in newly cleared and cultivated sites than in woodland. *M. subhyalinus* was the most abundant species in all vegetation types except long-term cultivated maize where *M. lepidus* was the most abundant species. Changes in crop alter species abundance and *Microtermes* community structure.

Microtermes fungus comb abundance (n/m^2), individual dry weight (g) and total dry weight (g/m^2) to a soil depth of 1 metre in primary and secondary woodland and short- and long-term maize are examined in Chapter Five. Vegetation cover had an influence on seasonal changes in the abundance, individual and total dry weights of fungus combs. *M. subhyalinus* fungus combs showed the greatest seasonal changes, in secondary woodland and short-term maize.

Microtermes foraging activity on softwood baits with season, species and vegetation is examined in Chapter Six. Seasonal differences in foraging activity were recorded but differences over time were more significant. Foraging activity differed with vegetation and species. Percentage of baits attacked by species as a proportion of the total number of baits attacked by all species was the best indicator of foraging activity. Non-random foraging was identified for *Microtermes* with positive associations among *M. subhyalinus*, *M. aluco* and *M. lepidus*.

Microtermes foraging activity on baits is compared with soil abundance in Chapter Seven using diversity indices and simple linear regression analysis. Foraging activity can give a more accurate indication of species richness than soil sampling. Foraging activity can be correlated positively with soil abundance, most significantly with wet season assessments.

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CHAPTER ONE

GENERAL INTRODUCTION

Termites are one of the most important groups of soil organisms in the tropics and sub-tropics. They have an important role in the maintenance of soil fertility (Lee and Wood, 1971; Lobry de Bruyn and Conacher, 1990) while, on the other hand, their pest status is well documented (Cowie and Wood, 1989; Harris, 1969). Termites are eusocial insects (Order: Isoptera) with polymorphic, highly organised colonies developed around a nest system and with division of labour among different castes. Nests vary from single nests concentrated in one site to diffuse networks of subterranean galleries and chambers (Krishna and Weesner, 1969). Noirot (1970) described five main nest sites between which there are also intermediates (Figure 1.1):

1. nests within wood
2. subterranean nests
3. epigeal nests
4. arboreal nests
5. inquilinous nests

Polymorphism is demonstrated by the production of three main castes (reproductives, workers and soldiers) which exhibit both morphological and functional differences (Noirot, 1969; Watson, Okot-Kotber and Noirot, 1985, Lys and Leuthold, 1991). The main differences amongst these castes are given in Figure 1.2.

1.1 Termite Classification

Termite classification is founded on the work of Hagen (1858). Seven families and fourteen sub-families are currently recognised (Figure 1.3) which comprise, to date, of more than 2,500 species within 268 genera (Emerson, 1955; Krishna, 1970; Snyder, 1949; Pearce and Waite, 1994). The first six families are collectively known as the Lower termites. The seventh family is the Termitidae, also known as the Higher termites, and presently contains more than 80% of known genera and 74% of described species. This family is the most advanced and diverse exhibiting a wide range of social specializations (Harris, 1971; Krishna, 1970).

1.2 Geographical distribution and abundance

Termites are distributed widely between the 45^{o} north and south latitudinals, which encompasses almost two thirds of the Earth's total land surface; distribution is limited only by extreme aridity, lack of vegetation and altitude; termites are rarely found above 3000 m (Kemp, 1955; Kayani, Sheikh and Ahmad, 1979; Johnson and Wood, 1980; Wood, 1988). The geographical distribution of individual families and sub-families is shown in Figure 1.3.

Figure 1.1 : An illustration to show the five main nest sites of termites:

Nests within wood; within fallen and standing dead wood and dead wood on trees.

Subterranean nests; concentrated or diffuse in the soil.

Epigeal nests; constructed above ground level from soil or carton.

Arboreal nests; on tree trunks and branches

Inquilinous nests; within the nest of another species.

Figure 1.2 The caste system in Isoptera and the main differences in morphology and behaviour.

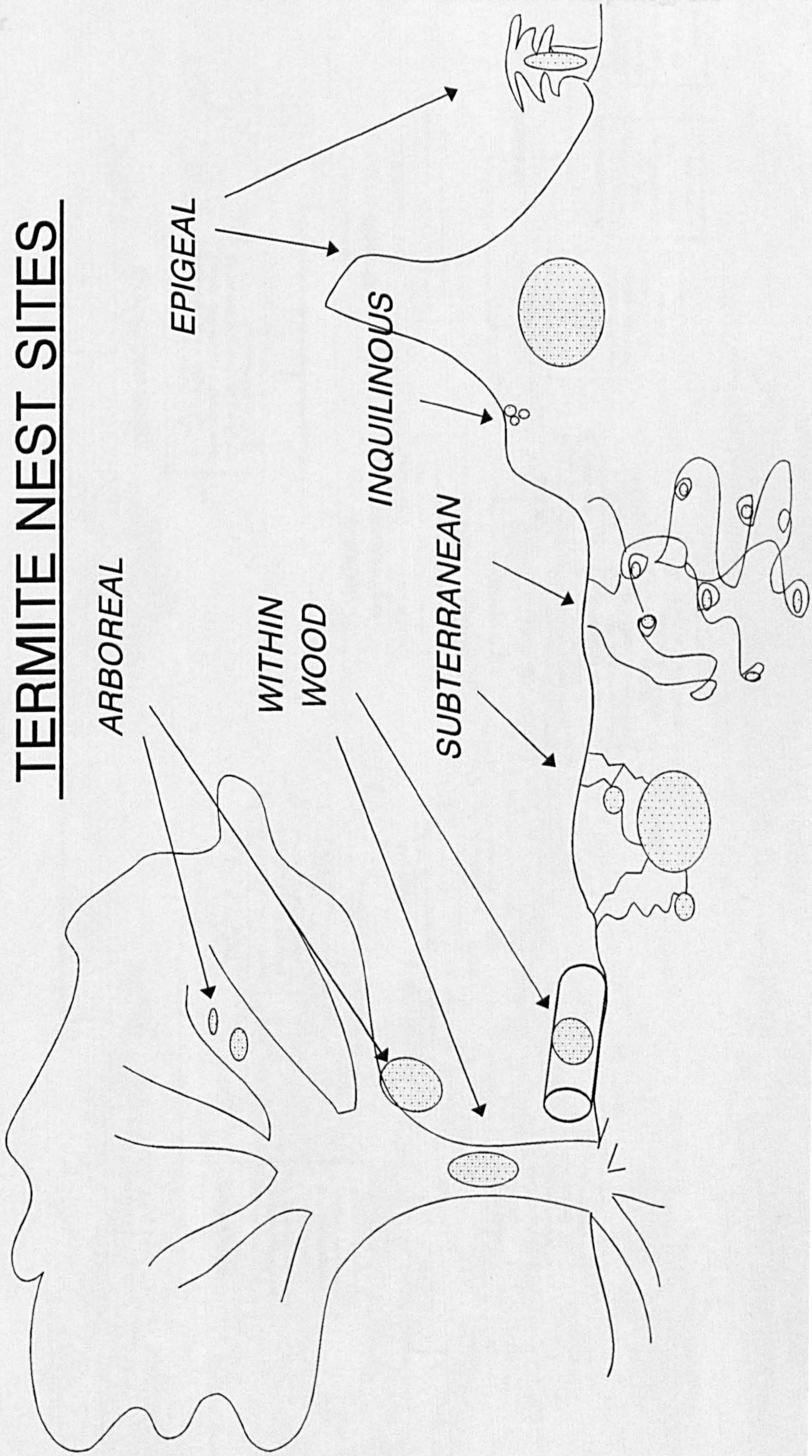


Figure 1.2 : The caste system in Isoptera and the main differences in morphology and behaviour.

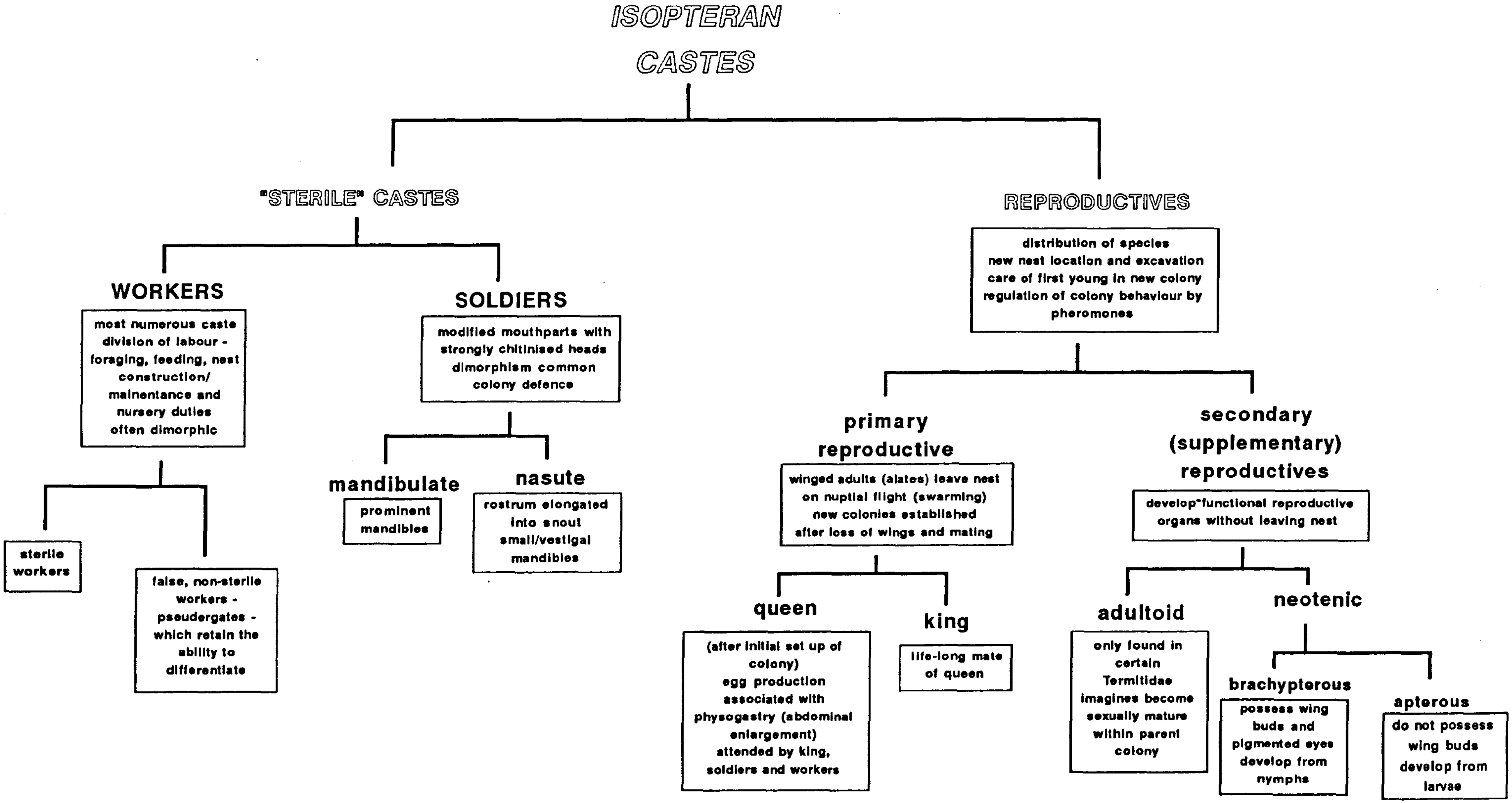

ISOPTERAN CASTES
"STERILE" CASTES
REPRODUCTIVES
distribution of species
new nest location and excavation
care of first young in new colony
regulation of colony behaviour by pheromones
WORKERS
most numerous caste
division of labour - foraging, feeding, nest construction/ mainentance and nursery duties
often dimorphic
SOLDIERS
modified mouthparts with strongly chitinised heads
dimorphism common
colony defence
sterile workers
false, non-sterile workers - pseudergates - which retain the ability to differentiate
mandibulate
prominent mandibles
nasute
rostrum elongated into snout
small/vestigal mandibles
primary reproductive
winged adults (alates) leave nest on nuptial flight (swarming)
new colonies established after loss of wings and mating
secondary (supplementary) reproductives
develop functional reproductive organs without leaving nest
queen
(after initial set up of colony)
egg production associated with physogastry (abdominal enlargement)
attended by king, soldiers and workers
king
life-long mate of queen
adultoid
only found in certain Termitidae
imagines become sexually mature within parent colony
neotenic
brachypterous
possess wing buds and pigmented eyes
develop from nymphs
apterous
do not possess wing buds
develop from larvae

Figure 1.3 : The classification and geographical distribution of termites according to family and sub-family.

FAMILY	SUB-FAMILY	GEOGRAPHICAL REGION
LOWER TERMITES		
Mastotermitidae		AUSTRALIAN
Kalotermitidae		ALL REGIONS
Termopsidae		ALL REGIONS, except PALEARCTIC & MALAGASY
	Termopsinae	INDOMALAYAN & NEARCTIC
	Porotermitinae	AFROTROPICAL, AUSTRALIAN & NEARCTIC
	Stolotermitinae	AFROTROPICAL & AUSTRALIAN
Hodotermitidae		PALEARTIC, AFROTROPICAL & INDOMALAYAN
Rhinotermitidae		ALL REGIONS
	Coptotermitinae	ALL REGIONS
	Heterotermitinae	ALL REGIONS, except MALAGASY & PAPUAN
	Psammotermitinae	AFROTROPICAL, MALAGASY, INDOMALAYAN, NEOTROPICAL & PALEARCTIC
	Termitogetinae	INDOMALAYAN
	Stylotermitinae	INDOMALAYAN
	Rhinotermitinae	MALAGASY, NEOTROPICAL & PALEARCTIC
	Prorhinotermitinae	MALAGASY, INDOMALAYAN, NEOTROPICAL, NEARCTIC & PAPUAN
Serritermitidae		NEOTROPICAL
HIGHER TERMITES		
Termitidae		ALL REGIONS
	Macrotermitinae	MALAGASY, INDOMALAYAN & AFROTROPICAL
	Apicotermitinae	NEARCTIC, NEOTROPICAL, INDOMALAYAN, AUSTRALIAN & AFROTROPICAL
	Termitinae	ALL REGIONS
	Nasutitermitinae	ALL REGIONS, except NEARCTIC

The greatest species diversity and abundance is found in tropical and subtropical regions with tropical forests maintaining the greatest species diversity (Emerson, 1955; Harris, 1969; Lee and Wood, 1971; Wood and Johnson, 1986).

The modification of the environment by human activities for agricultural land use may also alter the overall species diversity and abundance often producing an increase in the abundance of certain, often potential pest species (Dangerfield, 1990; Collins, 1980; Kooyman and Onck, 1987; Lepage, 1980; Roy-Nöel, 1978; Sands, 1965; Wood, Johnson and Ohiagu, 1977).

1.3 Biology and Nutrition

Termites are primary consumers and decomposers with cellulosic matter of several, not mutually exclusive, types as their main food source (Collins, 1981; Noirot and Noirot-Timothée, 1969; Whitford, Freckman, Parker, Schaefer, Santos and Steinberger, 1983; Wood, 1976 and 1978; Wood and Sands, 1977). Food is collected by foraging workers and distributed within the colony, as required (Lee and Wood, 1971). The workers feed the various castes by trophallaxis, either from stomodeal or proctodeal feeding or saliva. Food digestion is completed with the aid of symbionts.

Lower termites have a relatively uniform intestinal structure but possess symbiotic gut protozoa and bacteria. These, largely xylophagous, termites have a mutualism with protozoan flagellates which anaerobically breakdown cellulytic material in the hindgut to produce organic acids which can then be absorbed by the host (Honigberg, 1970; Breznak, 1983; Breznak and Pankrantz, 1977). The Higher termites exhibit a more varied digestive system which reflects their utilisation of a greater variety of plant matter which ranges from wood through to humus. All Higher termites, except Macrotermitinae, harbour gut enzymes, symbiotic bacteria and protozoa. Cellulose digestion in these termites appears to be accomplished by complementary functions of gut enzymes and bacteria while the protozoa present are not xylophagous species and are relatively low in numbers (Bignell, Oskarsson and Anderson, 1979; Breznak, 1983; Sands, 1969; Wood and Johnson, 1986; Wood and Thomas, 1989).

The Macrotermitinae have a fairly simple gut structure and the primary symbiont is a basidiomycete (Amanitaceae) fungus, *Termitomyces* Heim. Konig (1779) first observed this symbiosis and recent work indicates that there is a complex and specialised relationship of mutual dependency between termite and fungus (Thomas, 1981). There are many hypotheses as to the role of *Termitomyces* in termite nutrition; lignin decomposition (Rohrmann and Rossman, 1980), a source of concentrated nutrients (Rohrmann, 1978; Veivers, Mühlemann, Slaytor, Leuthold and Bignell, 1991), involvement in cellulose breakdown either external or internal to the termite gut (Rouland, Mora, Matoub, Renoux and Petek, 1986). However, it is certain that the combined enzyme system of the fungus and termite is an efficient method for the conversion of plant matter into energy and nutrients (Wood and Thomas, 1989; Rouland, Lenoir and Lepage, 1991).

1.4 *Termitomyces* and the Macrotermitinae

Macrotermitinae (Termitidae) are found throughout the Afrotropical and Indomalayan region. There are twelve genera in this sub-family. Ten of these occur in the Afrotropical region while the more advanced genera, *Macrotermes*, *Odontotermes* and *Microtermes*, have reached as far as the Philippines in the Indomalayan region (Bouillon, 1970).

Termitomyces only exists in association with Macrotermitinae and is cultivated in the nest on specialised structures called fungus combs which are constructed from faecal pellets of finely chopped, lightly digested plant tissue (Johnson, 1981; Josens, 1971a; Grassé and Noirot, 1958).

Faecal pellets from the first workers in a new colony are used to produce the first fungus comb. The fungus comb is then inoculated with *Termitomyces* from spores within faeces added to the comb. The source of the inoculum varies amongst the genera; spores may be carried in the gut of the founding pair of reproductives or collected from sporulating *Termitomyces* at the soil surface by the first foraging workers (Johnson, Thomas, Wood and Swift, 1981).

The maintenance of fungus combs is a dynamic process with the continual addition of new faecal matter as older material is removed and consumed (Josens, 1971a; Johnson, 1981; Grassé, 1978; Rohrmann, 1978; Garnier-Sillam, 1987; Noirot, 1969; Wood, 1981; Sands, 1969). Josens (1971a) estimated, by using soot as a tracer, that the complete turnover of fungus comb maybe accomplished in 5 to 8 weeks.

The number and location of fungus combs in a nest also differ amongst the genera. Fungus combs may be located in a single centralised hive or brood chamber e.g. in *Macrotermes* and *Odontotermes* nests. Where there is no centralised nest, as in the nests of many subterranean species e.g. *Microtermes*, fungus combs are found in small chambers which vary in location and number with depth, season and species (Josens, 1971a & b, Wood and Johnson, 1978; Grassé, 1978; Sands, 1969; Thomas, 1981).

The necessity for more detailed knowledge of fungus comb dynamics in the soil is, partly, a result of the recent interest in the use of fungicides as a selective chemical method of controlling fungus-growing termites, especially *Microtermes*. Toxicity testing of fungicides on laboratory colonies of *Microtermes* has produced encouraging results on the efficacy of the chemicals (Barnett & Cowie, 1990; El Bakri, Eldein, Kambal, Thomas and Wood, 1989). However field testing of fungicide impregnated baits has not, to date, proved effective in *Microtermes* control (El Bakri, 1986). There appears to be a dilution effect from naturally occurring sources of food whereby bait material is returned to the fungus comb in too low concentrations to allow the fungicide to be effective (Logan, pers. comm.). Recent preliminary results from monitoring the use of systemic fungicides on sugar-cane to control *Microtermes* in Central Africa have shown reduced damage to the sugar-cane and a reduction in the abundance of fungus combs (Mora, pers. comm.).

1.5 Population Ecology

In order to understand the role of termites in ecosystem functioning, it is essential to obtain accurate information on termite population ecology (Brian, 1978; Lavelle, 1983; Josens, 1983; Usher, 1988). This section summarises published data on population estimates and discusses general trends. Problems with obtaining accurate quantitative and qualitative estimates of population parameters are discussed, in conjunction with the following section on sampling methods.

There is a wide range in estimates of termite populations, even between and within similar biotypes (c.f. Abe, 1978; Collins, 1983; Wood et al., 1982; Lepage, 1974). In tropical savannas of West Africa, termite abundance estimates range from 861/m^2 in Senegal to 4602/m^2 in Nigeria while in semi-arid grasslands of N. America, termite abundance ranges from 0 to 9000/m^2 (Josens, 1972; Wood et al. 1977a; Ueckert, 1976). In can be generalised, however, that termite species richness and abundance increases with decreasing latitude which is linked to increasing rainfall (Wood, 1976; Josens, 1983). The influence of rainfall and other environmental factors will be discussed in greater detail later in this section.

Species richness and abundance would appear to decline with the clearing and cultivation of natural/semi-natural vegetation types (Lavelle and Pashanasi, 1989; Bandiera, 1979; Kouassi and Lepage, 1988). However, there are exceptions where pest species of termite are present. Wood et al.(1979) estimated that termite abundance was greater, although overall termite species richness was much reduced, in maize cultivated for more than 8 years (> 6000/m^2) than in adjacent undisturbed Southern Guinea savanna woodland (<4500/m^2). The high populations were due to *Microtermes*, a serious termite pest in the region.

Estimates of the density and dispersion of mounds differ between and ecotypes i.e. the density of all termite mound in African Guinea savanna range from 13.6/ha to 530.6/ha (Bodot, 1967; Sands, 1965) while mound dispersion has been recorded from low contagious (Hebrant, 1970), aggregated (Sands, 1965) to overdispersed (Wood and Lee, 1971). There are a few published studies on the soil abundance of subterranean nests and these have concentrated on the fungus combs of fungus growing termites. Fungus combs fluctuate in density, distribution and dry weight between wet and dry season (Wood and Johnson, 1978; Sands; 1969; Josens, 1972).

Species composition and foraging activity have been monitored from baits, natural food sources and foraging galleries/runways while consumption rates have been studied using baits and litter removal. Both these parameters are influenced by food type, seasonal climate and soil moisture and temperature regimes; foraging is often highest in the wettest periods of the year while peaks in diurnal foraging patterns can be linked to soil moisture and temperature levels as effected by rainfall, irrigation and vegetation cover shading (Abushama and Al Houty, 1988; El Bakri, 1986; Buxton, 1981; Ferrar, 1981a; Haverty et al., 1975; Usher, 1975; Johnson and Whitford, 1975; Ohiagu, 1979; Collins, 1977; La Fage et al., 1973; Abensperg-Traun, 1993; Sands, 1961; Whitford et al., 1983; Nutting, Haverty and La Fage; 1973).

Spatial distribution of species has been studied from the occurrence of species on baits. These indicate that some species have overlapping foraging territories while foraging is random for certain species (Haverty et al., 1975; Jones and Nutting, 1987; Jones and Trosset, 1991; Wood, 1981; Usher, 1975). Qualitative estimates of termite foraging have been achieved using a mark-recapture technique in the Sonoran desert; *Heterotermes aureus* foraging populations ranged from 67,819 to 302,411 individuals (Jones and Nutting, 1987).

Intrinsic, often inter-related, environmental factors are important influences on termite activity at both the macro and microscale. Four main factors can be defined for discussion purposes:

(1) altitude
(2) soils
(3) food type and availability
(4) rainfall

As stated earlier, termites are rarely found above 3000 m while soil characteristics influence termite abundance; termites are rare on soils of high clay content (Ratcliffe, Gay and Greaves, 1952; Lee and Wood, 1971; Holt and Coventry, 1982) while mound density has been show to relate to various soil characteristics (Josens, 1972; Sands, 1965). The soil micro-climate, especially soil temperature and moisture content, influence termite foraging activity. The micro-climate is itself influenced by a combination of seasonal climate, vegetation cover (i.e. shading) and soil characteristics. Seasonal climate will be discussed below while the presence/absence of vegetation shading has been shown to influence termite densities (El Bakri, 1986; Johnson and Whitford, 1975; Dangerfield, 1990; Sands, 1965).

Food type and availability have an obvious influence on termite population dynamics. Differences in termite activities between similar biotypes may relate to local differences in vegetation composition, litter formation and decomposition (c.f.Collins, 1983 and Abe 1979). Food type is especially important in the comparison of foraging activity studies where palatability and preference is often not considered (c.f. Abensperg-Traun, 1993).

The history of land use, especially when examining termite populations in agroecosystems has been shown to be important in termite community composition and abundance. Species diversity of termites tends to decrease with cultivation with a corresponding increase in termite biomass, as a few pest species increase in abundance (Biggar, 1966; Wood et al., 1982; Dangerfield, 1990). This is an especially important factor when considering pest control strategies and when examining the role of termites in soil processes (Whitford et al., 1983; Sands, 1977).

Rainfall is a main limiting/controlling factor in food type/availability and soil characteristics which,as discussed above,are important in termite population dynamics (Lee and Wood, 1971). Wood, 1976, defined a relationship between termites and latitude. However, this can now be more clearly defined as a relationship between termite abundance and rainfall/primary productivity (Brain, 1978; Josens, 1983). Species richness and abundance increase with increasing rainfall, with a few exceptions which can be explained by extensive sampling (i.e. Bodot, 1967).

Josens, 1983, examined species richness and abundance from the African region and formulated the following hypotheses. (1) species richness within a 'cluster' of biotypes increases with increasing rainfall (c.f Lepage, 1974; Wood et al., 1982; Josens, 1972). (2) species richness and predominance of humus feeding termites increases with increasing rainfall. Localised high numbers of species in relatively drier areas can be explained by suitable local micro-climates and availability of organic matter (Roy-Nöel, 1978). (3) species richness of termites feeding on decomposing wood follows the same humidity gradient as humus feeding termites. Species richness of Macrotermitinae reduces in drier areas where the production of woody matter is low and in more humid areas where decomposition of wood is more rapid. (4) Species richness and abundance of grass feeding termites is reduced in the driest savannas due to low primary productivity and

reduced in more humid areas where there is rapid decomposition of dead grass matter.
(5) The amount of annual rainfall with the amount and quality of food are main determinants of termite community structure and abundance.

The above synopsis mainly considers the increase in rainfall with decrease in latitude. However there is also the important consideration of seasonal rainfall, especially within the sub-tropical and tropical regions. Termite populations within nests and in foraging, along with nest construction activities, fluctuate with seasonal rainfall. These often present problems when comparing data, especially population estimates and abundance of nest sites (mainly fungus combs) as few studies have carried out seasonal comparisons. Many studies have only sampled in one season and in some cases mean populations are given for both seasons, while studies carried out solely in the drier seasons of the year examine termite activity at its least active (c.f wet season data only; Wood et al., 1977a; Lavelle and Pashanasi, 1989; Sands, 1965; Ohiagu, 1979).

There is extensive literature to indicate that the onset of rains corresponds to increases in populations, nest construction and, especially, foraging activity, in most species, a notable exception is *Hodotermes* (Kouassi and Lepage, 1988; Bodot, 1969; Ferrar, 1982a; Coaton and Sheasby, 1975). Subterranean termite activity is also closely relate to seasonal rainfall with an increase in abundance and density of fungus combs in the upper soil regions during the wet season (Wood et al., 1977a; Wood and Johnson, 1978; Josens, 1971 & 1974). Further reviews of the literature are given in the relevant Chapters for *Microtermes* soil populations, fungus combs and foraging activity.

Diurnal differences in soil moisture and soil temperature, which are often related to seasonal climate, are important influences on termite activity. Mound populations of certain species aggregate in the central core of the mound during daily periods of higher soil temperature i.e. *Trinervitermes geminatus* in West Africa (Sands, 1965), *Nasutitermes* and *Coptotermes* (Holdaway and Gay, 1948; Greaves, 1962). Foraging activity on baits and in the upper soil regions is often lower in the hotter drier periods of the day. Species separation may be achieved by differences in daily foraging patterns.

1.6 Sampling methods

All estimates of abundance and distribution are dependant on sampling methodology (Baroni-Urbani, Josens and Peakin, 1978). Detailed reviews of sampling methodologies are given in Lee and Wood, 1971; Baroni-Urbani et al., 1978 and Sands, 1972. This section presents a brief overview of the most widely used sampling techniques and examines constraints to obtaining accurate population estimates. The following four categories will be examined:

(1) Type of sampling
(2) Sampling regime
(3) Sorting of individuals
(4) Identification of termites

Quantitative methods of estimating populations involve sampling mounds, nests and soils while qualitative methods have concentrated on foraging studies either on baits or from removal of litter. The estimation of mound populations is carried out by destructive sampling either by taking a portion of the nest or by sampling the whole nest (Sands, 1965). Accuracy in population estimation depends on the reduction of losses due to escaping termites (i.e. the use of fumigants before sampling), the number of mounds sampled, the age of mounds sampled and the seasonal/diurnal timing of sampling (Darlington, 1984; Sands, 1965; Bouillon and Lekie, 1964).

Two methods, soil cores and soil pits, are commonly use to sample subterranean termite nesting or foraging (which often includes foragers from mound building termites). There are large differences in accuracy between different sizes of cores and pits however there is general agreement the use of small numerous plots/cores provides more accurate quantitative data that a few large pits, as reviewed in Baroni-Urbani et al, 1978.

The study of termite foraging was first carried out using 'graveyard' trials where wooden stakes were placed on the soil surface or buried to assess timber resistance to termite damage and the efficiency of chemical control agents (Harris, 1969). Since the 1970's, the study of termite foraging has diversified considerably with several techniques now commonly employed though the use of baits has been the most widely used method to study the feeding habits of termites, especially polyphagous and wood feeding species (Wood and Sands, 1978; French and Robinson, 1981). A more detailed review of baiting techniques is given in Chapter Five.

Any sampling procedure must also consider differences in population activities with seasonal and diurnal environment, as discussed earlier. There are also localised niches of certain species i.e. subterranean - soil feeding termites (c.f. Wood et al., 1982).

The method of sorting of individuals is often not mentioned by studies. Comparative work on different sorting methods was carried out by Wood et al., 1979b. Salt Hollick flotation was effective at separating out termites but it is very time consuming. The efficiency of hand-sorting was determined against flotation and found to be dependant on the size of individuals and on their colour; termites with darker gut contents were more efficiently collected than those with light coloured guts i.e. soil feeders compared to

Microtermes spp. A correction factor was incorporated to correct hand-sorted estimates of different termite genera for the differences in sorting efficiency.

1.7 Termites as pests

Sands (1973) suggested that every plant used by man has been (or will be) at some stage in its growth attacked by at least one species of termite in some part of the tropics. In Africa, termites damage a wide variety of crops and exotic trees , such as maize, groundnuts and *Eucalyptus*, are particularly prone to attack (Brown, 1965; Cowie, Logan and Wood, 1989; Harris, 1971; Johnson, Lamb and Wood, 1981; Wood, Johnson and Ohiagu, 1980; Wood, Smith, Johnson and Komolafe, 1980). Some species cause significant yield losses in annual, perennial and tree crops as well as damage to timber in the construction industry (Harris, 1969; Cowie, Wood and Logan, 1989; Wood and Cowie, 1988).

The importance of termites as pests of staple foods and economically important crops emphasises the need to understand the changes in termite populations and species composition as habitats are modified and land use is intensified; the degree of damage and yield losses are frequently related to the cultivation history of the land; crop types and the length of cultivation (Sands, 1977). Certain species often decline as nest sites are destroyed and preferred food sources are removed while other termites, often with subterranean nests, increase in abundance (Kooyman and Onck, 1987; Lavelle and Pashanasi, 1989; Lepage, 1980; Roy-Nöel, 1978; Sands, 1965; Wood, Johnson and Ohiagu, 1977).

However, not all termites encountered in agricultural ecosystems are pests. The majority are harmless or even beneficial. Less than 10% of all known termite species are classified as "economically important". The family Termitidae contains over 60% of all known pest species and the fungus-growing Macrotermitinae are the major termite pests in the tropical regions of Africa and Indo-Malaysia (Cowie and Wood, 1989; Cowie, Wood, Barnett, Sands and Black, 1990; Harris, 1971; Sands, 1973).

With a few exceptions, crop damaging termites are entirely subterranean (Wood et al. 1980a). Their populations are highly aggregated and their nest systems widely distributed, depending on the soil and vegetation type of the area. Consequently, there are many sampling problems to consider when estimating population densities of subterranean termites. The most accurate method of sampling is quantitative soil sampling which is both labour intensive and time-consuming requiring the digging/coring of numerous samples and hand-sorting to collect termites.

1.8 *Microtermes* (Wasmann)

Microtermes (Termitidae; Macrotermitinae) originated in the Afrotropical region during the Tertiary Period, spread from there to the Orient and is now established in the Afrotropical, Malagasy and Indomalayan regions (Emerson, 1955). At present there are over 60 species described with over 40 from Africa. However, specific identification is notoriously difficult due to inadequate descriptions, confusion among types series and the morphological similarity between species (Wood, 1981).

Microtermes are widespread throughout the Afrotropical and Indomalayan regions with the largest populations found in the semi-arid and savanna vegetation zones (Buxton, 1981; Ferrar 1981a, b & c; Kooyman and Onck, 1987). *Microtermes* is known to increase in abundance with cultivation. However, it was not known whether or not all *Microtermes* species followed this trend.

This genus is considered the major termite pest of annual crops, especially cereal and legume staples, throughout Africa and Indomalaysia (Johnson and Gumel, 1981; Sands, 1973 & 1977; Thakur, 1977; Wood, Johnson, Ohiagu, Collins and Longhurst, 1977; Wood and Johnson, 1978). Table 1.1 lists crops recorded being attacked and damaged by *Microtermes*, the country of record and the species responsible, when given in the source text.

Microtermes are principally polyphagous wood feeders, though they will also consume litter. Foragers search for food from subterranean galleries. They remove fine roots and excavate root systems and stems, replacing their cores with soil. Food at the soil surface is attacked from galleries below in response to differing environmental gradients i.e. humidity and temperature.

The species construct widely dispersed, subterranean nest systems which contain highly aggregated and mobile populations. A network of narrow galleries link small chambers (3 - 4 cm diameter) which are used as nurseries and to house fungus combs for the cultivation of the symbiotic fungus *Termitomyces* (Krishna and Weesner, 1969). A single subterranean nest may cover an area up to 250 m^2, include 560 fungus comb chambers and have galleries (800 - 1200 μm cross section diameter) which may penetrate to a depth of 8 - 10 metres to obtain water (Biggar, 1966; Josens, 1971b & 1974; Kooyman and Onck, 1987; Lepage, 1972, 1973 & 1974; Pearce, Tiben, Kambal, Thomas and Wood, 1984). This poses enormous sampling problems and population density is inevitably underestimated (Sands, 1972).

Table 1.1: Records of crops attacked by *Microtermes* in countries of the Afrotropical and Indomalayan geographical regions.

Crops with recorded attack	Species (if known)	Country	Source
Abutilon	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Apricot	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Bamboo	*Microtermes sp.*	India	Thakur, 1988
Banana	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Barley	*M. obesi*	India	Reddy, 1968
	Microtermes sp.	India	Bhanot, Verma & Kashyap, 1984
Cajuput	*M. insperatus*	Java	Intari & Wiraadinata, 1984
Chickpea	*Microtermes sp.*	India	Reed, Lateef, Sithanantham and Pawar, 1989
Chillies	*M. obesi*	India	Sharma & Bohra, 1966
Citronella	*M. obesi*	India	Sontakke, Mohanty & Kole, 1991
Citrus	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Cocoa	*Microtermes sp.*	Nigeria	Sands, 1962
Coconut palm	*M. bugnoni*	Ceylon	Jepson, 1931
Coffee	*M. insperatus*	Java	Le Pelley, 1968
	M. insperatus	Malaya	Le Pelley, 1968
	M. insperatus	Indonesia	Le Pelley, 1968
	M. pallidus	Malaya	Le Pelley, 1968
Cotton	*M. mycophagus*	India	Thakur, 1985
	M. unicolor	India	Thakur, 1985
	M. mycophagus	Pakistan	Akhtar and Shahid, 1991
	M. obesi	Pakistan	Akhtar and Shahid, 1991
	M. najdensis	Sudan	Tiben, Pearce, Wood, Kambal & Cowie, 1990
	M. najdensis	Yemen	Wood, Bednarzik & Aden, 1987
	M. aluco	W. Africa	Harris, 1971
	M. kasaiensis *	Zambia	Harris, 1971
	M. thoracalis *	Sudan	El Amin and Ahmed, 1991
	Microtermes sp.	Tanzania	Pearson, 1958
	Microtermes sp.	Zimbabwe	Mitchell, 1980
Egg-plant	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Eucalyptus	*M. obesi*	India	Jamaluddin and Joshi, 1989
	Microtermes sp.	Africa	Cowie, Logan & Wood, 1989
	Microtermes sp.	Zimbabwe	Mitchell, Gwaze & Stewart, 1987
Fig	*M. unicolor*	India	Thakur, 1985
Groundnuts	*M. thoracalis* *	Burkina Faso	Lynch, Ouedraogo & Some, 1990
	M. thoracalis *	Sudan	Feakin, 1973
	M. thoracalis *	India	Smith & Barfield, 1982
	M. lepidus	Nigeria	Johnson & Gumel, 1981
	M. lepidus	Sudan	Hebblethwaite & Logan, 1985
	M. subhyalinus	Nigeria	Perry, 1967
	M. obesi	South Asia	Roonwal, 1979
	M. obesi	India	Logan, Rajagopal, Wightman & Pearce, 1992
	M. najdensis	Yemen	Wood, Bednarzik and Aden, 1987
	Microtermes sp.	Zambia	Wightman, Dick, Ranga Roa, Shanower & Gold, 1990
	Microtermes sp.	Malawi	Wightman, Dick, Ranga Roa, Shanower & Gold, 1990
	Microtermes sp.	Zimbabwe	Wightman, Dick, Ranga Roa, Shanower & Gold, 1990
	Microtermes sp.	Botswana	Wightman, Dick, Ranga Roa, Shanower & Gold, 1990
	Microtermes sp.	Tanzania	Harris, 1971
	Microtermes sp.	Sudan	Logan, Rajagopal, Wightman & Pearce, 1992
	Microtermes sp.	Ethiopia	Cowie & Wood, 1989
Guava	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Hyphaene palm	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Jute	*M. obesi*	India	Dutt, 1962
	M. obesi	Pakistan	Kabir & Hossain, 1970

* synonym

cont.

M. thoracalis syn. M. tragardhi
M. kasaiensis syn. M. congoensis

Table 1.1: Records of crops attacked by *Microtermes* in countries of the Afrotropical and Indomalayan geographical regions. cont.

Crops with recorded attack	Species (if known)	Country	Source
Maize	*M. lepidus*	Nigeria	Wood, Johnson & Ohiagu, 1980
	M. najdensis	Yemen	Wood, Bednarzik and Aden, 1987
	Microtermes sp.	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
	Microtermes sp.	Yemen	Wood, Bednarzik & Aden, 1987
	Microtermes sp.	India	Thakur, 1985
	Microtermes sp.	Ethiopia	Cowie & Wood, 1989
	Microtermes sp.	Tanzania	Bohlen, 1973
	Microtermes sp.	Uganda	Dunbar, 1969
	Microtermes sp.	Zimbabwe	Mitchell, 1980
Mango	*M. obesi*	India	Thakur, 1985
	M. mycophagus	India	Thakur, 1985
	Microtermes sp.	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Millet	*Microtermes sp.*	India	Thakur, 1985
Oats	*M. obesi*	India	Reddy, 1968
Okra	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
	M. najdensis	Yemen	Wood, Bednarzik & Aden, 1987
	Microtermes sp.	India	Reddy, 1968
Papaya	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Pepper	*M. najdensis*	Yemen	Wood, Bednarzik & Aden, 1987
	Microtermes sp.	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Pigeon-pea	*M. obesi*	India	Reddy, Yule, Reddy and George, 1992
	Microtermes sp.	Kenya	Khamala, Oketch & Okeyo-Owour, 1978
Prunus	*Microtermes sp.*	India	Reed, Lateef, Sithanantham and Pawar, 1989
Rice	*Microtermes sp.*	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
	Microtermes sp.	India	Variar, Chauhan, Maiti & Chauhan, 1991
Sesame	*M. najdensis*	Yemen	Wood, Bednarzik & Aden, 1987
Sorghum	*Microtermes sp.*	Nigeria	IITA, 1971
Soybean	*Microtermes sp.*	Malawi	Logan, 1991
Stylosanthes	*Microtermes sp.*	Kenya	Singh, van Emden and Taylor, 1978
Sugarcane	*M. mycophagus*	India	Thakur, 1985
	M. mycophagus	Pakistan	Akhtar and Shahid, 1990
	M. unicolor	India	Thakur, 1985
	M. tragardhi	Sudan	Abushama and Kambal, 1977
	M. obesi	Pakistan	Akhtar and Shahid, 1990
	M. obesi	India	Agarwala & Ramanujam, 1959
	Microtermes sp.	Tanzania	Bohlen, 1973
	Microtermes sp.	Nigeria	Wood and Johnson, 1978
Sunflower	*Microtermes sp.*	Nigeria	Sands, 1962
Tamarix	*M. najdensis*	Yemen	Wood, Bednarzik & Aden, 1987
Tea	*M. pallidus*	Malaysia	Harris, 1971
	M. jacobseni	Java	Harris, 1971
	Microtermes sp.	India	Reddy, 1968
	Microtermes sp.	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Teak	*Microtermes sp.*	Malaya	Corbett & Miller, 1936
Tomato	*M. obesi*	India	Thakur, 1985
	M. najdensis	Yemen	Wood, Bednarzik & Aden, 1987
	Microtermes sp.	Saudi Arabia	Badawi, Al-Kady & Faragalla, 1986
Vegetable seedlings	*Microtermes sp.*	Yemen	Wood, Bednarzik & Aden, 1987
Wheat	*M. obesi*	India	Thakur, 1977
	M. vadschaggae	Tanzania	Harris, 1971
	Microtermes sp.	Zimbabwe	Mitchell, 1980
	Microtermes sp.	Ethiopia	Hill, 1989
Yam	*Microtermes sp.*	Ethiopia	Cowie & Wood, 1989

* synonym

M. thoracalis syn. M. tragardhi

M. kasaiensis syn. M. congoensis

1.9 Termite Research Project 1973 to 1979

From 1956 to 1960, The Termite Unit of The Centre for Overseas Pest Research (COPR), U.K., carried out field studies in West Africa and highlighted the need to investigate the role of termites in the agricultural ecosystem (Harris, Sands and Wilkinson, 1960). To this aim, the Termite Research Project was established to determine termite abundance, distribution and feeding habits in relation to crop damage and to assess crop yield loss due to termites. The ultimate objective was provide information for the development of control strategies that were both safe and economic (Wood, Johnson, Ohiagu, Collins and Longhurst, 1977).

The following topics were examined :

(1) Population studies on mound building and subterranean termites and the assessment of baiting as an index of population density.

(2) Foraging and food consumption of grass and wood feeding termites and predation by ants.

(3) Assessments of damage and yield loss caused by termites to the main crops of the region.

(4) Termite biology, nest structure and colony development.

(5) Chemical studies on defense secretions and repellents.

This project was jointly financed by Ahmadu Bello University (ABU), Nigeria (through the Institute for Agricultural Research (IAR), Government of Nigeria) and the Ministry of Overseas Development (ODM), UK, through COPR (Sands, 1977). The Agricultural Research Station at Mokwa in the Southern Guinea savanna vegetation zone of Nigeria provided a base for the project which started in June 1973 and ran for six years. Project staff consisted of three full-time scientists, two from COPR (Dr T.G Wood and Dr R.A Johnson) and one from ABU (Mr C.E. Ohiagu), and a graduate research fellow (Mr N.M. Collins). Two other research fellows visited the site for study purposes (Mr C. Longhurst and Mr A. Davies).

The Macrotermitinae were of particular interest to the project as they were important pests of crops in Nigeria and elsewhere in Africa. One conclusion of this project was that the genus *Microtermes* was the major crop pest in Nigerian Guinea savanna, with respect to yield loss in annual crops, especially cereal staples and groundnuts (Johnson, Lamb and Wood, 1981; Sands, 1973 & 1977; Wood, Johnson, Ohiagu, Collins and Longhurst, 1997; Wood, Johnson and Ohiagu, 1977). However, at the time of the project, it was not possible to identify *Microtermes* to species and as a result all collections were returned to U.K. and stored at COPR. During the 1980's, COPR merged with several other institutions within ODM and now forms part of the Natural Resources Institute (NRI). ODM was also renamed the Overseas Development Administration (ODA).

1.10 The relationship of this study with the Termite Research Project

In 1986, an extra-mural contract was provided by ODA to support the author, a research assistant from Queen Mary & Westfield College, in a laboratory based project to identify crop-damaging *Microtermes* from Africa. This work required training in the taxonomy of *Microtermes*, assistance in the verification of a West African and Sudan *Microtermes* key and the identification of the TRP termite samples (over 5,000 samples). This project started in September 1986 and was completed in March 1991.

In this thesis, these identifications were utilised, in conjunction with TRP field data, to investigate population dynamics of *Microtermes* spp. and individual species in uncultivated and cultivated sites in the Southern Guinea savanna vegetation zone of Nigeria.

1.11 HYPOTHESES

As discussed earlier, termite community structure and population dynamics are influenced seasonal climate, vegetation type and cultivation history. Therefore the following hypotheses are to be tested with reference to *Microtermes* population dynamics. More detailed literature reviews of each topic are given in the relevant Chapters.

The hypotheses to be tested are:

(1) SOIL POPULATIONS

The community structure and abundance of *Microtermes* will be influenced by vegetation cover and seasonal climate. Changes in abundance will correspond to changes in soil distribution[1*], notably lower populations in the dry season compared to the wet season with corresponding movements down in the soil. Successional changes in community structure and abundance of species will be identified as woodland is cleared and different crops cultivated. These changes may have predictive value in assessing populations of pest species and therefore potential yield losses.

[1*] the term *soil distribution* refers to *vertical soil distribution* unless otherwise stated.

(2) FUNGUS COMBS

The abundance of fungus combs of *Microtermes* spp. and individual species will be influenced by vegetation type and seasonal climate and will correspond to changes in the community structure and abundance of *Microtermes* species. Differences in the abundance of fungus combs will correspond to changes in soil distribution, notably a movement down in the soil with a decline in weight in the dry season compared to the wet season.

(3) FORAGING ACTIVITY

The community structure and foraging activity of *Microtermes* will be influenced by vegetation type and seasonal climate, notably reduced foraging in the dry season compared to the wet season, with further successional changes identified as woodland is cleared and different crops cultivated. Spatial distribution of species can be detected from foraging activity. Foraging activity by *Microtermes* species correspond to soil populations and therefore foraging activity can be used as a qualitative index of abundance and as a predictor of populations especially pest species.

CHAPTER TWO

MICROTERMES OF THE SOUTHERN GUINEA SAVANNA VEGETATION ZONE OF WEST AFRICA

Recent taxonomic studies at the Natural Resources Institute, U.K. have produced a key of West African and Sudanese species (unpublished). In the production of this key, *Microtermes* species were examined from the Termite Research Project collections and material from the British, Stockholm and Smithsonian Museums. This key is given in Appendix 1, listing species and synonyms. Eighteen species can be identified from the key. Twelve species are present in the Southern Guinea savanna vegetation zone. Of these, *M. congoensis* (Sj.) Sjöstedt (1911)., *M. depauperata* Silv. Silvestri (1914), *M. sp. J ?n.sp.* and *M. comprehensa* Silv. Silvestri (1914) are predominantly forest species which occasionally occur in savanna woodland. *M. tragardhi* (Sj.) Sjöstedt (1904) is a species from Sahel/Northern Guinea savanna zones which is occasionally found in Southern Guinea savanna.

The remaining seven species (from 12) were shown by Wood, 1981, to be sympatric in Southern Guinea savanna woodland. Dispersal flights of the reproductives (alates) are not spatially isolated, subterranean colonies are spatially interlocked and species frequently occur in both the same soil area and food source. Three species are new species and, as yet, formally undescribed; *M. sp.K n.sp.*, *M. sp.Y n.sp.* and *M. sp.C n.sp.*. *M. sp.Y n.sp.* (*M. sp. Z*, in Wood, 1981) is very rare and may have specialized niche requirements. The soldiers of this species cannot be differentiated morphologically from those of *M. lepidus* or *M. sp. K.* but all species have distinctive dispersal flight times and behaviour. At the start of the wet season, alates of *M. sp. Y* fly after dark on the third or fourth day after the rains commence. *M. lepidus* alates fly before dark, in the mid-afternoon, on the first day after the rains from specially constructed soil turrets. *M. sp. K* alates also fly on the first day after the rains but after dark in early evening. Soldiers of *M. sp. C* can be differentiated from the above species by slight morphological differences. Alates of this species have a similar flight time range to *M. sp. K* but tends to fly earlier in the evening.

The remaining species, *M. aluco*, *M. subhyalinus* and *M. grassei*, can all be differentiated morphologically and have different flight times. *M. aluco* flies after dark from the first to third day after the rains start. *M. subhyalinus* also flies in the early evening after dark on the first day after the rains but differs from other species as mating is accomplished in the air. *M. grassei* flies in the afternoon before dark two days after the rains.

Microtermes in this study were collected from woodland and sites derived from woodland in the Southern Guinea savanna vegetation zone of Nigeria. All identifications were carried out from the unpublished key of West African and Sudanese species (Appendix 1). Five of the seven sympatric species described above, were present in the samples available; *M. aluco*, *M. n. sp. C*, *M. grassei*, *M. lepidus* and *M. subhyalinus*. Plates 2.1 to 2.5 show the morphology of the soldier and worker heads of these species.

Plate 2.1 *Microtermes lepidus* Sjöstedt; soldier and worker. Magnification x 25.

Plate 2.2 *Microtermes grassei* Ghidini; soldier and worker. Magnification x 25.

Plate 2.3 *Microtermes aluco* Sjöstedt; soldier and worker. Magnification x 25.

Plate 2.4 *Microtermes subhyalinus*; Silvestri soldier and worker. Magnification x 25.

Plate 2.5 *Microtermes n.sp. C*; soldier and worker. Magnification x 25.

CHAPTER THREE

DESCRIPTION OF EXPERIMENTAL AREA

The main experimental area was based at the Agricultural research station approximately 6 km north of Mokwa village, 9°, 18'N; 5°, 4'E (Figure 3.1). The climate is typical of the Southern Guinea savanna with pronounced wet and dry seasons; the latter usually from mid-October to mid-April. Mean annual rainfall is 1175 mm often with a bi-modal yearly distribution pattern; August usually being the driest month within the wet season. Figure 3.2 shows the mean monthly rainfall at Mokwa from 1974 to 1976. The annual temperature regime shows large diurnal range in the dry season (day 38°C/night 12°C) and a low wet season range from 33°C to 20°C (Walter, 1968; Agboola, 1979).

The soils of the area are a mosaic of two soil series of the Kulfo association, either the Dangappe or Kulfo series. They are both developed on coarse - grained Nupe sandstone and are mainly deep, undifferentiated red Ferrisols constructed of a shallow sandy upper layer and a B horizon (30 - 150 cm depth) of sandy clay to clay with clay content increasing with depth (Valette, 1973). The natural vegetation is open canopy deciduous woodland (12 - 15 m height) and a dense stand of grasses up to 2 m in height (Collins, 1977). The dominant vegetation is -

1. TREE SPECIES
    Burkea africana Hook (Caesalpiniaceae)
    Afzelia africana Sm. (Caesalpiniaceae)
    Detarium microcarpum Guill & Per (Caesalpiniaceae)

2. GRASSES
    Andropogon gayanus Kunth
    Eragrostis tremula (Hochst, ex Steud)
    Hyparrhenia dissoluta (Hochst, ex Steud)

The study sites were chosen to give a range of habitats from undisturbed natural vegetation to long term monocultures in order to study changing termite populations within different cultivation practices. A main randomised block experiment was established from secondary woodland early in 1974 and additional sites were chosen from the surrounding area at this time. The sites are described below.

Mokwa randomised block of 12 plots (Figure 3.3):

Block history : secondary woodland cleared during 1949 - 53 and mechanically cultivated in one season for sorghum; regrowth prevented by cutting until 1959 when secondary regrowth proceeded unchecked except for light cutting for fuelwood. The following plots (numbered as in italics) were established in 1974 and continued to 1976. Each plot was 50 m x 100 m with 2 replicates of 6 treatments. In 1977, the cereal and root crops were rotated as indicated in parentheses (*77:crop*).

Randomised block:

1. Secondary woodland *1* + *12*
2. Grazed pasture *4* + *5*
3. Short term maize *7* + *9* (77:*sweet potato*)
4. Groundnut *2* + *11* (77:*yam*)
5. Yam *3* + *6* (77:*groundnut*)
6. Sweet potato *8* + *10* (77:*maize*)

Additional sites:

7. Primary woodland (plots 13 + 14): never cultivated or cut for firewood.
8. Long term (Ranch) maize (plots, 19 + 20): cultivated from 1949 - 59 then secondary re-growth of woodland until cropping restarted in 1965.
9. Long term (Farm) maize (plots 21 + 22): continuously cultivated since, 1949.

All cultivation was carried out mechanically with the use of a disc cultivator and plough, to a depth of 20 cm. The management of individual crops is given below.

MAIZE : discing was carried out after the first rains in April then a broadcast application of Nitrophoska (152.4 kg/0.5 ha) was applied. Seed was planted late April or early May at 30.5 cm intervals (rows 90 cm apart) by a 4-tined cultivator. A second application of fertiliser (76.2 kg/0.5 ha) was made 3 to 4 weeks after planting and was immediately followed by ridging. Harvesting usually started in early September.

GROUNDNUTS : discing after the first rains in April, followed by broadcast application of superphospate (50.3 kg/0.5 ha). Ridging at 90 cm intervals then planting at 22.9 cm intervals occurred in early April. Harvesting was in mid-September.

SWEET POTATO : Discing and ridging at 90 cm intervals then planting at 61 cm intervals began in early July. Harvesting in mid-November.

YAM : discing mid-January, then ridges constructed by hand at 182 cm intervals. Setts planted mid to late February at 61 cm intervals. Harvesting early December.

Figure 3.1 : Location of Agricultural Research Station at Mokwa in the Southern Guinea savanna vegetation zone of Nigeria (from Wood et al., 1977a & b).

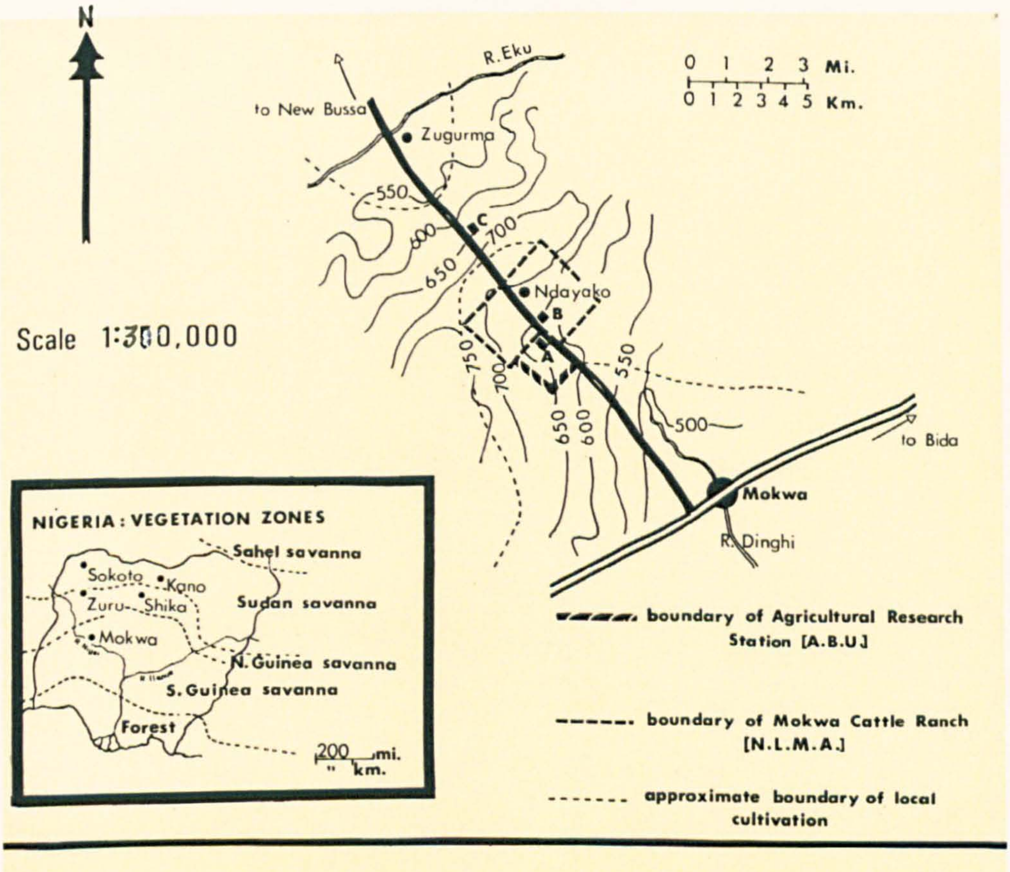

N
R. Eku
to New Bussa
Zugurma
0 1 2 3 Mi.
0 1 2 3 4 5 Km.
550
600
650
700
750
C
Ndayako
B
A
Scale 1:300,000
500
to Bida
Mokwa
R. Dinghi
NIGERIA : VEGETATION ZONES
Sahel savanna
Sokoto
Kano
Zuru
Shika
Sudan savanna
Mokwa
N. Guinea savanna
S. Guinea savanna
Forest
200 mi.
" km.
boundary of Agricultural Research Station [A.B.U.]
boundary of Mokwa Cattle Ranch [N.L.M.A.]
approximate boundary of local cultivation

Figure 3.2 : Monthly rainfall at Mokwa from 1974 to 1977; adapted from Wood <u>et al</u>., 1977b.

Figure 3.3 : Layout of the randomised block experiment established in 1974 from clearing and cultivating secondary woodland at Mokwa, Nigeria.

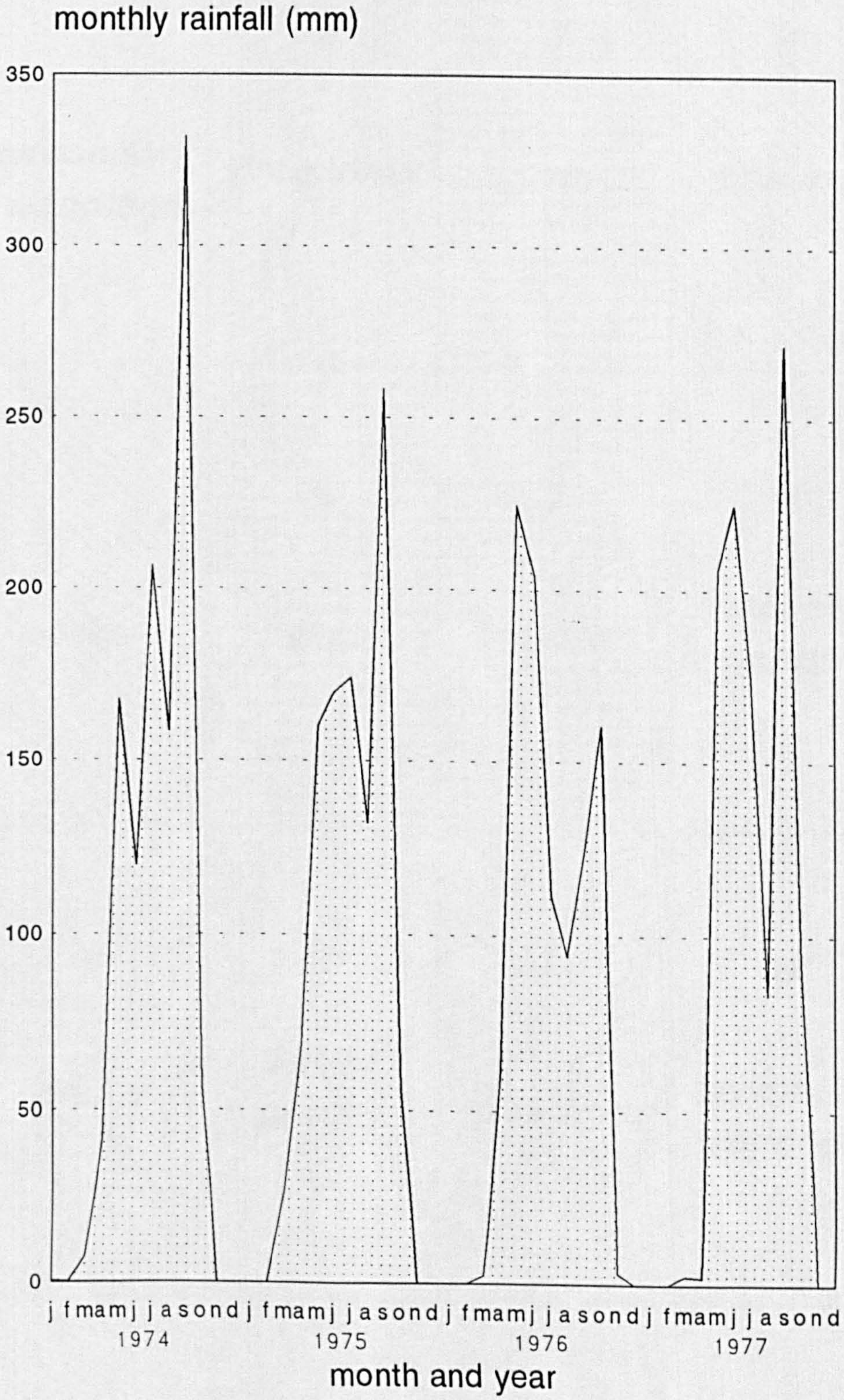
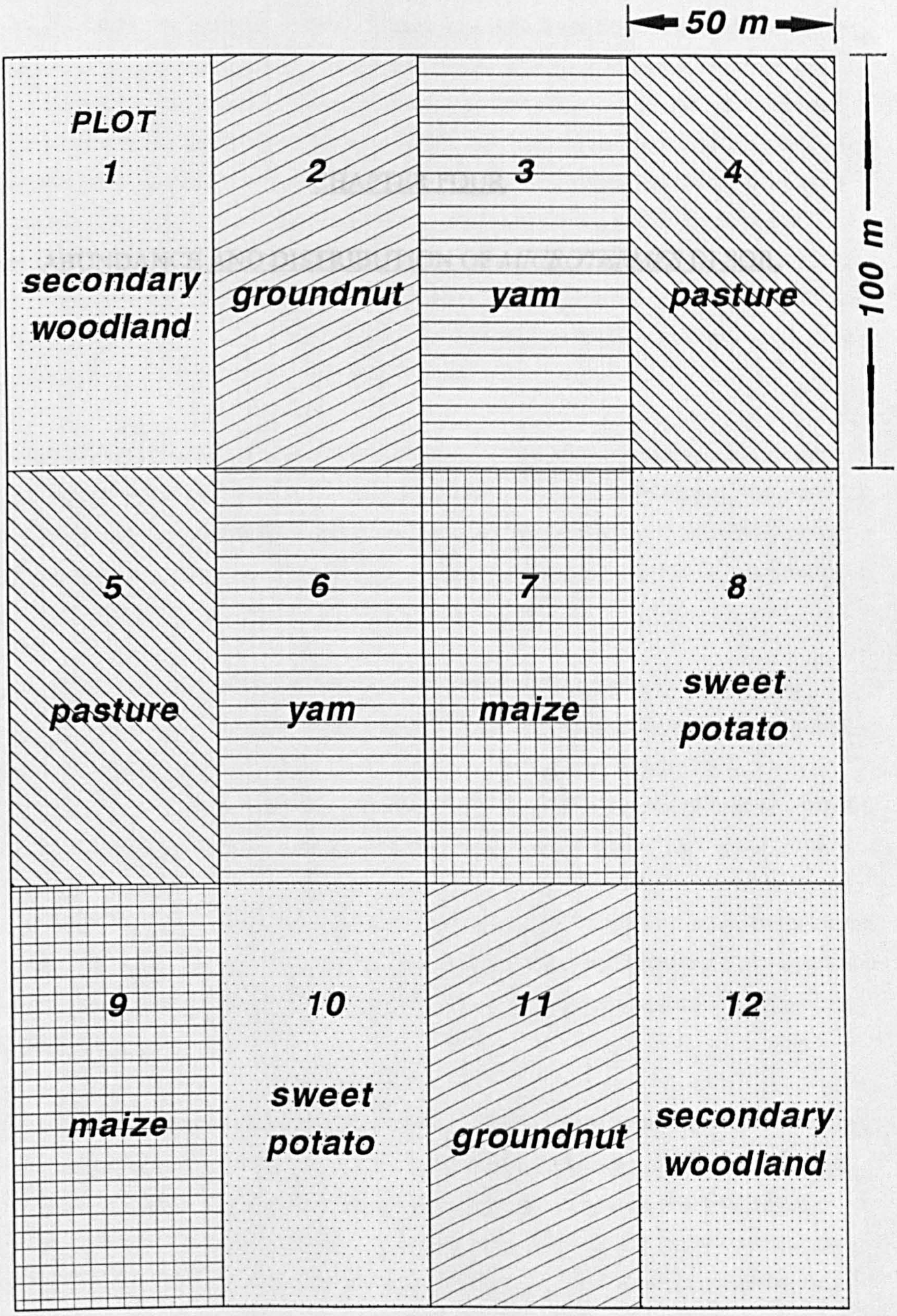


Figure 3.3 : Layout of the randomised block experiment established in 1974 from clearing and cultivating secondary woodland at Mokwa, Nigeria.


50 m
100 m
PLOT
1
secondary woodland
2
groundnut
3
yam
4
pasture
5
pasture
6
yam
7
maize
8
sweet potato
9
maize
10
sweet potato
11
groundnut
12
secondary woodland

CHAPTER FOUR

ABUNDANCE AND DISTRIBUTION OF *MICROTERMES* IN SOIL

4.1 INTRODUCTION

The intensity of termite attack on crops is often related to prior cultivation history (Harris, 1971; Sands, 1977; Wood et al., 1980). Clearing of woodland removes food and nesting sites while mechanical cultivation destroys mounds and termite nests in the upper soil layers, resulting in an alteration in termite species composition and abundance. Several studies note the decline in certain species with the introduction of agriculture as nest sites are destroyed and preferred food sources are removed, while other termites, often with subterranean nests, increase in abundance (Kooyman and Onck, 1987; Kouassi and Lepage, 1988; Lepage, 1972; Roy-Nöel, 1978; Sands, 1965; Wood et al., 1977a). This has important economic implications as many subterranean termites cause significant yield losses in tropical agriculture and have diverse and important roles in soil processes (Lee & Wood, 1971; Lobry de Bruyn & Conacher, 1990).

Within this context, the genus *Microtermes* is one of the most important subterranean termites within the Southern Guinea savanna of West Africa. In this region, the pest status of termite species is directly linked to agricultural operations, with *Microtermes* considered the most significant termite pest, especially of cereal crops and groundnuts (Sands, 1977; Wood et al., 1977a & b; Johnson et al., 1981a).

Quantifying subterranean termite populations, such as *Microtermes*, is notoriously difficult and there has been inconsistency in published population estimates corresponding to different sampling methodologies, as reviewed by Wood and Sands, 1978. *Microtermes*, as with other subterranean termites, show a high degree of spatial variation in distribution with populations both aggregated and diffuse throughout the soil profile. Individuals congregate around fungus combs and move within an extensive network of galleries, as discussed in Chapter One. *Microtermes* are also relatively small termites and can escape sampling if disturbance during sampling provides sufficient time for termites to move from the soil being sampled (c.f. Josens, 1983; Wood and Sands, 1978; Eggleton and Bignell, in press).

Several methods have been used to quantify subterranean termite populations from large pits or trenches (Abe and Matsumoto, 1979), soil monoliths or small pits (Dangerfield, 1990; Josens, 1974) to soil cores (Wood et al. 1982). In each case, the time taken to sample the soil is vitally important; soil must be sampled before the termites can escape (c.f. Josens, 1972). The number of soil samples must be sufficient to encompass the spatial variation across a habitat and within the soil. Wood et al., 1977b, inoculated an area of soil with a known number of termites to assess the accuracy of soil coring using a Jarret auger of 10 cm diameter to a depth of 2 m. A major problem with sampling subterranean termites must be retrieving the termites. To date, the most efficient and cost-effective method has been hand-sorting. Wood et al., 1977a & b, have shown that the accuracy of this method depends on the termite species being sampled; active termites with light coloured guts (i.e. *Microtermes* and *Amitermes*) are often collected more efficiently than slower termites with dark guts (*Microcerotermes* and *Trinervitermes*). The study of Wood et al., 1977a, was carried out as part of the Termite Research Project. *Microtermes* identified for this present study were collected during the Termite Research Project and the methodology is discussed in full below, in Section 4.2.

Previous published results from Africa indicate that *Microtermes* abundance and distribution in soil differs with seasonal weather conditions, habitat and termite species composition; populations are often highest the wet season and in disturbed and cultivated habitats where overall termite species richness is reduced.

In south-western Kenya, Kooyman and Onck (1987) collected termite species from soil pits dug to 2 m in pasture, perennial and annual crops. *Microtermes sp.* and *M. vadschaggae* were more abundant under annual crops than perennial crops. The authors concluded that this was due three factors; i. *Microtermes* ability to survive cultivation disturbance; ii. a decrease in competition from other termite species (species richness was lower in annual crops than pasture or perennial crops) and, iii. an increase in preferred food type.

Ferrar, 1982c, sampled termite populations in South African *Acacia* savanna and broad-leaved savanna from soil cores (auger diameter 7.5 cm) taken to a depth of 18 cm. *Microtermes* were more abundant in the *Acacia* savanna (326/m^2) than the broad-leaved savanna (59/m^2) with movement down in the soil during heavy rainfall and in drier periods. This movement was most pronounced in *Acacia* savanna where tree cover and litter layer on the soil surface were more sparse than in broad-leaved savanna. Tree cover and litter layer may help to reduce water evaporation from the soil surface and so maintain soil moisture levels. In a study of the termite community in Guinea savanna of Côté d'Ivoire, *M. toumodiensis* (now *M. subhyalinus*) populations ranged from 14.4 to 244/m^2 with a movement down the soil profile in the dry season (Josens, 1972 and 1974). In the Northern Guinea savanna vegetation zone, Sands (1965) sampled *Microtermes* from soil pits in cleared woodland, undisturbed and disturbed woodland. *Microtermes* were most abundant in the cleared plot and least abundant in undisturbed woodland.

Previously published results from the Termite Research Project have examined *Microtermes* populations in various habitats in Nigeria. Summaries of these results are given below. Table 4.1.1 summarises previously published results from Mokwa which show the differences in the abundance and species richness of termites and the relative abundance of *Microtermes* spp. in uncultivated and cultivated sites.

Table 4.1.1 : Mean wet season species richness and abundance of termites and the relative abundance of *Microtermes* in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria (adapted from Wood et al. 1977a)

	primary undisturbed woodland	secondary woodland since 1959	plots newly established from cleared secondary woodland					maize cultivated since 1949
			grazed pasture	sweet potato	ground-nuts	yam	maize	
Total number of species	24	11	11	10	11	12	13	5
Mean abundance of species (n/m2)	2023	1807	1709	702	1391	1510	1683	4073
Relative abundance of Microtermes (%)	20.46	52.29	68.89	77.35	84.9	90.9	83.36	77.29

Wood et al., 1982, sampled the termite community of Southern Guinea riperian forest in Nigeria. *Microtermes* abundance, to a soil depth of 1 m, was 48/m² with a concentration in the top 25 cm of the soil in the wet season and between 25 to 50 cm in the dry season.

Microtermes abundance and distribution were sampled in soil to a depth of 1 m in one wet season and one dry season from 1974 to 1975 in savanna woodland and agricultural ecosystems (Wood and Johnson, 1978). These sites are the uncultivated and cultivated vegetation types discussed in this study and described in Chapter Three and were preliminary results from the Termite Research Project covering the first two years of sampling. The highest abundance of *Microtermes* was shown in the wet season in eight and twenty-four year old cultivated maize sites (4196/m² and 4335/m², respectively) with *Microtermes* concentrated in the top 25 cm of the soil. Also in the wet season, *Microtermes* abundance in groundnuts was 600.5/m² with the highest abundance in the top 25 cm. Wet and dry season abundance of *Microtermes* were, respectively, 507/m² and 178/m² in undisturbed (primary), 1100/m² and 993/m² in disturbed (secondary) woodland, 1216.5/m² and 272/m² in pasture, 235/m² and 371/m² in sweet potato, 516/m² and 480/m² in yam and, 924/m² and 590/m² in short-term maize.

There were seasonal differences in the relative depth distribution of *Microtermes* in 25 cm depth intervals to a soil depth of 1 m. In the newly cleared and cultivated sites *Microtermes* were more abundant in the top 25 cm in the wet season than other soil depth intervals while in the dry season, there was an increase in the relative abundance of. In both woodland sites, *Microtermes* populations in the wet season were lower in the lowest soil depth interval (75 to 100 cm) while the reverse was shown in the dry season.

Black and Wood (1989) describe *Microtermes* spp. abundance and the relative abundance of five *Microtermes* species in soil at 25 cm depth intervals to a depth of 2 m in secondary woodland and (short-term) maize, newly cultivated from cleared woodland. *Microtermes* spp. were concentration in the top 50 cm of soil. *M. subhyalinus* and *M. lepidus* were more abundant in maize than woodland. In secondary woodland, *Microtermes* spp., *M. lepidus* and *M. grassei* were more abundant in the dry compared to the wet season with an increase in abundance below 1 m. In maize, *Microtermes* spp. *M. grassei M. aluco* and *M. subhyalinus* were more abundant in the wet season compared to the dry season with an increase in abundance in the top 50 cm while *M. lepidus* increased in abundance from the first to second year.

These published studies show that *Microtermes* abundance and distribution in soil can differ with season, habitat, cultivation type and species. This study aims to carry out a more intensive examination of the population dynamics of *Microtermes* spp. and individual species in uncultivated and cultivated sites to examine the following hypotheses:

The community structure and abundance of *Microtermes* will be influenced by vegetation type and seasonal climate. Changes in abundance will correspond to changes in soil distribution, notably lower populations in the dry season compared to the wet season with corresponding movements down in the soil. Successional changes in community structure and abundance of species will be identified as woodland is cleared and different crops cultivated. These changes may have predictive value in assessing populations of pest species and therefore potential yield losses.

These hypotheses will be examined through the following procedures;

1. Identification of *Microtermes* species collected from soil cores by the Termite Research Project and matching of identifications with available field records from TRP.

2. Examination of the abundance and distribution of *Microtermes* in uncultivated and cultivated sites with season and years for;

    (i) all vegetation types

    (ii) a randomised block experiment of woodland and plots derived from cleared woodland and cultivated with different crops.

    (iii) a change in crop

4.2 METHODS

4.2.1 Fieldwork by the Termite Research Project

Soil sampling was carried out from 1974 to 1977 during wet and dry seasons in primary woodland, a randomised block experiment, involving uncultivated and cultivated plots, and in long-term maize. Each vegetation type is described in full in Chapter Three. Quantitative sampling for termites was accomplished by stratified random sampling using a Jarret soil auger (7.2 cm diameter) to a depth of 1 m with 48 sample units taken per plot for each sampling occasion. Each 1 m core was divided into 4 successive 25 cm depths permitting each species sampled to be assigned to one of the four available depths. The number of sampling occasions for each vegetation type is given in Table 4.2.1. The extraction of termites was carried out using careful hand-sorting with random checks on efficiency using the Salt and Hollick soil washing apparatus and flotation in salt solution. Hand-sorting was estimated to be 85% efficient at collecting *Microtermes* (Wood et al. 1977b). A correction factor adjusted the number of termites to 100% values.

4.2.2 Identification of *Microtermes* species and analysis of data

Identification of species was carried out at NRI, U.K., using an unpublished key for West African and Sudanese *Microtermes* (Appendix one). Abundance of *Microtermes* spp. and individual species were recorded for available plots (see Table 4.2.1) in wet and dry seasons from year one to year four as total soil abundance to 1 m and at four 25 cm depth intervals to 1 m from each plot. Mean abundance ($n/m^2 \pm 1$ standard error, SE) for *Microtermes* spp. and individual species was calculated for each vegetation type using the above.

The following measures of diversity were calculated to examine the community structure of *Microtermes* in each vegetation type at soil depths 0 to 1 m and 0 to 25 cm for each wet and dry season.

(i) Species richness: calculated as a measure of the number of species in a defined unit (Magurran, 1988); therefore mean species richness is the mean number of species recorded per vegetation type.

(ii) Information Theory Indices: which take into account the proportional abundance of species.

Table 4.2.1 : Number of sampling occasions for each vegetation type in wet and dry seasons from 1974 to 1977
(48 sampling units per plot; diameter 7.2 cm to a soil depth of 1 metre).

Year and Season		1974		1975		1976		1977
Plot	Vegetation 1974-76*	wet	dry	wet	dry	wet	dry	wet
13+14	primary woodland	2	4	-	-	2	2	-
1+12	secondary woodland	4	2	2	2	2	-	-
4+5	pasture	4	2	2	2	-	-	-
8+10	sweet potato	4	2	4	2	4	2	2
2+11	groundnuts	6	-	4	-	2	-	2
3+6	yam	6	4	6	4	4	4	2
7+9	short-term maize	6	2	6	2	6	-	2
19+20	ranch maize	1	-	2	-	2	-	-
21+22	farm maize	1	-	2	-	-	-	-

* change in crop, see text.

(a) Shannon-Wiener index (H'): reaches a maximum value when all species are present in equal proportions, often called the Shannon Index of Diversity. When comparing even communities then the one with largest number of species will have greater value of H'. H' can be calculated using any log series however there is a trend to standardise on natural logs ($\log_e$) which is essential when calculating H' from a series equation. H' values tend to fall between 1.5 and 3.5. Calculated from mean species richness and mean abundance per vegetation type (Pielou, 1976; Magurran, 1988); formula in Appendix Two.

(b) Evenness index (J'): calculated from mean species richness and mean abundance per vegetation type. Evenness index provides as additional measure of the homogeneity of species abundance and ranges from 0 to 1.0, with 1.0 representing equal abundance of all species present (Pielou, 1974; Magurran, 1988); formula in Appendix Two.

The following statistics were calculated to determine differences in *Microtermes* abundance and distribution in soil amongst the vegetation types. Abundance data were transformed using $\log_{10}$ (n+1) before statistical analysis (Southwood, 1978; Zar, 1984). Analysis of variance (one and two way) was carried out on *Microtermes* abundance to a total soil depth of 1 m and at 25 cm intervals to 1 m for all seasons and each season from available plots. Tukey's multiple range test was executed on significant interactions to permit pair-wise comparisons of means where relevant (Zar, 1984). Statistical analysis was carried out with the aid of the computer software package Statsgraphics version 4.0 (STSC, 1989).

4.3 RESULTS

4.3.1. Community structure of *Microtermes*

In this section, results are presented for each measure of diversity as 1 m and 25 cm indicating indices calculated on *Microtermes* species occurrence and abundance in soil from 0 to 1 m and 0 to 25 cm respectively. Mean species richness of *Microtermes* in soil to depths of 1 m and 25 cm are shown in Figure 4.3.1. Shannon-Wiener diversity (H') of *Microtermes* in soil to depths of 1 m and 25 cm are shown in Figure 4.3.2. Evenness index (J') of *Microtermes* in soil to depths of 1 m and 25 cm are shown in Figure 4.3.3. Results for the changes in crop types in the fourth wet season are given in Section 4.3.5. The term *diversity*, used throughout the Results section, refers to the Shannon-Wiener index of diversity.

There were no seasonal differences in mean species richness of *Microtermes* for either 1 m or 25 cm amongst the vegetation types. In primary woodland, mean species richness was close to two species for both depths in all but the third wet season when species richness increased to 3 species for 25 cm and close to 5 for 1 m. Mean species richness in secondary woodland was consistently close to three species for 1 m and 2 species for 25 cm, except in the second wet season where there was a decrease in species richness from the previous season. Mean species richness for 1 m in the dry seasons was greater in secondary woodland (3 species) than primary woodland (2 species) but similar between the two woodland sites for 25 cm (2 species).

In all newly cleared and cultivated sites, species richness in the first wet season was similar to that in secondary woodland for both depths (between 2 and 3 species). In the first dry season, species richness for 1 m was similar amongst all newly cleared and cultivated sites (close to 3 species) and greater than for 25 cm. Species richness for 25 cm in this season was similar between sweet potato and short-term maize (1 species) and between pasture and yam (2 species). In all these sites, species richness in the first dry season was less than in secondary woodland for both depths.

In pasture, there was a small increase in species richness for 1 m from the first wet to dry season and a more pronounced increase for both depths from the first dry season to the second wet season when species richness (3 to 4 species) was greater than in secondary woodland. From the second wet to dry season species richness decreased for both depths; species richness for 1 m equivalent to the previous dry season (2 to 3 species) and 25 cm intermediate between the previous wet and dry seasons (close to 2 species).

Figure 4.3.1 : Mean species richness of *Microtermes* for wet and dry seasons from 1974 to 1977 in uncultivated and cultivated sites at Mokwa, Nigeria -
(i) to a soil depth of 0 to 1 m,
(ii) to a soil depth of 0 to 25 cm.

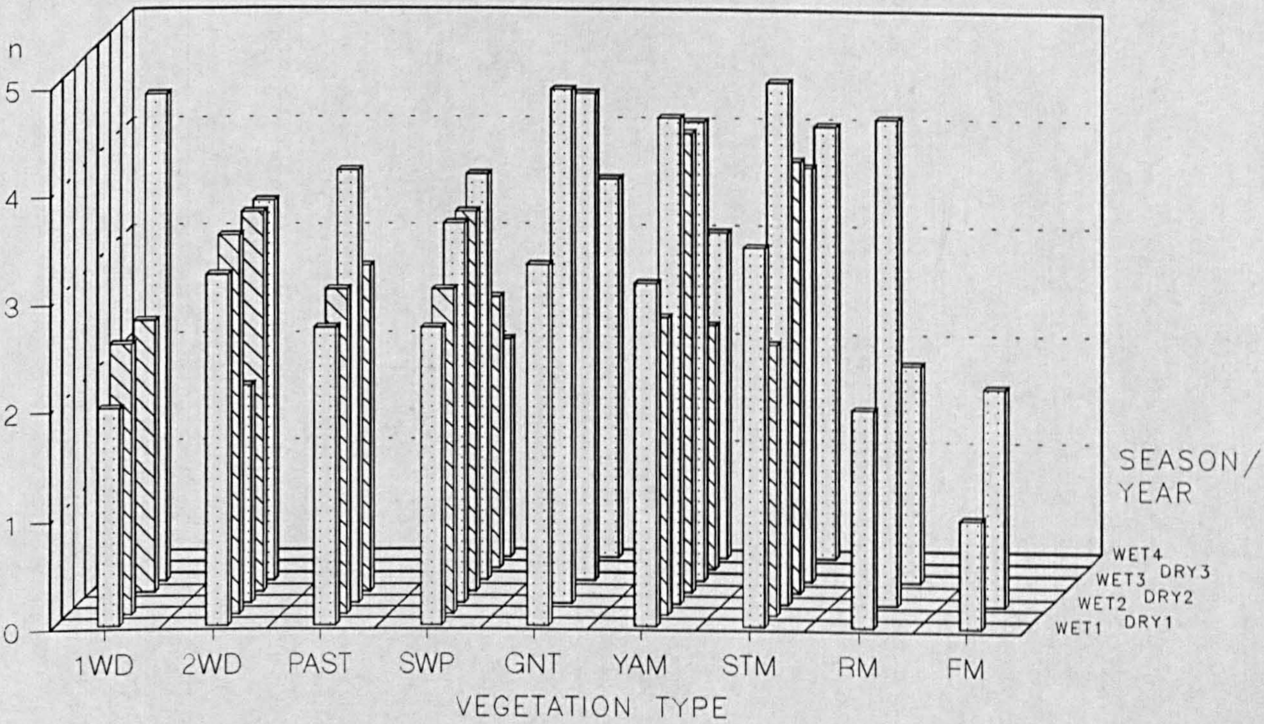
Key to vegetation types

1WD = primary woodland
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

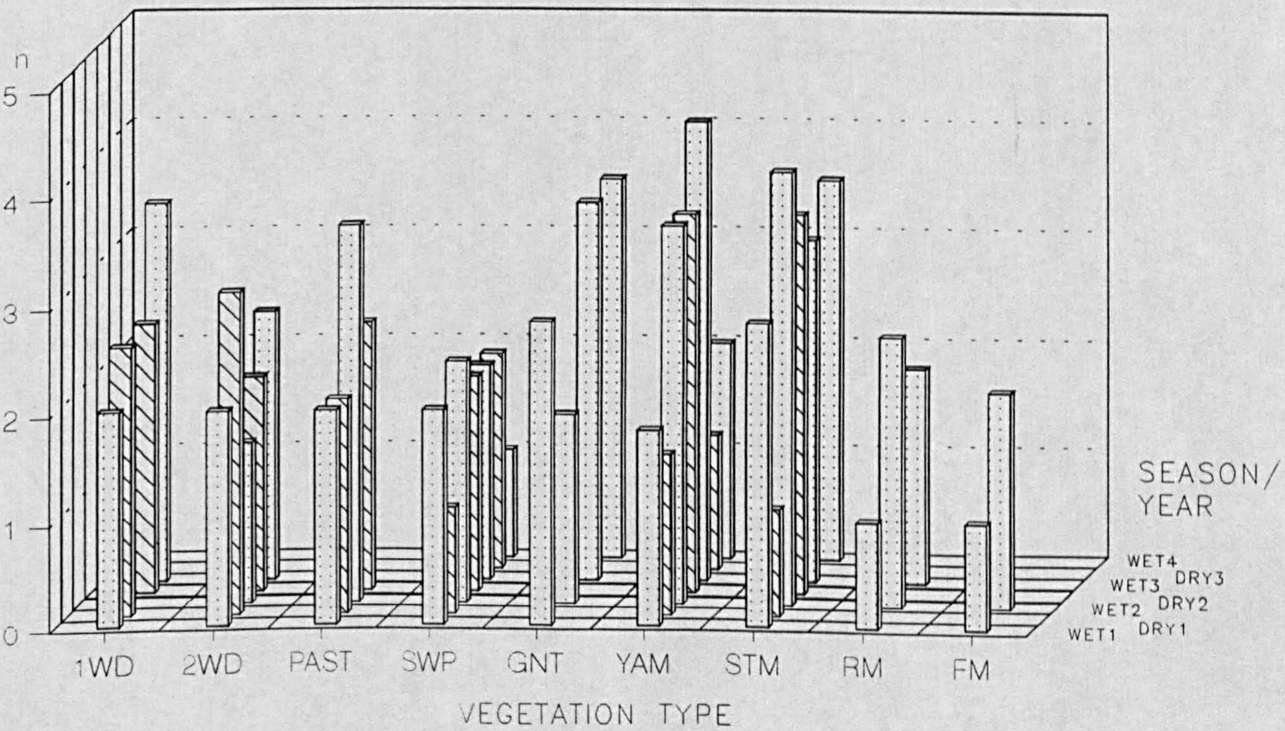
Key to seasons/years

W1 = wet season, 1974
D1 = dry season, 1974 to 1975
W2 = wet season, 1975
D2 = dry season, 1975 to 1976
W3 = wet season, 1976
D3 = dry season, 1976 to 1977
W4 = wet season, 1977; change of crop from 1976

(i) species richness
of Microtermes in soil to a depth of 1m.



(ii) species richness
of Microtermes in soil to a depth of 25 cm



In sweet potato, species richness for 1 m increased in each season from the first to third wet season to equal species richness for 1 m in pasture in the second wet season (3 to 4 species). Species richness decreased from the third wet to third dry season and was equivalent to species richness in the first year (2 species). For 25 cm, species richness decreased from the first wet to dry season (from 2 to 1 species) and increased from the first dry to the second wet season to become equal to species richness in the first season. There were no further changes.

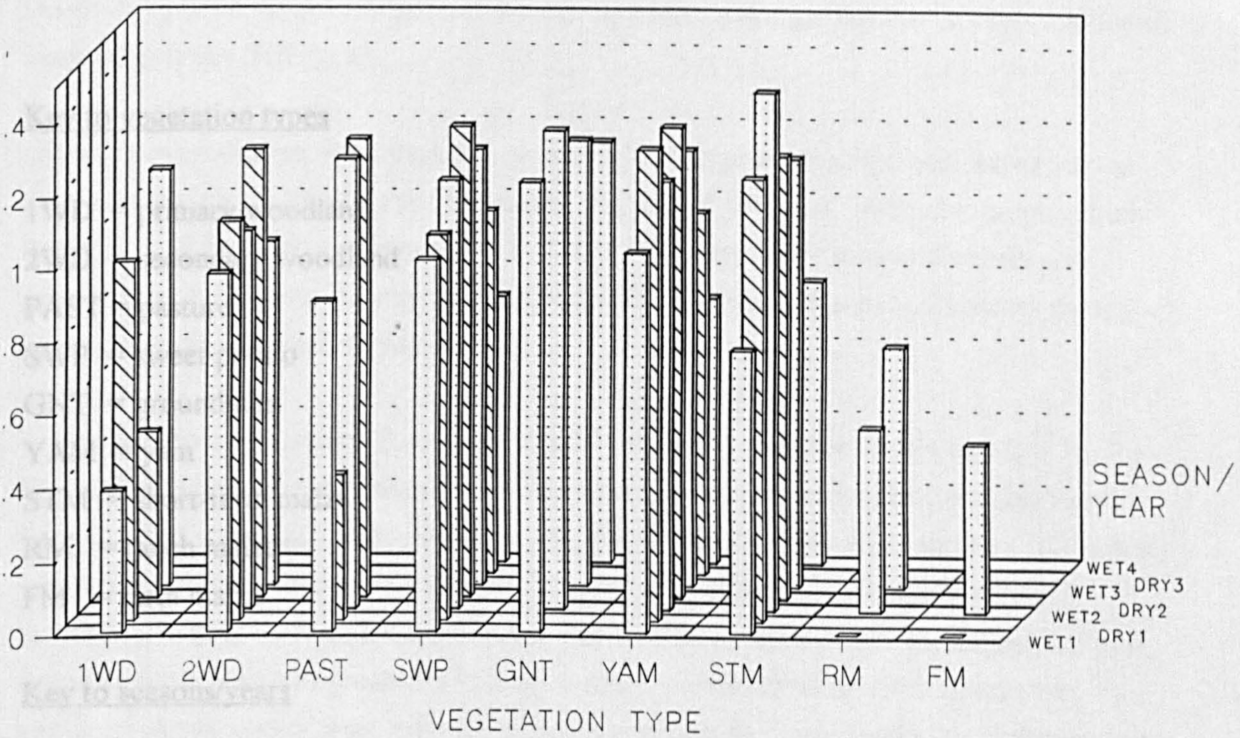
In groundnuts, where there were wet season samples only, species richness for 1 m increased from the first to second wet season which was similar to the third wet season (from 3 to close to 5 species). For 25 cm, species richness decreased from the first to second wet season (from 3 to 2 species) and increased from the second to third four wet season to become equivalent to species richness for 1 m (3 species).

In yam, species richness for 1 m in the wet season followed the same trend in described for 1 m in groundnuts (to four species) while there was an increase in species richness from the first dry to second wet season with no change in the following, second, dry season species richness (3 to 4 species). For 25 cm, species richness increased progressively from the first to third wet season (from close to 2 species to 4 species). For both depths, there was a decrease in species richness from the third wet to third dry season with species richness equivalent to that in the first dry season; 2 species for 1 m and 1 species for 25 cm.

In short-term maize, changes in species richness from the first wet to second dry season were similar to those in yam with an increase in both wet and dry seasons for both depths. From the second to third wet season, there was a decline in species richness, though there were still more species present than in the first wet season; 3 species for 25 cm and 4 species for 1 m.

In both long-term maize sites (ranch and farm maize), mean species richness at both depths was less than two species for both 1 m and 25 cm, excepting the second wet season in ranch maize where there were four species.

(i) Diversity (H')
of Microtermes in soil to a depth of 1m.



(ii) Diversity (H')
of Microtermes in soil to a depth of 25 cm

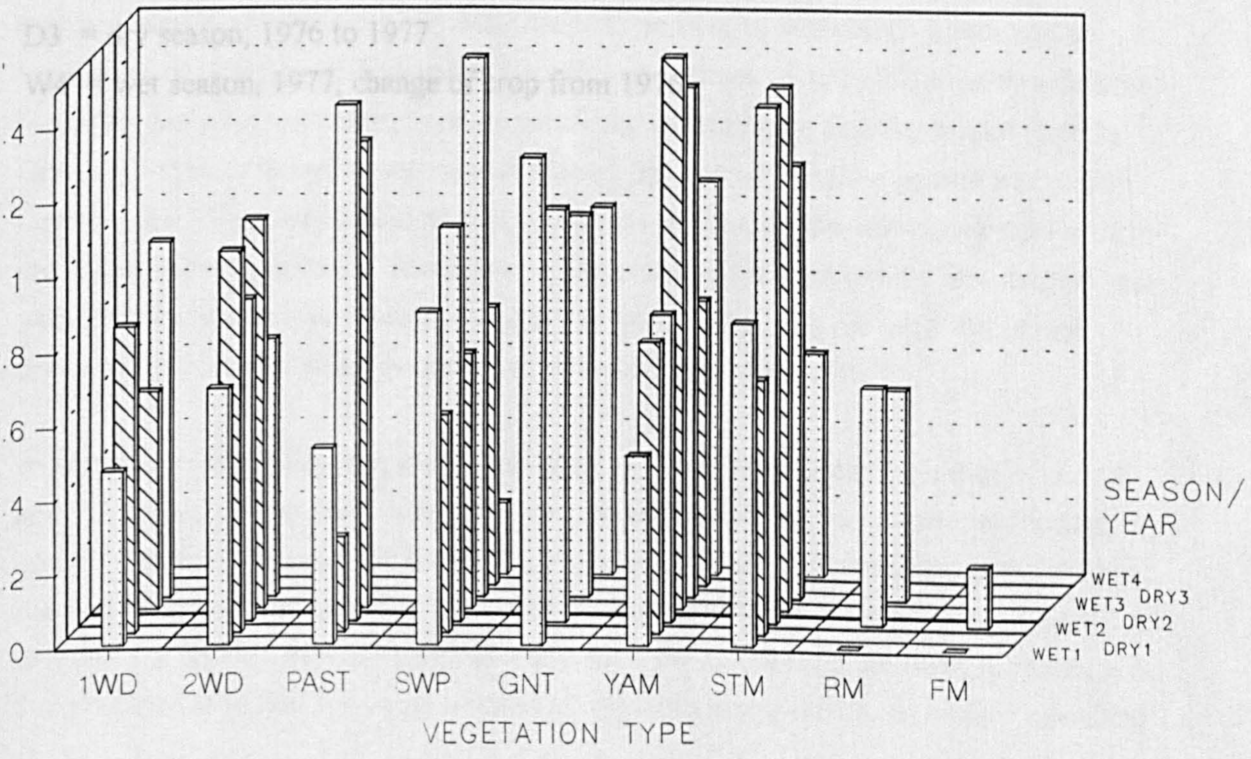


Figure 4.3.2 : Shannon-Wiener diversity of *Microtermes* for wet and dry seasons from 1974 to 1977 in uncultivated and cultivated sites at Mokwa, Nigeria -
(a) to a soil depth of 0 to 1 m, and
(b) to a soil depth of 0 to 25 cm.

Key to vegetation types

1WD = primary woodland
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

Key to seasons/years

W1 = wet season, 1974
D1 = dry season, 1974 to 1975
W2 = wet season, 1975
D2 = dry season, 1975 to 1976
W3 = wet season, 1976
D3 = dry season, 1976 to 1977
W4 = wet season, 1977; change of crop from 1976

Diversity in primary woodland was similar between 1 m and 25 cm, ranging from 0.4 to 1, with similar changes with season and year; diversity increased from the first wet to dry season (0.8 - 1.0), decreased to the second dry season to equal diversity in the first dry season and increased to the third wet season to equal diversity in the second dry season. Diversity in the first wet and second dry seasons were amongst the lowest recorded for all vegetation types (0.4 - 0.6).

Diversity in secondary woodland was similar to that in primary woodland, except in the third wet season. Diversity was consistently higher for 1 m than for 25 cm; ranging from 0.944 to 1.39 for 1 m and from 0.694 to 1.253 for 25 cm. Dry season diversity was greater than wet season diversity throughout the study with seasonal differences more pronounced for 25 cm diversity.

In pasture, diversity ranged from 0.26 to 1.39 for 25 cm and from 0.394 to 1.253 for 1 m. For both depths, diversity decreased from wet to dry season in the first year, increased from the first to second year where wet and dry season diversity were similar. In the first year diversity was greater for 1 m than 25 cm; 1 m diversity was similar to that in secondary woodland and 25 cm similar to that in primary woodland. By the second year, diversity for 25 cm was greater than in secondary woodland while for 1 m only wet season diversity was greater than secondary woodland; for both depths > 1.2 compared to < 1.0.

In sweet potato, diversity in the first three years ranged from 0.59 to 1.453 for 25 cm and 0.992 to 1.289 for 1 m. There were seasonal differences throughout, being most pronounced for 25 cm than 1 m, with dry season less than wet season diversity. In the first wet season, diversity for 1 m was similar to secondary woodland. There was an increase in diversity in each season to the third wet season (1.192) followed by a decrease to the third dry season where diversity was equal to that in the first dry season (0.992). Diversity in the third wet season was similar to that in pasture in the second wet season. Diversity for 25 cm was similar to 1 m in the first wet season but was higher than for 25 cm in secondary woodland. There was an increase in diversity from the first to third year with the increase was most pronounced in the wet seasons. By the third wet season, diversity for 25 cm in sweet potato was the highest recorded (1.453).

In groundnuts in the first wet season, diversity was similar between both depths (1.312 and 1.232) and greater than in secondary woodland in the first wet season, particularly for 25 cm. For 1 m, there was an increase and for 25 cm, a small decrease in diversity from the first to second wet season (1.11). For the first three years, diversity ranged from 1.03 to 1.312 for 25 cm and from 1.219 to 1.232 for 1 m. In the third wet season, diversity for 1 m was similar to that for sweet potato (1.219) and greater than in secondary woodland while for 25 cm diversity was less (1.03) than in sweet potato and similar to secondary woodland in the second dry season.

In yam, diversity ranged from 0.51 to 1.49 for 25 cm and 0.992 to 1.29 for 1 m. In the first wet season, diversity for 1 m was similar to secondary woodland and sweet potato while diversity for 25 cm was lower than for these two vegetation types and similar to pasture. Diversity for both depths increased to the third wet season where diversity was similar to sweet potato. As in sweet potato, there was a decrease in diversity from the third wet to dry season where diversity was similar to the first dry season.

In short-term maize, diversity ranged from 0.68 to 1.41 for 25 cm and 0.773 to 1.42 for 1 m. Diversity was similar between the depths in the first wet season. For 1 m, this was less than in secondary woodland while for 25 cm this was greater than in secondary woodland and similar to sweet potato. For both depths, diversity increased from the first wet to third wet season where diversity for 1 m was similar to and, for 25 cm, slightly lower than that in yam and sweet potato. For 1 m, diversity in the first dry was greater than in the first wet season and similar to that in the second wet season. For 25 cm, diversity in the first dry season was less than in the first wet season.

In both long-term maize sites (ranch and farm maize), diversity at both depths were amongst the lowest recorded, ranging from 0 to 0.658 in ranch maize and 0 to 0.456 in farm maize.

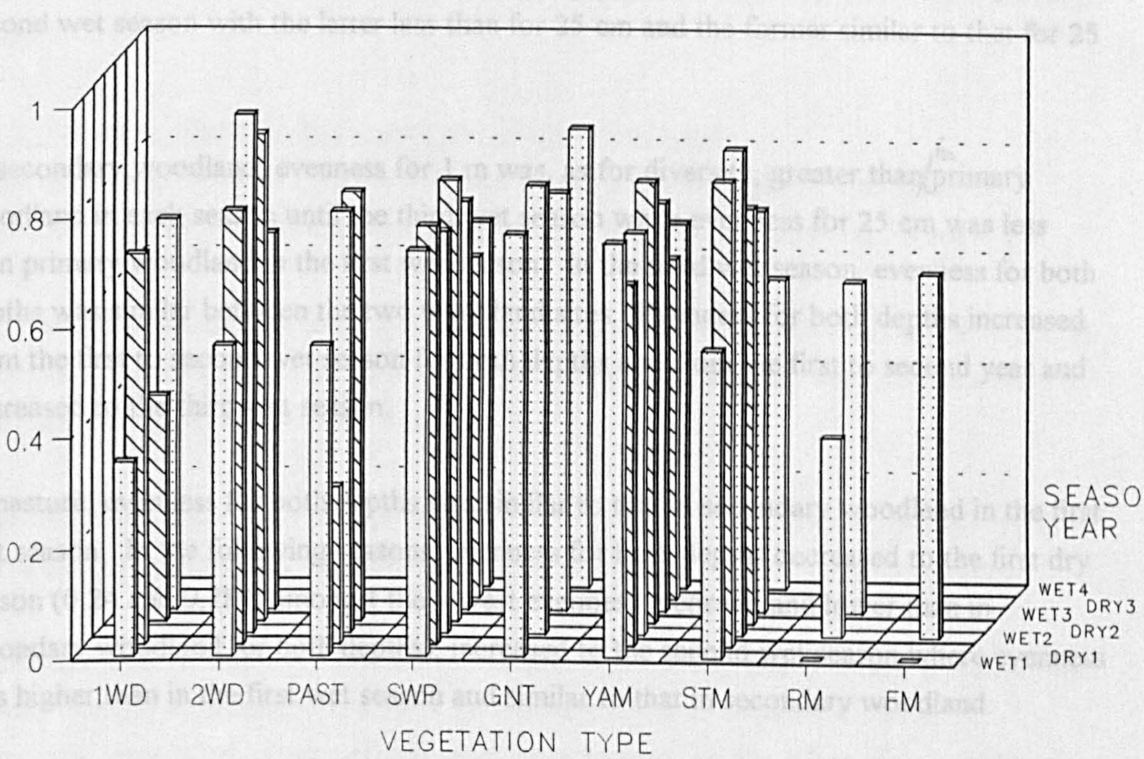
Figure 4.3.3 : Evenness index (J') of *Microtermes* for wet and dry seasons from 1974 to 1977 in uncultivated and cultivated sites at Mokwa, Nigeria -
(a) to a soil depth of 0 to 1 m, and
(b) to a soil depth of 0 to 25 cm.

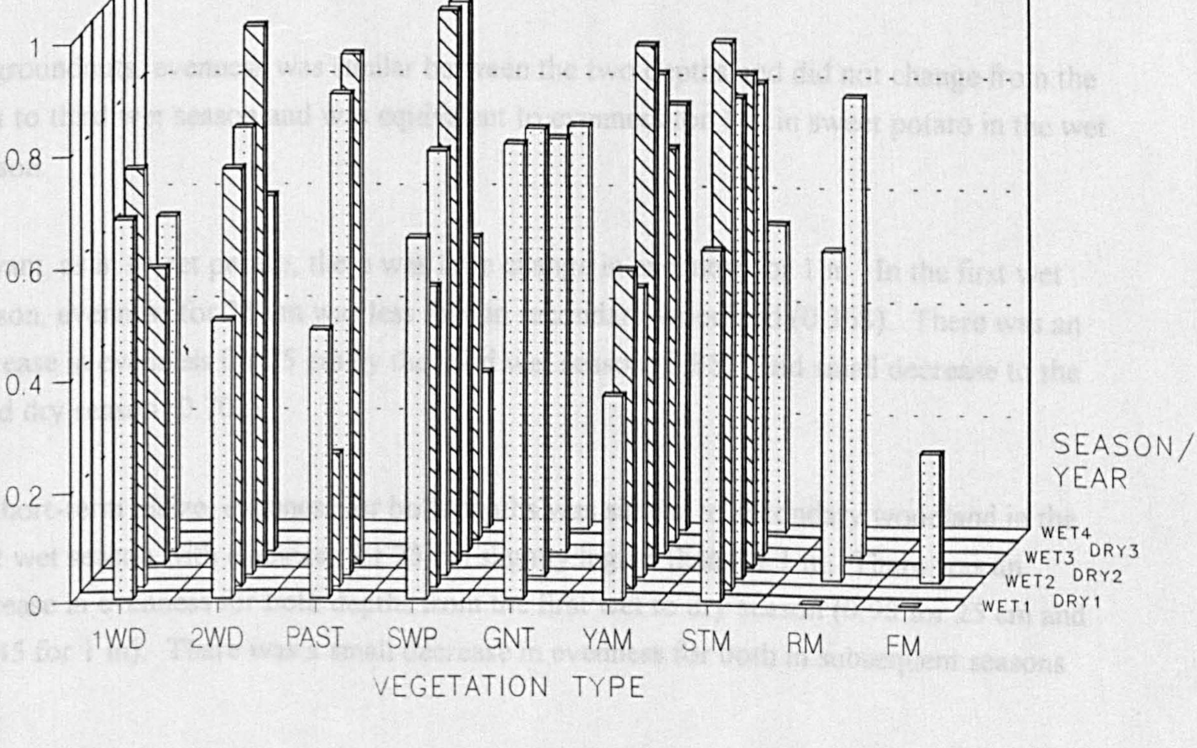
Key to vegetation types

1WD = primary woodland
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

Key to seasons/years

W1 = wet season, 1974
D1 = dry season, 1974 to 1975
W2 = wet season, 1975
D2 = dry season, 1975 to 1976
W3 = wet season, 1976
D3 = dry season, 1976 to 1977
W4 = wet season, 1977; change of crop from 1976


(i) Evenness (J') of Microtermes in soil to a depth of 1 m


(ii) Evenness (J') of Microtermes in soil to a depth of 25 cm

Evenness exhibited similar changes to diversity with season and years for 1 m in primary woodland, pasture and short-term maize and for 25 cm in pasture and yam. In primary woodland, evenness for 25 cm was similar amongst all wet seasons. Evenness for 1 m was similar between the first wet and second dry season and between the third dry and second wet season with the latter less than for 25 cm and the former similar to that for 25 cm.

In secondary woodland, evenness for 1 m was, as for diversity, greater than in primary woodland in each season until the third wet season while evenness for 25 cm was less than primary woodland in the first wet season. In the third wet season, evenness for both depths was similar between the two woodland sites. Evenness for both depths increased from the first to second wet season for both depths and from the first to second year and decreased to the third wet season.

In pasture, evenness for both depths was similar to that in secondary woodland in the first wet season. In the following seasons, evenness for both depths decreased to the first dry season (0.24 and 0.284; amongst the lowest evenness recorded and lower than in secondary woodland for both depths), increased to the second wet season where evenness was higher than in the first wet season and similar to that in secondary woodland.

In sweet potato in the first wet season, evenness for both depths was higher than in secondary woodland and pasture (0.734 for 1 m and 0.648 for 25 cm). Evenness for 1 m did not alter with season or year while evenness for 25 cm increased from year one to three to equal 0.983 in the third wet season; the second highest recorded evenness. There was a decrease in evenness for 25 cm to the third dry season (0.541) to a similar level in the first dry season.

In groundnuts, evenness was similar between the two depths and did not change from the first to third wet season and was equivalent to evenness for 1 m in sweet potato in the wet season.

In yam, as in sweet potato, there was little change in evenness for 1 m. In the first wet season, evenness for 25 cm was less than in secondary woodland (0.368). There was an increase in evenness for 25 cm by the third wet season (0.857) and small decrease to the third dry season (0.702).

In short-term maize, evenness for both depths was similar to secondary woodland in the first wet season with evenness for 25 cm slightly higher than for 1 m. There was an increase in evenness for both depths from the first wet to dry season (0.98 for 25 cm and 0.845 for 1 m). There was a small decrease in evenness for both in subsequent seasons.

In long-term maize sites, evenness was relatively higher than diversity compared to other vegetation types and ranged from 0 to 0.82 in ranch maize and from 0 to 0.658 in farm maize. Evenness was higher in the second wet compared to the first wet season in ranch maize.

4.3.2 Seasonal effects on abundance and distribution in soil

Mean abundance (n/m^2 ± 1 SE) of *Microtermes* in soil to a depth of 1 m for each vegetation type in wet and dry seasons from 1974 to 1977 are shown in Figure 4.3.4.

Mean seasonal abundance (n/m^2 ± 1 SE) and distribution of *Microtermes* in soil at 25 cm intervals to a depth of 1 m for each vegetation type in wet and dry seasons from 1974 to 1977 are displayed in Figure 4.3.5 to 4.3.13.

In each figure, there was a change in crop from 1976 to 1977 for the following crops; sweet potato, groundnuts, yam and short-term maize.

Significant interactions from analysis of variance and corresponding Tukey comparisons of *Microtermes* abundance from 1974 to 1976 are given in Tables 4.3.1 to 4.3.7 Significant interactions from analysis of variance to examine the effect of crop changes on wet season *Microtermes* abundance from 1976 to 1977 are given in Table 4.3.8 Sections 4.3.2 - 4.3.4 deal with the results from 1974 to 1976 while section 4.3.5 deals with the change in crops from 1976 to 1977.

Figure 4.3.4 : Mean total abundance (n/m² ± 1 SE) of *Microtermes* spp. and individual species to a soil depth of 1 metre for wet and dry seasons in uncultivated and cultivated sites from 1974 to 1977 at Mokwa in the Southern Guinea savanna vegetation zone of Nigeria.

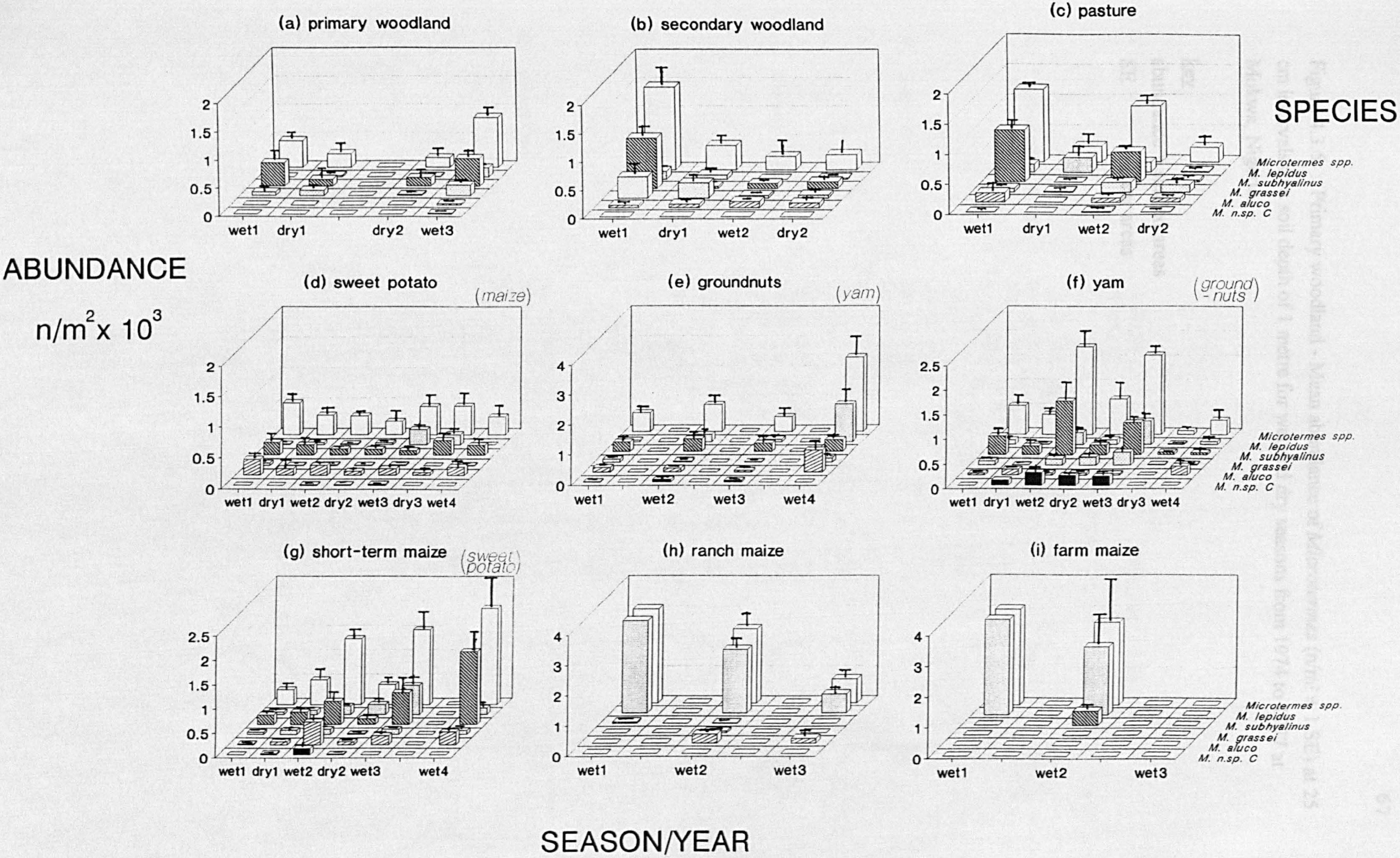

ABUNDANCE
n/m² x 10³
SPECIES
SEASON/YEAR
(a) primary woodland
wet1 dry1 dry2 wet3
(b) secondary woodland
wet1 dry1 wet2 dry2
(c) pasture
wet1 dry1 wet2 dry2
(d) sweet potato
(maize)
wet1 dry1 wet2 dry2 wet3 dry3 wet4
(e) groundnuts
(yam)
wet1 wet2 wet3 wet4
(f) yam
(ground-nuts)
wet1 dry1 wet2 dry2 wet3 dry3 wet4
(g) short-term maize
(sweet potato)
wet1 dry1 wet2 dry2 wet3 wet4
(h) ranch maize
wet1 wet2 wet3
(i) farm maize
wet1 wet2 wet3
Microtermes spp.
M. lepidus
M. subhyalinus
M. grassei
M. aluco
M. n.sp. C
0 0.5 1 1.5 2 2.5
0 1 2 3 4

Figure 4.3.5 : Primary woodland - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

Figure 4.3.6 : Secondary woodland - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

key

abundance = shaded areas

SE = clear areas

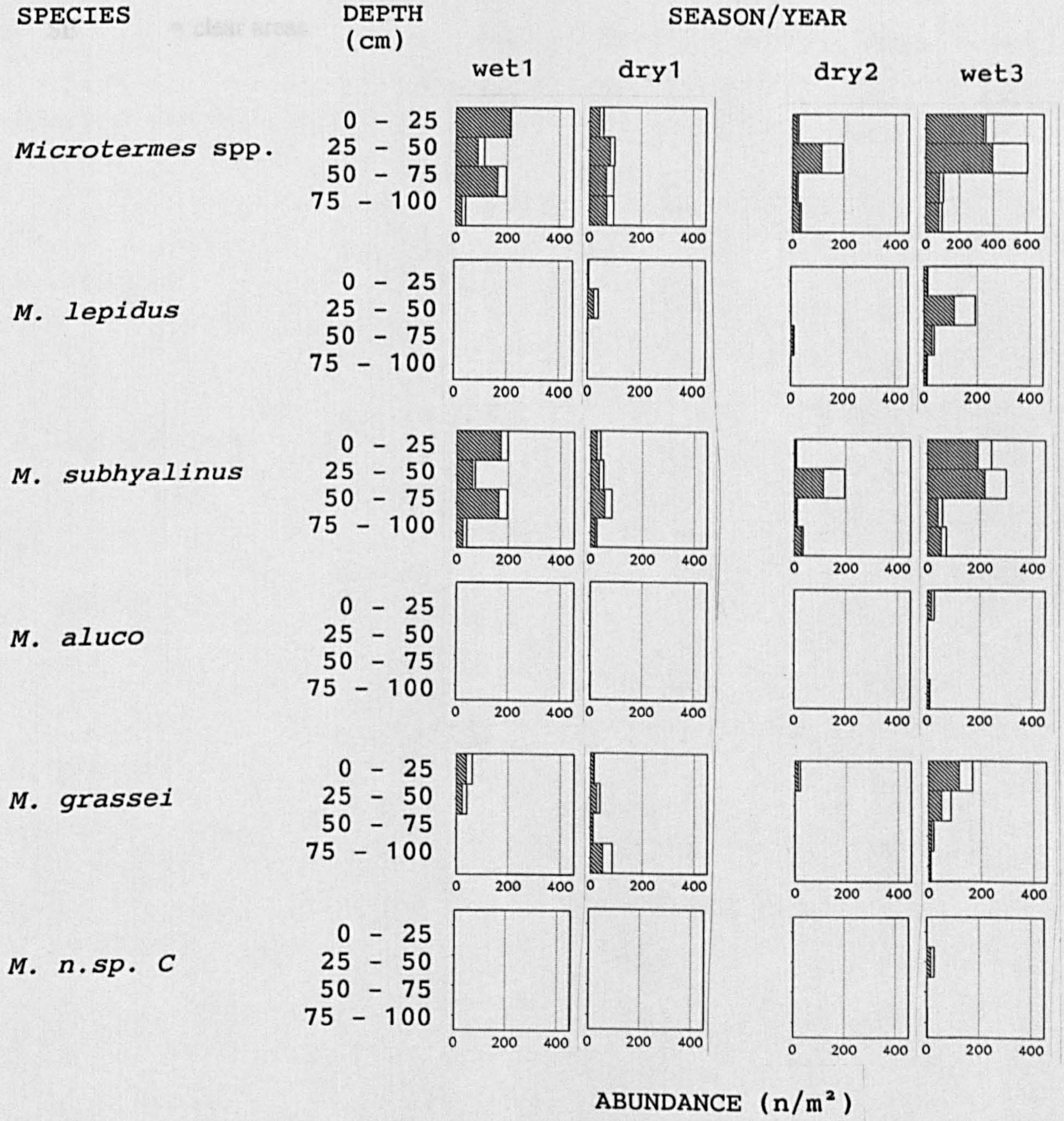


Figure 4.3.6 : Secondary woodland - Mean abundance of *Microtermes* (n/m^2 ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

Figure 4.1.7 Pasture - Mean abundance of *Microtermes* ($n/m^2 \pm 1$ SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

key:

mean = shaded areas

SE = clear areas

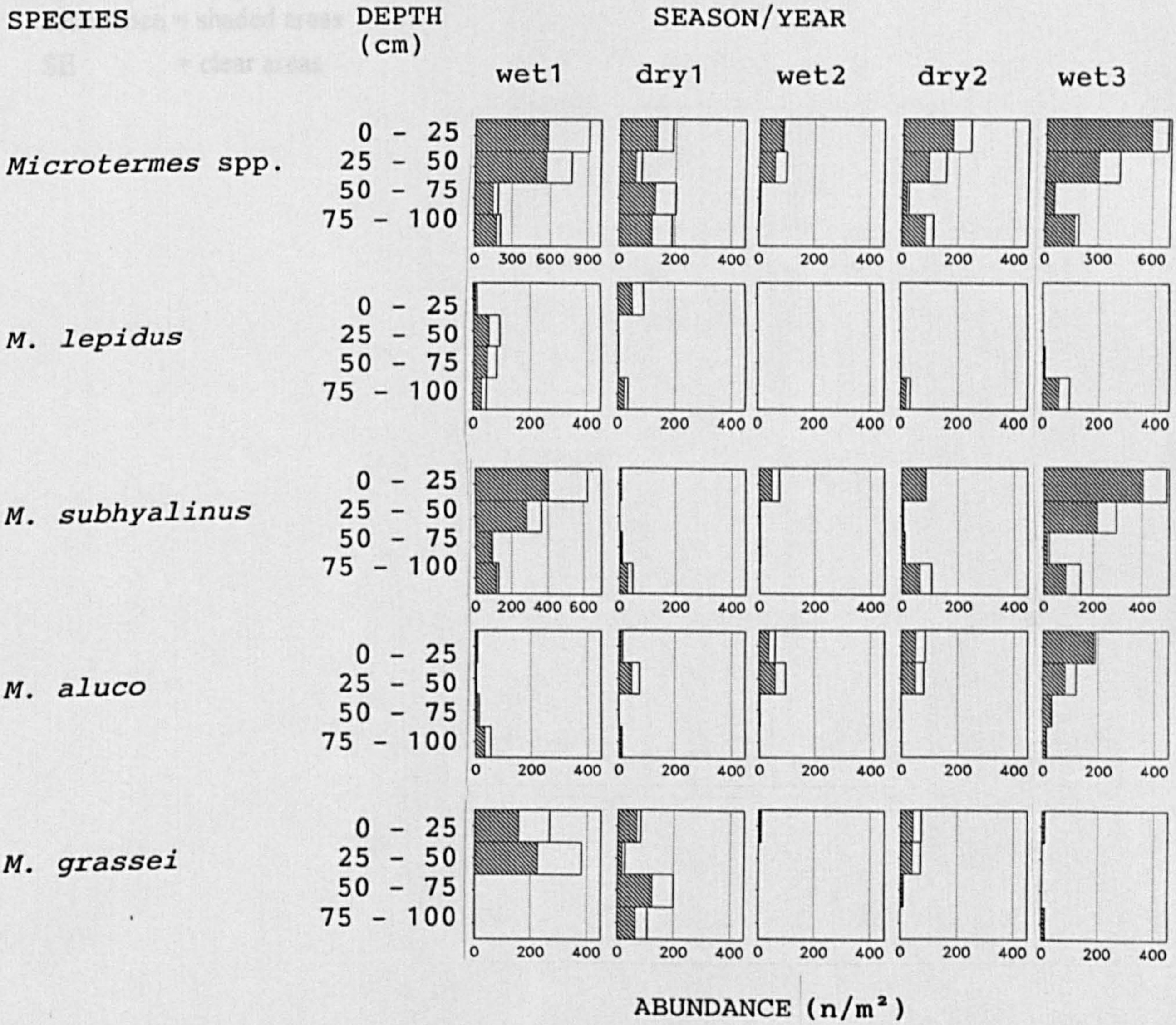


Figure 4.3.7 : Pasture - Mean abundance of *Microtermes* (n/m^2 ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

key
abundance = shaded areas
SE = clear areas

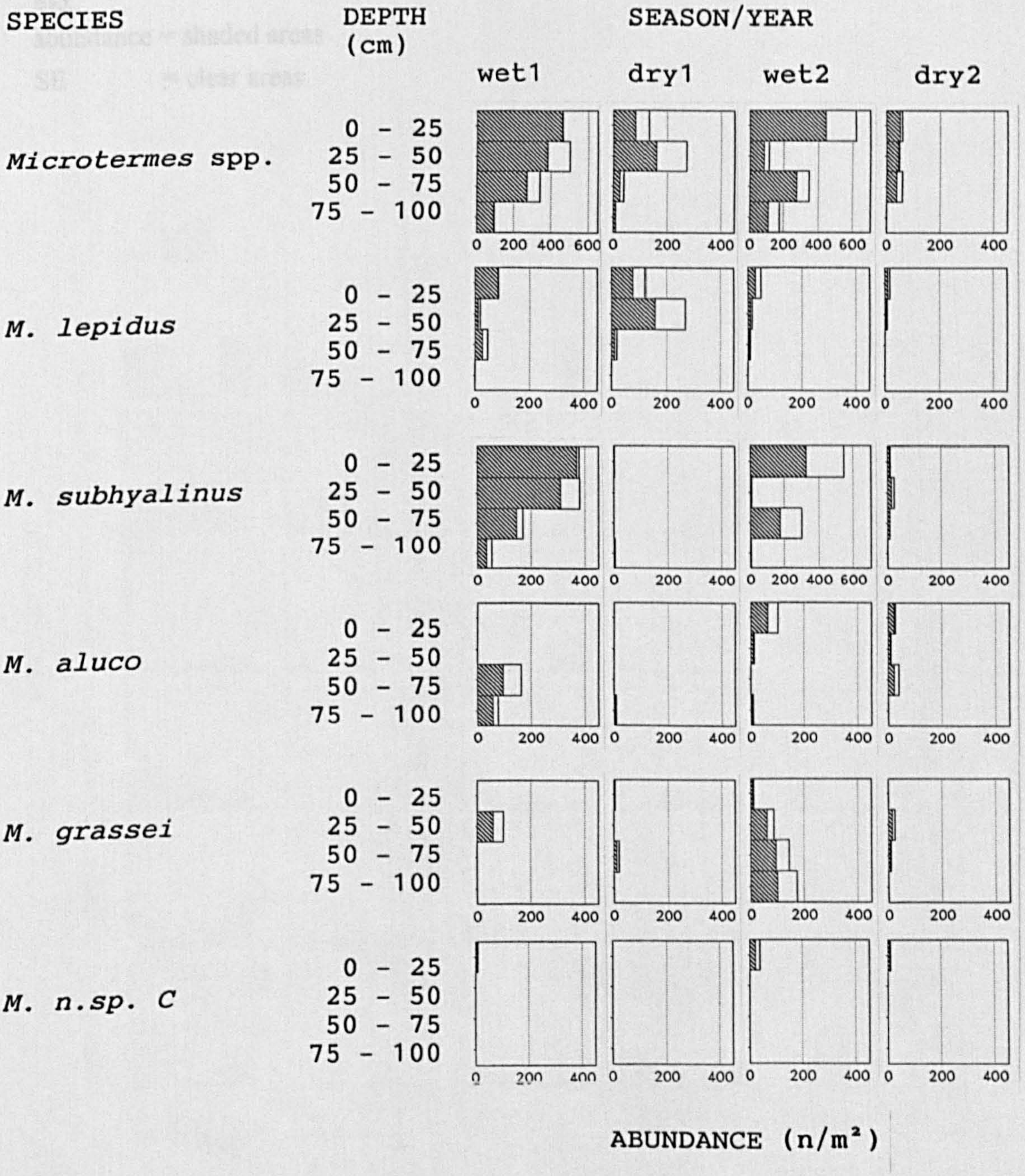

SPECIES
DEPTH (cm)
SEASON/YEAR
wet1
dry1
wet2
dry2
Microtermes spp.
M. lepidus
M. subhyalinus
M. aluco
M. grassei
M. n.sp. C
0 - 25
25 - 50
50 - 75
75 - 100
0
200
400
600
ABUNDANCE (n/m²)

Figure 4.3.8 : Sweet potato (crop change to maize in wet season 4) - Mean abundance of *Microtermes* (n/m^2 ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

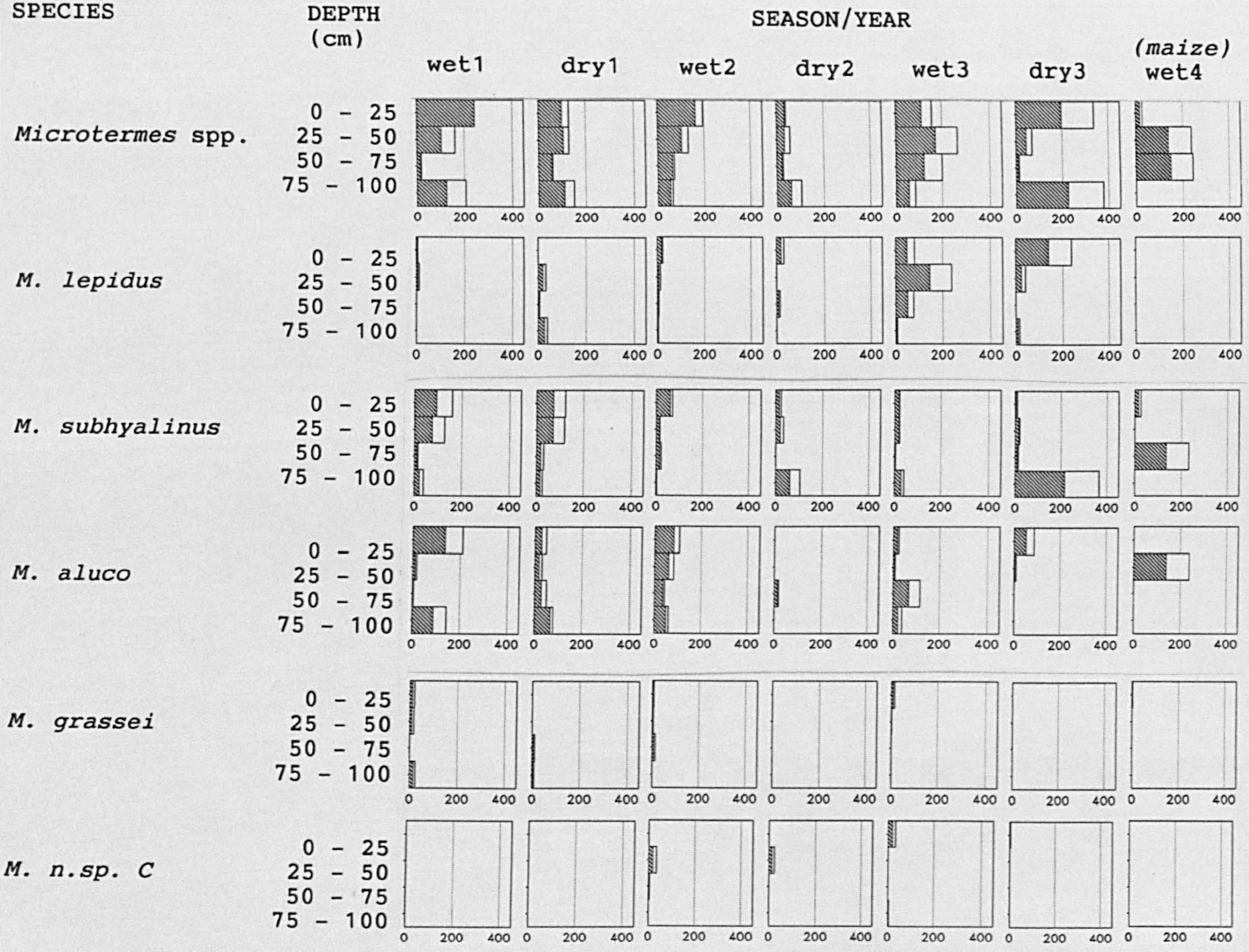


Figure 4.3.9 Groundnuts (crop change to yam in wet season 4) - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

Key
abundance = shaded areas
SE = clear areas

Figure 4.3.9 : Groundnuts (crop change to yam in wet season 4) - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

Figure 4.3.10 Yam (crop change to groundnuts in wet season 4) - Mean abundance of *Microtermes* ($n/m^2 \pm 1$ SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

Key

abundance = shaded areas
SE = clear areas

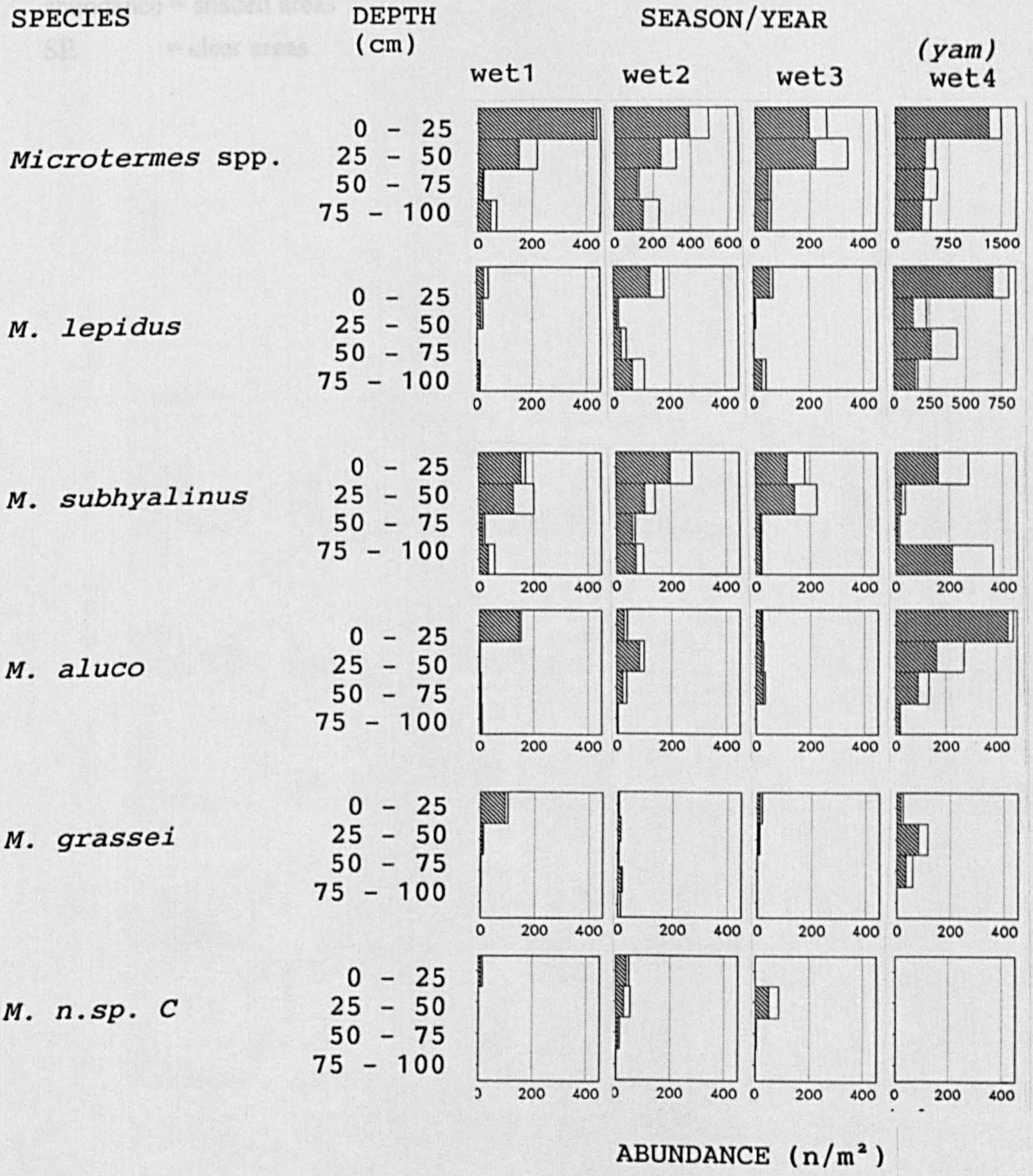


Figure 4.3.10 : Yam (crop change to groundnuts in wet season 4) - Mean abundance of *Microtermes* (n/m^2 ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

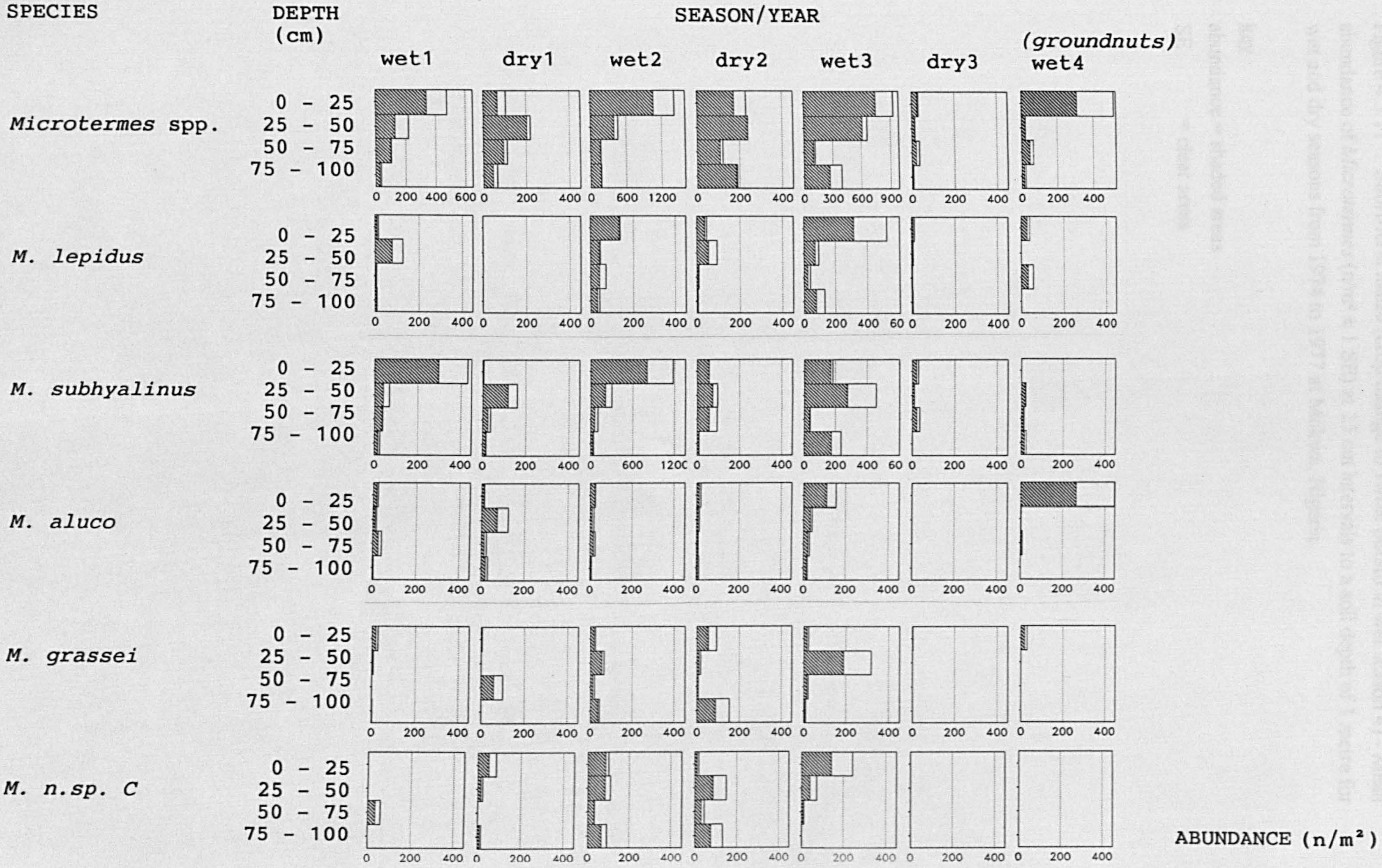

SPECIES
DEPTH (cm)
SEASON/YEAR
wet1
dry1
wet2
dry2
wet3
dry3
(groundnuts)
wet4
Microtermes spp.
M. lepidus
M. subhyalinus
M. aluco
M. grassei
M. n.sp. C
0 - 25
25 - 50
50 - 75
75 - 100
0 200 400 600
0 200 400
0 600 1200
0 300 600 900
0 200 400 60
ABUNDANCE (n/m²)

Figure 4.3.11 : Short-term maize (crop change to sweet potato in wet season 4) - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

Figure 4.3.12 Ranch maize - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

key
abundance = shaded areas
SE = clear areas

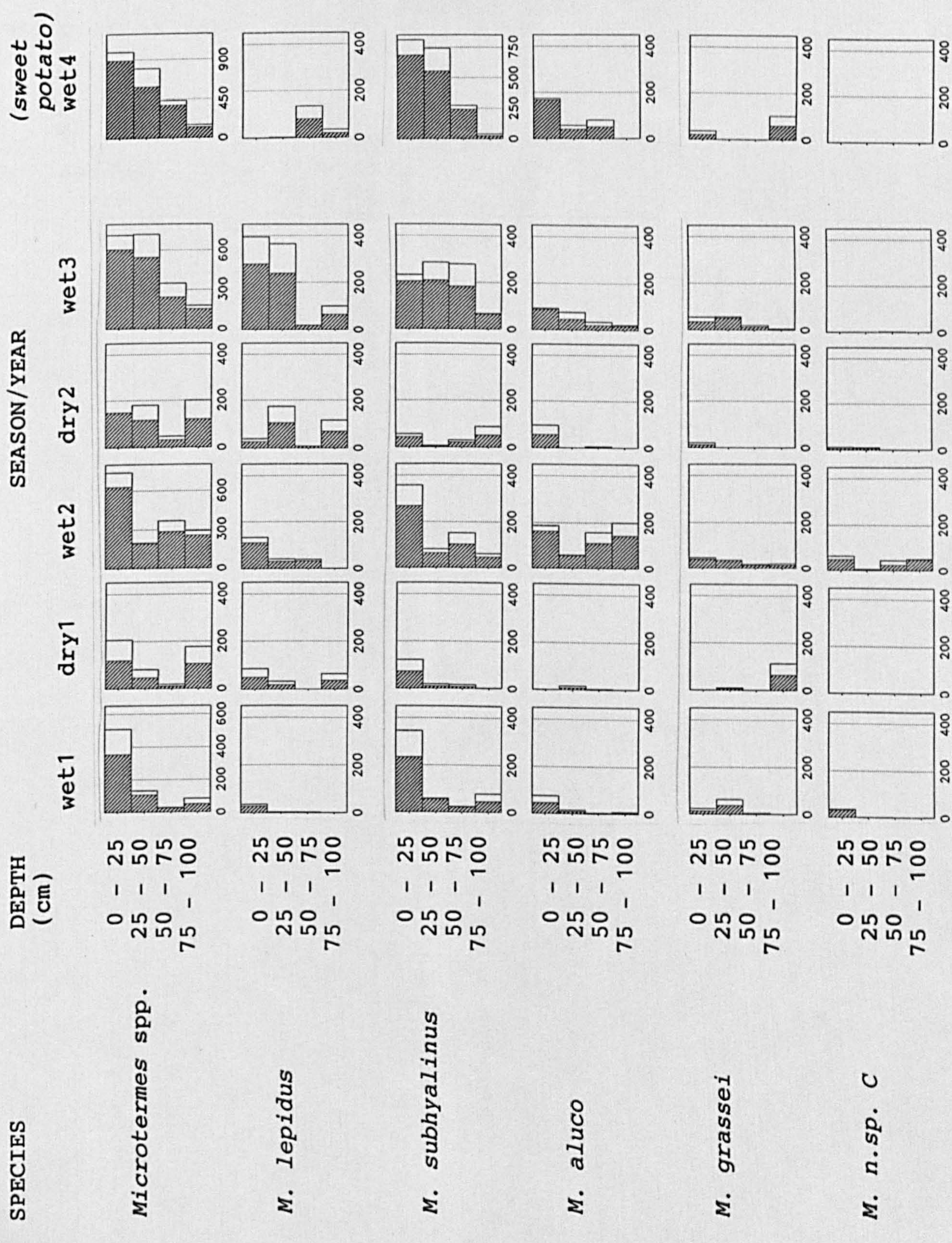


Figure 4.3.12 : Ranch maize - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

Figure 4.3.13 Farm maize - Mean abundance of *Microtermes* (n/m² ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

KEY

abundance = shaded areas

SE = clear areas

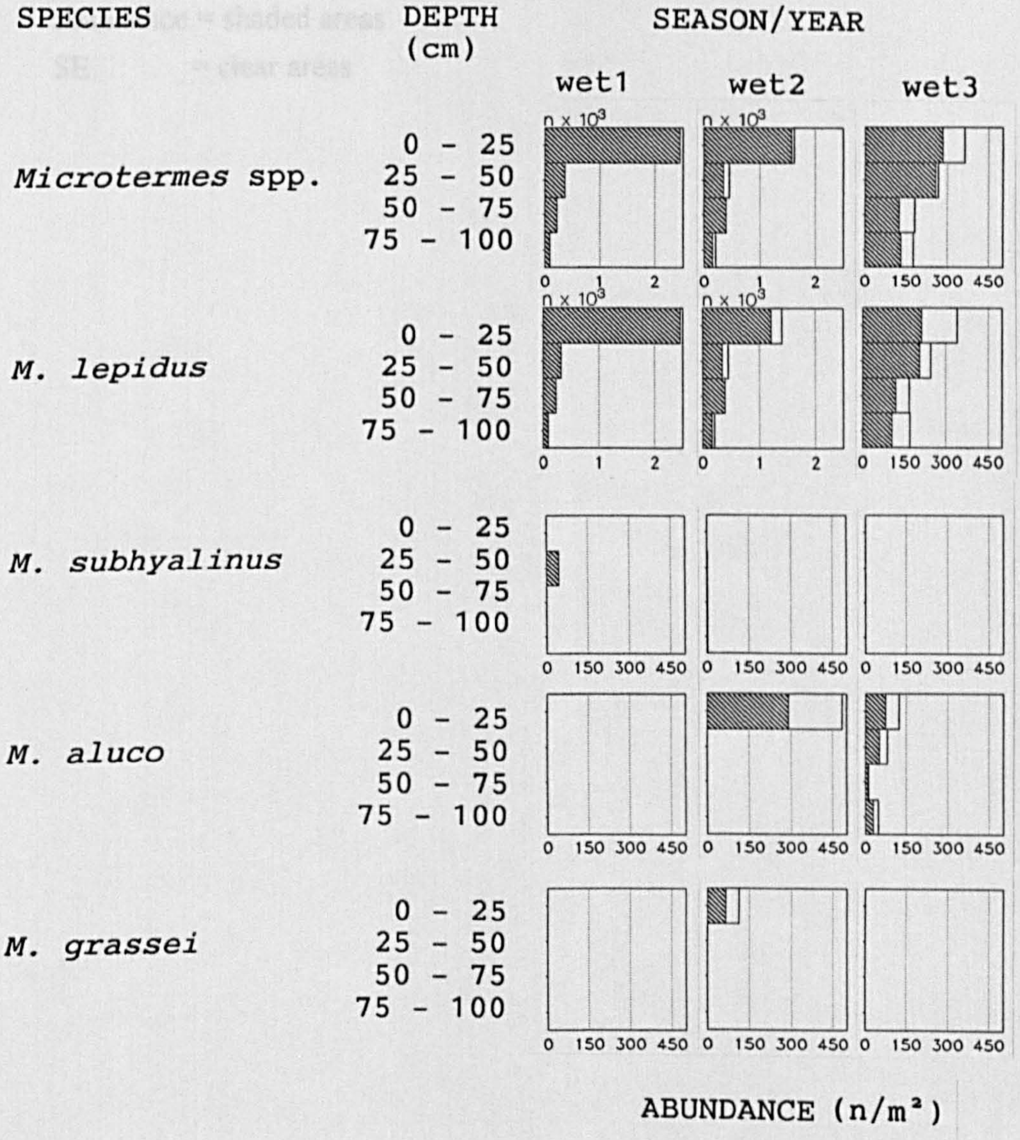


Figure 4.3.13 : Farm maize - Mean abundance of *Microtermes* (n/m^2 ± 1 SE) at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons from 1974 to 1977 at Mokwa, Nigeria.

<u>key</u>

abundance = shaded areas
SE = clear areas

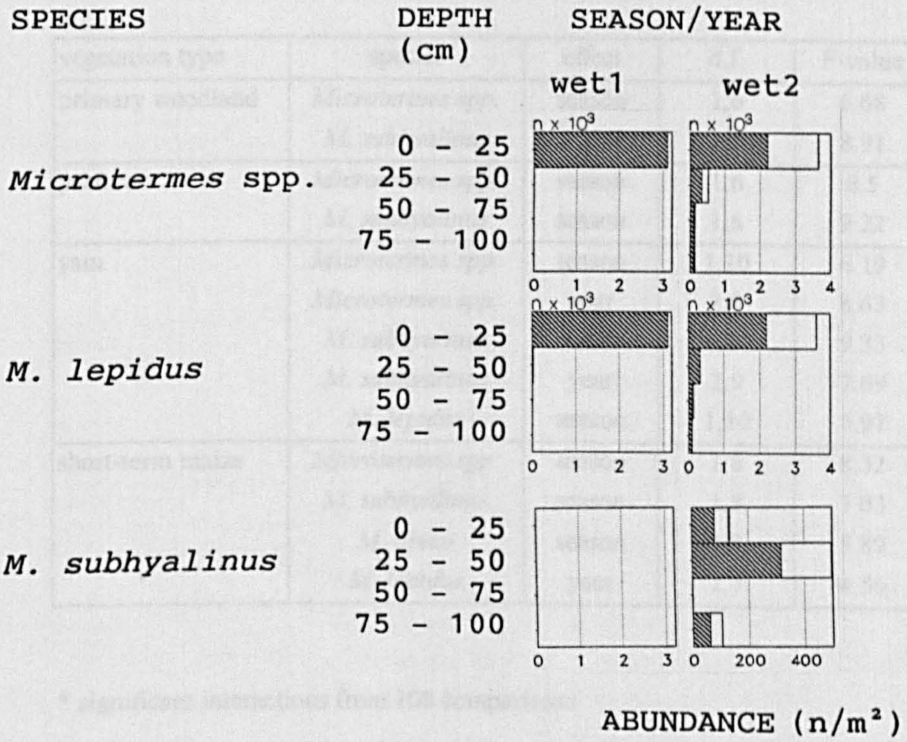

SPECIES
DEPTH (cm)
SEASON/YEAR
wet1
wet2
n x 10³
Microtermes spp.
M. lepidus
M. subhyalinus
0 - 25
25 - 50
50 - 75
75 - 100
0
1
2
3
4
200
400
ABUNDANCE (n/m²)

Table 4.3.1 : Significant interactions* from analysis of variance and Tukey comparisons for season and year effects on the abundance of *Microtermes* to a soil depth of 1 metre in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

vegetation type	species	effect	d.f.	F-value	P	Tukey
primary woodland	*Microtermes spp.*	season	1,6	6.68	<0.05	wet>dry
	M. subhyalinus	season	1,6	8.91	<0.05	wet>dry
pasture	*Microtermes spp.*	season	1,6	8.5	<0.05	wet>dry
	M. subhyalinus	season	1,6	9.22	<0.05	wet>dry
yam	*Microtermes spp.*	season	1,10	6.19	<0.05	wet>dry
	Microtermes spp.	year	2,9	8.63	<0.05	1<2=3
	M. subhyalinus	season	1,10	9.33	<0.05	wet>dry
	M. subhyalinus	year	2,9	7.69	<0.05	1<2=3
	M. lepidus	season	1,10	5.97	<0.05	wet>dry
short-term maize	*Microtermes spp.*	season	1,8	8.32	<0.05	wet>dry
	M. subhyalinus	season	1,8	7.03	<0.05	wet>dry
	M. aluco	season	1,8	5.89	<0.05	wet>dry
	M. lepidus	year	2,7	4.56	<0.05	1<2<3

* significant interactions from 108 comparisons

KEY TO TUKEY COMPARISONS

means not significantly different; =
means significantly greater or less than; > , <

1 = year one
2 = year two
3 = year three

Table 4.3.2 : Significant interactions* from split-plot analysis of variance and Tukey comparisons for depth, season and year effects on the abundance of *Microtermes* at 25 cm depth intervals to a soil depth of 1 metre in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

vegetation type	species	effect	d.f.	F-value	P	Tukey
primary woodland	*Microtermes spp.*	season	1,12	5.56	<0.05	wet>dry
	M. subhyalinus	season	1,12	7.86	<0.05	wet>dry
secondary woodland	*Microtermes spp.*	year	1,12	14.36	<0.01	2<1=3
	Microtermes spp.	season.year	1,12	9.7	<0.01	
	M. subhyalinus	year	1,12	7.6	<0.05	2<1=3
	M. subhyalinus	season.year	1,12	31.18	<0.01	
	M. aluco	year	1,12	5.51	<0.05	2=3<1
pasture	*Microtermes spp.*	season	1,12	17.09	<0.01	wet>dry
	M. subhyalinus	season	1,12	25.21	<0.01	wet>dry
	M. subhyalinus	season.year	1,12	11.59	<0.01	
	M. aluco	year.depth	3,12	3.93	<0.05	
sweet potato	*M. aluco*	season	1,20	9.98	<0.01	wet>dry
yam	*Microtermes spp.*	season	1,20	22.94	<0.01	wet>dry
	Microtermes spp.	year	2,20	9.04	<0.01	1<2=3
	Microtermes spp.	season.year	2,20	8.6	<0.01	
	M. subhyalinus	season	1,20	12.48	<0.01	wet>dry
	M. aluco	season	1,20	7.78	<0.05	wet>dry
	M. aluco	season.year	2,20	6.82	<0.01	
	M. grassei	season	1,20	5.99	<0.05	wet>dry
	M. grassei	year	2,20	4.03	<0.05	1=2<3
	M. lepidus	season	1,20	15.57	<0.01	wet>dry
	M. lepidus	year	2,20	4.76	<0.05	1<2<3
	M. n. sp. C	year	1,10	7.13	<0.01	1=3<2
short-term maize	*Microtermes spp.*	season	1,12	14.31	<0.01	wet>dry
	Microtermes spp.	year	1,12	4.49	<0.01	1<2<3
	M. subhyalinus	season	1,12	21.39	<0.05	wet>dry
	M. aluco	season	1,12	30.17	<0.01	wet>dry
	M. aluco	year	1,12	5.06	<0.05	1<3<2
	M. grassei	season	1,12	11.02	<0.01	wet>dry
	M. lepidus	year	1,12	10.6	<0.01	1<2<3
	M. n. sp. C	year	1,12	18.16	<0.01	1=3<2

* significant interactions from 378 comparisons

KEY TO TUKEY COMPARISONS

means not significantly different; =
means significantly greater or less than; > , <

1 = year one
2 = year two
3 = year three

Table 4.3.3 : Significant interactions* from analysis of variance and Tukey comparisons for year effects on the wet season abundance of *Microtermes* to a soil depth of 1 metre in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

vegetation type	species	d.f.	F-value	P	Tukey
secondary woodland	*Microtermes spp.*	2,3	8.34	<0.05	2<1=3
	M. subhyalinus	2,3	6.72	<0.05	2<1=3
yam	*Microtermes spp.*	2,3	6.51	<0.05	1<2=3
	M. subhyalinus	2,3	4.58	<0.05	1<2=3
	M. aluco	2,3	4.36	<0.05	1<2<3
short-term maize	*Microtermes spp.*	2,3	5.21	<0.05	1<2=3
	M. subhyalinus	2,3	18.96	<0.01	1<2<3
	M. aluco	2,3	24.02	<0.01	1=3<2
	M. lepidus	2,3	19.67	<0.01	1<2<3
ranch maize	*Microtermes spp.*	2,3	13.2	<0.05	3<2<1
	M. lepidus	2,3	133.81	<0.005	3<2<1
farm maize	*M. subhyalinus*	2,3	18.15	<0.05	2<1

* significant interactions from 54 comparisons

KEY TO TUKEY COMPARISONS

means not significantly different; =
means significantly greater or less than; > , <

1 = year one
2 = year two
3 = year three

Table 4.3.4 : Significant interactions* from analysis of variance and Tukey comparisons for year and depth effects on the wet season abundance of *Microtermes* at 25 cm depth intervals to a soil depth of 1 metre in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

vegetation type	species	effect	d.f.	F-value	P	Tukey
primary woodland	*M. lepidus*	year	1,8	10.26	<0.05	1<2
secondary woodland	*Microtermes spp.*	year	2,12	23.43	<0.005	2<1=3
	M. subhyalinus	year	2,12	38.87	<0.005	2<1=3
pasture	*M. subhyalinus*	year	1,8	6.58	<0.05	2<1
	M. grassei	year	1,8	5.38	<0.05	1<2
sweet potato	*M. lepidus*	year	2,12	4.34	<0.05	1=2<3
groundnuts	*Microtermes spp.*	depth	3,12	7.06	<0.01	4=3<2<1
yam	*Microtermes spp.*	depth	3,12	4.09	<0.05	4=3<2<1
	Microtermes spp.	year	2,12	6.41	<0.05	1<3=2
	M. subhyalinus	year	2,12	6.31	<0.05	1<3<2
	M. grassei	year	2,12	4.55	<0.05	1<2=3
	M. lepidus	year	2,12	8.04	<0.01	1<2<3
short-term maize	*Microtermes spp.*	depth	3,12	4.44	<0.05	4=3=2<1
	Microtermes spp.	year	2,12	8.66	<0.005	1<2<3
	M. subhyalinus	depth	3,12	5.67	<0.01	4=3=2<1
	M. subhyalinus	year	2,12	17.58	<0.005	1<3=2
	M. subhyalinus	year.depth	6,12	3.42	<0.05	
	M. aluco	year	2,12	9.39	<0.005	1=3<2
	M. lepidus	depth	3,12	18.27	<0.005	4=3=2<1
	M. lepidus	year	2,12	35.5	<0.005	1<2<3
	M. lepidus	year.depth	6,12	3.7	<0.05	
ranch maize	*Microtermes spp.*	depth	3,12	22.88	<0.005	4=3=2<1
	Microtermes spp.	year	2,12	8.54	<0.005	3<2<1
	Microtermes spp.	year.depth	6,12	3.06	<0.05	
	M. aluco	year	2,12	7.96	<0.01	1<3=2
	M. lepidus	depth	3,12	6.09	<0.01	4=3=2<1
	M. lepidus	year	2,12	6.11	<0.05	3<2<1
farm maize	*Microtermes spp.*	depth	3,8	16.8	<0.005	4=3=2<1
	Microtermes spp.	year	1,8	17.65	<0.005	1<2
	Microtermes spp.	year.depth	3,8	5.28	<0.05	
	M. subhyalinus	year	1,8	13.23	<0.01	1<2
	M. lepidus	depth	3,8	34.5	<0.005	4=3=2<1
	M. lepidus	year.depth	3,8	12.72	<0.005	

* significant interactions from 162 comparisons

KEY TO TUKEY COMPARISONS

1 = year one

means not significantly different; =

2 = year two

means significantly greater or less than; > , <

3 = year three

Table 4.3.5 : Significant interactions* from analysis of variance and Tukey comparisons of year and depth effects on the dry season abundance of *Microtermes* at 25 cm intervals to a soil depth of 1 metre in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

vegetation type	species	effect	d.f.	F-value	P	Tukey
yam	*Microtermes spp.*	year	2,12	15.64	<0.005	3<1=2
short-term maize	*M. lepidus*	year	2,12	5.51	<0.05	1<2

Microtermes spp. and *M. subhyalinus* populations (total abundance to 1 m) were higher in the wet season in primary woodland, pasture, yam and short-term maize both for total abundance to 1 m and at 25 cm intervals to 1 m (Tables 4.3.1 and 4.3.2). *M. aluco* in short-term maize and *M. lepidus* in yam were more abundant, as a total abundance to 1 m, in the wet season while the 25 cm interval abundance of *M. aluco*, *M. grassei* and *M. lepidus* in yam, *M. aluco* in sweet potato and *M. grassei* in short-term maize were more abundant in the wet season.

The depth distribution of *Microtermes* spp. was not significantly different between seasons. During the wet season, *Microtermes* spp. in yam and *Microtermes* spp., *M. subhyalinus* and *M. lepidus* in short-term maize were concentrated above 25 cm (Table 4.3.4). In primary woodland, *M. subhyalinus* and *M. grassei* were more abundant above 50 cm in the wet season compared to dry. In pasture, *M. subhyalinus* was more abundant at all depths, especially above 50 cm, in the wet season. In short-term maize, *M. aluco* was more abundant above 50 cm in the wet season.

4.3.3 Vegetation cover effects on abundance and distribution in soil

Significant differences in *Microtermes* abundance between and within all vegetation types are given in Tables 4.3.6 and 4.3.7. Only wet season abundance figures are quoted below due to the generally low dry season abundance of *Microtermes* spp..

Microtermes spp. were significantly more abundant in long term cultivated maize sites than in other vegetation sites; ranging from 700 to 3200/m^2 (rarely below 2000/m^2) and concentrated above 25 cm in the soil (Table 4.3.4; Figures 4.3.12 and 4.3.13). This reflects the significant differences in depth distribution of *M. lepidus* which was the dominant species (over 75% of the total population). The remaining species, *M. subhyalinus*, *M. aluco* and *M. grassei*, were mainly present in low numbers above 50 cm in the soil. There were large fluctuations in *Microtermes* spp. abundance and depth distribution between years in both sites which correspond to changes in *M. lepidus* abundance and to a lesser extent *M. subhyalinus* and *M. aluco* (Tables 4.3.3 and 4.3.4).

The next highest populations of *Microtermes* spp. were found during the second and third wet seasons in yam and short-term maize with a range of 1350 to 1800/m^2. *M. subhyalinus* and *M. lepidus* were the most abundant species. *M. subhyalinus* was dominant in the first two wet seasons and co-dominant with *M. lepidus* in the third wet season. At this time, the depth distribution of *Microtermes* spp. and of individual species were similar in both crops. *Microtermes* spp. and *M. lepidus* populations were most abundant above 25 cm and declined with depth. *M. subhyalinus* was concentrated above 50 cm, with its highest abundance between 25 - 50 cm. Although the abundance of both

M. aluco and *M. grassei* was low, the distribution of the former was similar to that of *M. lepidus* and the latter that of *M. subhyalinus*.

Microtermes spp. abundance in secondary woodland and pasture ranged from 900 to 1450/m² and was concentrated above 50 cm throughout the study, excluding the second wet season in secondary woodland. *M. subhyalinus* was dominant and concentrated above 50 cm with greatest abundance above 25 cm. Of the remaining species, all of which were infrequent, *M. lepidus* (in pasture) and *M. aluco* (in woodland) were most abundant above 50 cm and *M. grassei* below 25 cm in pasture and above 50 cm in woodland. *M. n.sp. C* was rare and significantly less abundant than the other species (Table 4.3.7)

In primary woodland, sweet potato and groundnut, *Microtermes* spp. populations ranged from 200 to 900/m² but rarely exceeded 500/m². *M. subhyalinus* was the most abundant species in primary woodland and groundnuts and equally abundant as *M. aluco* in sweet potato. *M. n.sp. C* was rare. All species were generally most abundant above 50 cm.

The succession of secondary woodland to cultivation produced different abundance and distribution patterns depending on crop type. Here also, results concentrate on the wet seasons; dry season populations were low and often no single species was dominant.

In secondary woodland, *Microtermes* spp. abundance was similar in the first and third wet seasons of the block experiment (ranging from 1000/m² to 1500/m²) while dry season populations were low (< 500/m²). The second wet season sample in secondary woodland indicated significantly lower *Microtermes* spp. abundance than the previous or following wet seasons (Table 4.3.4). This was due to lower abundance of *M. subhyalinus* and, to a lesser extent, *M. aluco*. In all wet seasons, *Microtermes* spp. were most abundant above 50 cm. *M. subhyalinus* was the dominant species, concentrated above 50 cm, and *M. aluco* and *M. grassei* were the next most abundant species in the first and third years, respectively. *M. grassei* was most abundant above 50 cm whilst *M. aluco* was concentrated below 50 cm in the first season and above 50 cm by the third wet season. *M. lepidus* was low in abundance throughout the study, with no clear depth distribution, while *M. n.sp. C* was not recorded.

In the first wet season of pasture, *Microtermes* spp. abundance was similar to secondary woodland (> 1000/m²) with *M. subhyalinus* the dominant species. This species was also concentrated above 50 cm. *M. aluco* was noticeably less abundant in pasture than secondary woodland; similar abundance to *M. grassei* and *M. lepidus*. In the second wet season, there was small, non-significant, decline in *Microtermes* spp. abundance reflecting the significant decline in *M. subhyalinus* (Table 4.3.4); especially below 25 cm. *M. aluco* showed a significant change in depth distribution, similar to that secondary woodland (Table 4.3.2); populations highest below 50 cm in the first season and above 50 cm by the third wet season. *M. grassei* was concentrated below 25 cm and showed a significant increase in abundance from first to second year (Table 4.3.4). *M. lepidus* was concentrated above 50 cm throughout.

In all newly cultivated plots, initially, *Microtermes* spp. were less abundant than in secondary woodland (< 700/m²) due to fewer numbers of *M. subhyalinus* and, to a lesser extent, *M. grassei*. *M. subhyalinus* was still the most abundant species, except in sweet potato were it was co-dominant with *M. aluco*.

There was no significant change in *Microtermes* spp. abundance and distribution with three years of sweet potato cultivation; populations were less than 500/m² and concentrated above 50 cm; similar to woodland. However, *M. lepidus* populations were significantly higher in the third year, making this the most abundant species in the wet season and co-dominant with *M. subhyalinus* in the dry (Table 4.3.4; Figure 4.3.4). *M. aluco*, initially co-dominant with *M. subhyalinus*, reduced in numbers progressively, irrespective of season, while *M. subhyalinus* numbers declined until the third dry season. *M. subhyalinus* and, to a lesser extent, *M. aluco* showed a trend in concentrating numbers further down in the soil; *M. subhyalinus* became most abundant below 75 cm. *M. grassei* and *M. n.sp. C* were rare.

Three years of groundnut cultivation resulted in little change in the abundance or distribution of *Microtermes* spp., with numbers concentrated above 50 cm and *M. subhyalinus* the most abundant species. The significant depth distribution of *Microtermes* spp. (Table 4.3.4) highlights the predominance of species in the top 50 cm and the subsequent decline in abundance with depth. *M. n.sp. C* was more abundant in this crop than in woodland.

In the first year of yams, *Microtermes* spp. were most abundant above 25 cm, *M. subhyalinus* was concentrated above 25 cm and all other species above 50 cm, except *M. n.sp. C*, which was found between 50 and 75 cm. *Microtermes* spp. increased rapidly from the first to the second wet season (Table 4.3.4) when abundance was slightly higher than in secondary woodland. This increase was reflected in the significant difference between seasons with years (Table 4.3.2). Both these results can mainly be attributed to *M. subhyalinus* which increased from 400 to 1200/m²; predominantly above 25 cm. *M. lepidus*, *M. grassei* and *M. n.sp. C* also increased significantly in this period, the latter irrespective of season. *M. lepidus* continued to increase from the second to third wet season and became co-dominant with *M. subhyalinus*, which declined slightly to 750/m². The increase in *Microtermes* spp. abundance was seen in all depth intervals but numbers were still concentrated above 25 cm. There were no significant changes in depth distribution. However from Figure 4.3.10 it can be seen that *M. lepidus* increased in all depth intervals, especially above 25 cm where it became the most common species. *M. subhyalinus, M. grassei* and *M. n.sp. C* initially increased in all depth intervals; *M. subhyalinus* especially above 25 cm. By the third wet season *M. subhyalinus* and *M. grassei* were more abundant at lower soil intervals, becoming the most abundant and co-dominant species between 25 and 50 cm while *M. n.sp. C* was most abundant above 25 cm. *M. aluco* showed no change in total abundance to 1 m but was more abundant in the top 25 cm of the soil than in previous seasons.

In short-term maize, *Microtermes* spp. were again most abundant above 25 cm with *M. subhyalinus* concentrated above 25 cm and all other species above 50 cm. *Microtermes* spp. also increased dramatically from the first to second year, irrespective of season; abundance greater than 1200/m^2. Unlike yam, this continued on a smaller scale from the second to third wet season to reach 1500/m^2 (Table 4.3.2). The first increase related to increases in all species, in particular *M. subhyalinus* and *M. aluco* which became co-dominant. The second increase resulted from an increase in *M. lepidus* and, to a lesser extent, *M. subhyalinus* while *M. aluco* and *M. n.sp. C* declined. *M. lepidus* increased throughout the study irrespective of season (Table 4.3.2). Similar to yam, *M. lepidus* became co-dominant with *M. subhyalinus* by the third wet season. Throughout the study *Microtermes* spp. were concentrated above 25 cm, declining with depth (Table 4.3.4). Increases in abundance occurred in all depths and especially above 50 cm. From the first to second wet season *M. subhyalinus* and *M. aluco* increased in all depths; *M. subhyalinus* remained concentrated above 25 cm and *M. aluco* became concentrated below 50 cm. *M. grassei* and *M. n.sp. C* increased to show equal abundance in all depths. *M. lepidus* increased above 75 cm and in particular above 25 cm. In the first two years *M. subhyalinus* was most common and the most abundant species in the top 25 cm. By the third wet season *M. lepidus* increased above 50 cm and was the most common species above 25 cm replacing *M. subhyalinus*. *M. subhyalinus* increased in abundance between 25 and 75 cm and was the most abundant species between 50 and 75 cm. These two species were equally abundant between 25 and 50 cm. The decline in *M. aluco* and *M. grassei* occurred mainly below 50 cm and in all depths for *M. n.sp. C*

4.3.4 Comparison of abundance to 1 m and to 25 cm in soil

As stated earlier, *Microtermes* spp. abundance to 1 m soil depth was highest in long-term maize sites, followed by short-term maize and yam (in years two and three), then secondary woodland and pasture and, finally, groundnuts, sweet potato and primary woodland. Abundance of individual species to 1 m also differed significantly amongst the vegetation types (Table 4.3.6). Both *M. subhyalinus* and *M. n.sp. C* were most abundant in yam, groundnuts and maize. *M. grassei* was most abundant in both woodland sites and least abundant in long-term maize. *M. lepidus* was most abundant in long-term maize followed by yam and short-term maize. *M. aluco* was least abundant in farm maize and primary woodland. *Microtermes* spp. abundance to 25 cm highlighted certain similar differences as shown by abundance to 1 m (Table 4.3.6); highest populations were found in long-term maize and lowest in primary woodland, sweet potato and groundnuts. However, there were no further differences in *Microtermes* spp. abundance to 25 cm amongst the remaining vegetation types.

M. lepidus abundance to 25 cm results were consistent with those of abundance to 1 m; this species was most abundant in long-term maize followed by short-term maize and yam. Although there were no further significant differences amongst the vegetation types for *M. lepidus* abundance to 1 m, abundance to 25 cm was lower in both woodland sites than in sweet potato, pasture and groundnuts.

M. subhyalinus abundance was lowest in ranch maize for both depths. Abundance to 1 m was highest in yam, short-term maize, groundnuts, primary woodland, while abundance to 25 cm was highest in these, along with pasture and secondary woodland. There were no significant differences in the abundance of *M. n.sp. C*, *M. aluco* or *M. grassei* to 25 cm although there were differences in the 1 m abundance amongst the vegetation types.

In pasture and all maize sites, differences in abundance amongst the species were the same at both depths. *M. subhyalinus* was the most abundant species at both depths (along with *M. aluco* in sweet potato), except in long-term maize sites where *M. lepidus* was dominant (Table 4.3.7). In primary woodland and sweet potato, abundance to 25 cm further separated the remaining species. *M. grassei* was more abundant than *M. lepidus*, *M. n.sp. C* and *M. aluco* in primary woodland. *M. grassei* and *M. lepidus* were more abundant than *M. n.sp. C* and *M. aluco* in sweet potato. *M. n.sp. C* was the least abundant species at 1 m in secondary woodland and yam. However, at 25 cm, the least abundant species were *M. n.sp. C* and *M. lepidus* in secondary woodland and *M. n.sp. C*, *M. aluco* and *M. grassei* in yam. In groundnuts, where *M. n.sp. C* and *M. grassei* were the least abundant species at 1 m, *M. n.sp. C* was the single least abundant species at 25 cm.

Table 4.3.6 : Interactions from analysis of variance and Tukey comparisons of *Microtermes* abundance to a soil depth of 1 m and 25 cm amongst uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

species	depth	d.f.	F-value	P	Tukey
Microtermes spp.	1 m	8,65	2.09	<0.05	1w=sw=gn<2w=pa<ym=stm<rm=fm
	25 cm	8,65	3	<0.05	1w=sw=gn<2w=pa=ym=stm<rm=fm
M. subhyalinus	1 m	8,65	3.55	<0.005	rm<fm=sw<2w=pa=ym=stm=gn=1w
	25 cm	8,65	4.08	<0.005	rm<fm=sw=2w=pa<ym=stm=gn=1w
M. lepidus	1 m	8,65	5.86	<0.005	1w=2w=sw=pa=gn<ym=stm<rm=fm
	25 cm	8,65	8.95	<0.005	1w=2w<sw=pa=gn<ym=stm<rm=fm
M. grassei	1 m	8,65	3.09	<0.005	fm<pa=sw=rm=ym=stm=gn<2w=1w
	25 cm	8,65	2.59	<0.05	n/s
M. aluco	1 m	8,65	4.43	<0.005	fm<2w<rm=pa=ym<stm=2w=sw=gn
	25 cm	8,65	2.49	<0.05	n/s
M. n. sp. C	1 m	8,65	4.42	<0.005	fm=rm=2w<1w=pa=sw<stm=ym=gn
	25 cm	8,65	2.43	<0.05	n/s

Key to Tukey comparisons

means not significantly different; =
means significantly greater or less than; > , <
n/s ; not significant

Key to vegetation types

fm = farm maize
rm = ranch maize
stm = short-term maize
ym = yam
gn = groundnuts
sw = sweet potato
pa = pasture
2w = secondary woodland
1w = primary woodland

Table 4.3.7 : Interactions from analysis of variance and Tukey comparisons of the abundance of *Microtermes* to a soil depth of 1 metre and 25 cm in uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

species	depth	d.f.	F-value	P	Tukey
primary woodland	1 m	4,35	13.65	<0.005	g>b=a=d>c
	25 cm	4,35	9.56	<0.005	g>b>a=d=c
secondary woodland	1 m	4,45	8.56	<0.005	g>d=b=a
	25 cm	4,45	4.66	<0.005	g>b=d>a
pasture	1 m	4,35	2.84	<0.05	g>a=b=d>c
	25 cm	4,35	3.36	<0.05	g>a=d=b>c
sweet potato	1 m	4,55	8.32	<0.005	g=d>a=b=c
	25 cm	4,55	4.21	<0.005	g=d>a=b>c
groundnuts	1 m	4,25	3.97	<0.05	g>d=a>b=c
	25 cm	4,25	3.29	<0.05	g>a=d=b>c
yam	1 m	4,55	3.08	<0.005	g>a=d=b>c
	25 cm	4,55	2.9	<0.05	g>a>d=b=c
short-term maize	1 m	4,45	3.26	<0.05	g>a=d=b>c
	25 cm	4,45	3.55	<0.05	g>a=d=b>c
ranch maize	1 m	2,25	16.13	<0.005	a>d=g=b
	25 cm	2,25	16.6	<0.005	a>g=d=b
farm maize	1 m	4,15	15.78	<0.005	a>g
	25 cm	4,15	23.11	<0.005	a>g

Key to Tukey comparisons

means not significantly different; =
means significantly greater or less than: > , <

Key to species

a = *M. lepidus*
b = *M. grassei*
c = *M. n. sp. C*
d = *M. aluco*
g = *M. subhyalinus*

4.3.5 Effects of changing crops on abundance and distribution in soil

(1) Sweet potato to maize. There was no significant change in the abundance of *Microtermes* spp. although there was a reduction in abundance in the top 25 cm (Table 4.3.8; Figure 4.3.8). *M. lepidus* numbers declined significantly, mainly in the top 50 cm. There was a decrease in all measures of diversity, especially for 25 cm, to lower levels than in the first wet season of sweet potato. This change in community structure can be explained by the reduction in species in conjunction with a decline in abundance of all species with some species moving down in the soil. Species richness declined from close to 4 to 2 species for 1 m and from 2 to 1 species for 25 cm.

(2) Maize to sweet potato. There was no significant changes in *Microtermes* spp. abundance however *M. subhyalinus* numbers increased significantly above 50 cm coinciding with a decrease in the abundance of *M. lepidus* at the same depth (Figure 4.3.11). Species richness did not change but Shannon-Wiener and evenness indices declined corresponding to the changes in species abundance.

(3) Groundnut to yam. *Microtermes* spp. abundance increased significantly, at all depth intervals and mainly above 25 cm (Figure 4.3.9). *Microtermes* spp. population in 1977 was the highest for any crop in the randomised block throughout the study. There were significant increases in *M. lepidus* and *M. aluco* numbers, mainly above 25 cm and most dramatically by *M. lepidus*. The depth distribution of *M. subhyalinus* altered with numbers concentrated in the top 25 cm and below 75 cm. These changes did not alter community structure.

(4) Yam to groundnut. Community structure altered with this crop change; species richness and Shannon-Wiener index declined to similar levels shown in the first year of yam cultivation; a fall from 4.25 to 2 and 3 species for 25 cm and 1 m respectively. *Microtermes* spp. abundance decreased significantly, most noticeably in the top 50 cm, although numbers were still concentrated above 25 cm (Figure 4.3.10). *M. lepidus* and *M. subhyalinus* numbers also declined in the top 50 cm, especially above 25 cm. The remaining species exhibited non-significant changes in abundance. *M. aluco* numbers increased above 25 cm, where it replaced *M. subhyalinus* and *M. lepidus* as the most abundant species. *M. grassei* numbers decreased between 25 and 50 cm and *M. n.sp. C* numbers decreased in the top 25 cm. In this first year of yam, the abundance of each species, except *M. subhyalinus*, was similar to that in the first year groundnuts in the randomised block; *M. subhyalinus* was less abundant.

Table 4.3.8 : Significant interactions[*] from analysis of variance to examine the abundance of *Microtermes* at different depth intervals with a change of crop in cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria; (a) total abundance to a soil depth of 1 m, (b) abundance at four, 25 cm, intervals to a soil depth of 1 m, (c) abundance at two, 25 cm, intervals to a soil depth of 50 cm and, (d) abundance at two, 25 cm, intervals from a soil depth of 50 cm to 1 m

vegetation type	species	depth	d.f.	F-value	P
sweet potato to maize	*M. lepidus*	1 m	1,4	13.52	<0.05
	M. lepidus	0 - 100 m	1,22	9.41	<0.01
	M. lepidus	0 - 50 cm	1,11	5.74	<0.05
maize to sweet potato	*M. subhyalinus*	0 - 50 cm	1,14	7	<0.05
	M. lepidus	0 - 100 m	1,28	9.62	<0.005
	M. lepidus	0 - 50 cm	1,14	59.79	<0.005
groundnuts to yam	*Microtermes spp.*	0 - 100 m	1,22	14.12	<0.005
	Microtermes spp.	0 - 50 cm	1,11	19.81	<0.005
	M. aluco	0 - 100 m	1,28	7.75	<0.05
	M. lepidus	0 - 50 cm	1,11	7.72	<0.05
	M. lepidus	50 - 100 cm	1,11	6.16	<0.05
yam to groundnuts	*Microtermes spp.*	0 - 100 m	1,28	16.96	<0.005
	Microtermes spp.	0 - 50 cm	1,14	10.56	<0.005
	Microtermes spp.	50 - 100 cm	1,14	6.04	<0.05
	M. subhyalinus	0 - 100 m	1,28	8.4	<0.01
	M. subhyalinus	0 - 50 cm	1,14	4.98	<0.05
	M. lepidus	0 - 100 m	1,28	5.6	<0.05
	M. lepidus	0 - 50 cm	1,14	10.92	<0.01

[*] significant interactions from 96 comparisons.

4.4 DISCUSSION

4.4.1 Community structure of *Microtermes*

There were only three examples of seasonal differences the community structure of *Microtermes*; Shannon-Wiener index in secondary woodland was greater in the dry compared to the wet season for both 1 m and 25 cm and lower in sweet potato in the dry than wet season for 25 cm. These are unusual results as no seasonal differences were noted in the abundance of *Microtermes* spp. or individual species in either secondary woodland or sweet potato while wet season abundance of *Microtermes* and certain species was greater than dry season abundance in primary woodland, pasture, yam and short-term maize, as discussed below. In both secondary woodland and sweet potato, seasonal differences can be related to more equitable abundance amongst the species, as shown by the evenness index. In secondary woodland, abundance in the dry seasons tended to be less than in the wet seasons with reductions in the abundance of the predominant species to the soil depth of 1 m (*M. subhyalinus*, *M. aluco* and *M. grassei*) corresponding to a decline in foraging activity. In sweet potato, the least abundant species (*M. grassei* and *M. n. sp. C*) were only recorded in the top 25 cm of the soil in the wet season while the abundance of the remaining species was often higher in the wet season compared to the dry season corresponding to an increase in foraging activity.

In primary woodland, there was shown to be a high degree of variability in species richness and abundance which were reflected in Shannon-Wiener and evenness indices. This variability may be due to seasonal climatic conditions varying from one year to the next, particularly in the third wet season. It is also possible that *Microtermes* distribution is more patchy in undisturbed woodland due to the presence of other termite genera. If it is considered that species occurrence and abundance were unusual in the third wet season then it would appear that there were fewer *Microtermes* species in primary woodland compared to secondary woodland when soil was sampled to a depth of 1 m; *M. lepidus* and the rare species *M. n. sp. C* were not recorded in primary woodland where it is likely that these species have low abundance and/or localised distribution. Diversity, as shown by Shannon-Wiener and evenness indices, was also generally lower in primary than secondary woodland and this relates to the infrequent occurrence of certain species plus the predominance of *M. subhyalinus* in primary woodland. Further discussion of these differences is given below.

Species richness was shown to differ little in secondary woodland while Shannon-Wiener and evenness indices varied throughout the study reflecting seasonal differences in community structure with relative abundance of species. These differences were most apparent in the top 25 cm and, as for primary woodland, may be related to seasonal climate differences. However, the years with the greatest differences in species richness and abundance were not the same for the two woodland sites and therefore it may be suggested that factors other than or in conjunction with seasonal climate were likely to be responsible for a change in community structure i.e. food type and availability.

Clearing and cultivation of land from secondary woodland would appear to alter both community structure as shown by differences in species richness and Shannon-Wiener index, particularly in the top 25 cm. Changes differed with land use type and are discussed below in reference to *Microtermes* abundance and distribution.

Comparisons of the indices for 1 m and 25 cm show that species richness was greater for 1 m than 25 cm, suggesting that some species may forage and nest below 25 cm. Therefore sampling to depth is required to obtain a full description of species present.

4.4.2 Seasonal effects on abundance and distribution in soil

Throughout the study seasonal weather conditions were a major influence on both *Microtermes* species abundance and depth distribution as determined by soil sampling. Seasonal weather conditions dictate not only the availability of food but also soil characteristics, such as temperature and moisture profiles, which are known to effect termite abundance and distribution (Bodot, 1967; Buxton, 1981; Haverty, La Fage and Nutting, 1974; Kouassi and Lepage, 1988). In response to these environmental factors, subterranean termites move down to escape desiccation, while foraging is reduced in the top 25 cm of the soil during the dry season. Macrotermitinae utilise fungus combs maintained lower in the soil (Bodot, 1967; Buxton, 1981; Haverty et al., 1974; Kouassi and Lepage, 1988; Wood and Johnson, 1978; Black and Wood, 1989). Results from this study support previous work since *Microtermes* populations sampled in the dry season were generally less and found lower in the soil than those in the wet season, except in sweet potato where seasonal differences in *Microtermes* numbers were too low to be significant. Differences in *Microtermes* spp. abundance between wet and dry seasons were most pronounced where wet season abundance was greater than 500/m^2; dry season abundance was low and fairly constant.

The more pronounced differences in seasonal abundance and distribution with the cultivation of yam and short-term maize were as a result of increased wet season abundance and a pronounced change in the vertical distribution in the soil.

The change in community structure, especially in crops, as shown by increases in species richness and Shannon-Wiener index in the wet season, are a reflection of increased abundance. It should also be considered that a sampling procedure is more likely to record a species when it is more abundant.

4.4.3 Vegetation cover effects on abundance and distribution in soil

As described earlier, primary (undisturbed) woodland contains a more diverse and abundant termite population than other vegetation types, with *Microtermes* constituting only 23.59% of total numbers. Re-established (secondary) woodland supports a similar number of termite species but *Microtermes* forms a much greater proportion of the total population (62.18%) (Wood et al., 1977b). This is reflected in the results from this study, the number of *Microtermes* species was similar for primary and secondary woodland but in the latter, *Microtermes* spp. were more abundant and generally more diverse with a greater degree of evenness amongst the species.

Initial clearing and cultivation resulted in a slight further increase in the number of *Microtermes* species, with the presence of less common species.

Clearing of woodland to pasture led to change in community structure with an initial reduction in Shannon-Wiener index, although *Microtermes* abundance did not change. This initial change may be related to the disturbance of nesting sites and/or the removal of principal food sources. A further change in community structure was shown as Shannon-Wiener index and species richness increased in the top 25 cm in the second year. This change may be related to reduced competition from other termite genera (see below). Further study is required to determine whether this increase would be maintained in subsequent years.

The increases in measures of diversity, especially Shannon-Wiener index, may be a reflection of reduced competition for resources, in particular nesting sites, with the reduction in the number of other termite species in the initial years after clearing and cropping. Other termite species decline due to the destruction of nesting sites by ploughing and removal of food sources.

The similarity in *Microtermes* spp. abundance and distribution in pasture and secondary woodland suggests that, in the short-term, *Microtermes* spp. populations can be supported from residual plant material where soil disturbance is minimal. The removal of soil shading had no obvious initial effect in pasture.

The initial reduction in *Microtermes* spp. abundance in all newly cultivated sites is probably due to soil disturbance from tillage. *Microtermes* species, especially *M. subhyalinus*, were most abundant above 50 cm in both woodland and pasture where tillage would have the most effect, disturbing foraging and possibly nesting behaviour. The effects of cultivation on *Microtermes* spp. fungus combs are examined in greater detail in Chapter 7.

After clearing and cultivation, *Microtermes* spp. were concentrated in the top 25 cm. With the decline in residual woodland plant matter (roots and litter), particularly lower in the soil, foraging would become concentrated on crop roots, surface litter and plant residues. Therefore, the abundance, distribution and species composition of *Microtermes* relates to the availability and suitability of food from the various crops as well as reduced competition with other termite populations.

The introduction of sweet potato does not effect species richness. However, both Shannon-Wiener and evenness indices would appear to be higher in the wet seasons and lower in the dry seasons compared to secondary woodland, especially in the top 25 cm of the soil. These changes in community structure relate to changes in species abundance. Sweet potato is rarely susceptible to *Microtermes* spp. attack and *Microtermes* spp. were less abundant in this crop than in woodland. No one species was dominant and all species were represented, suggesting availability of a food type which did not favour any one species. Numbers of common species, *M. subhyalinus* and *M. aluco*, declined and were concentrated lower down in the soil, while *M. lepidus* became concentrated further up in the soil. This may be linked to the reduction of woodland residues and/or the initial reduction in *M. subhyalinus* in the top 25 cm, reducing competition for resources. Further study is required to determine whether continued cropping of sweet potato would result in further reductions in populations with the exhaustion of residual food sources in the soil.

Surprisingly, *Microtermes* abundance did not increase in groundnuts which is a crop prone to *Microtermes* attack (El Amin et al., 1983; Johnson and Gumel, 1981; Johnson et al., 1981a; Logan, Rajagopal, Wightman and Pearce, 1992; Kanshal and Deshpade, 1967; McDonald & Raheja, 1980). This was reflected in the constancy of Shannon-Wiener and evenness indices. However, there were initial changes in community structure as shown by the increase in species richness for 1 m and decrease for 25 cm. The increase for 1 m corresponds to minor increases in the abundance of *M. lepidus* and *M. n.sp. C* while the decrease for 25 cm corresponds to a change in the distribution of species within the soil; *M. aluco*, *M. grassei* and *M. n. sp. C* soil abundance decreased above 25 cm and increased below 25 cm. These minor changes in abundance and community structure may be related to initial changes in food type and availability and/or soil microclimate (including soil disturbance through ploughing).

The study of Johnson et al. (1981a) suggests possible reasons for the low, fairly constant *Microtermes* spp. populations. *Microtermes* attack on groundnuts was inversely related to annual rainfall and attack was low in areas which received more than 1000 mm annual. Mokwa is situated in a higher rainfall area (mean annual rainfall of 1175 mm p.a.) and this may account, in part, for the lower *Microtermes* spp. abundance. The study of Johnson et al. (1981a) also identified *M. lepidus* as the main termite pest species in Nigerian savanna. However, this species was not abundant in the groundnut fields at Mokwa. *M. lepidus* may take several cropping cycles to build up to potentially harmful population levels and/or the cultivar may have been resistant to attack.

Yam is also rarely susceptible to *Microtermes* attack but the use of wooden stakes to support plants provided a ready source of food. Community structure changed with increased years of cropping as shown by increased species richness, Shannon-Wiener index and evenness as the abundance of all species of *Microtermes* increased, including rare species, and particularly above 25 cm, where food provided by the stakes was concentrated.

Maize is well documented as being highly susceptible to *Microtermes* attack, with damage initiated by attack on roots followed by excavation of the stems (Wood et al., 1980; Wood & Cowie, 1988; Sands, 1972). This susceptibility is substantiated by the rapid increase in *Microtermes* (all species) after one year of maize cultivation and a change in community structure as shown by increases in species richness, Shannon-Wiener and evenness indices. These changes were most marked in the top 25 cm of the soil. Concentration in the upper soil levels indicates increased foraging activity which may be on roots and/or surface litter. Only *M. subhyalinus* and *M. lepidus* sustained the increase, in particular *M. lepidus* which rapidly built up a large population irrespective of seasons which were concentrated above 25 cm. All species identified are documented as attacking maize roots but *M. lepidus* is the most important cereal pest.

The long-term cultivation of maize leads to a further change in *Microtermes* community structure as species richness and Shannon-Wiener index are lower than in all other vegetation types, especially in the top 25 cm of the soil. Competition for a limited but favoured food source and disturbance from soil tillage as well as total reduction in woodland residues may singly or jointly, result in the decline in all species except *M. lepidus*, whose abundance is much greater than in all other vegetation types.

4.4.4 Comparison of *Microtermes* abundance to 1 m and to 25 cm in soil

Comparisons of *Microtermes* species total abundance to 1 m and 25 cm suggests that sampling from the top 25 cm can give an accurate indication of species composition and relative abundance within a vegetation type. When comparing the abundance of individual species among vegetation types then sampling from the top 25 cm will only show differences of the most abundant species.

4.4.5 Changing crops effects on *Microtermes* abundance and distribution in soil

The change in crops highlights the close link between food type and/or availability and *Microtermes* community structure and abundance.

The rapid reduction in *Microtermes* numbers with the introduction of groundnuts after yam and increase with the reverse crop change demonstrates the variability in *Microtermes* numbers from one year to the next as a result of changes in amounts of readily available food.

The decline in *M. lepidus* in all sites, except where yam was introduced, suggest that this species may initially react negatively to crop change in the top 50 cm of the soil, even when susceptible maize and groundnuts are introduced. The rapid increase in the abundance of *M. lepidus* and *M. aluco* in yam after groundnuts is more difficult to explain. Low species abundance in groundnuts may have reduced competition for the stakes, allowing these two species to increase. The increase may have been produced by a rapid expansion in species populations in the top 1 m of the soil but it is more likely that these species were more abundant below 1 m in the soil and moved up in the soil with the introduction of a favourable food source (wooden stakes).

The decline in numbers of *M. lepidus* in sweet potato following maize may have permitted *M. subhyalinus* populations to increase as a result of utilising maize residues.

These results suggest that the judicious use of crop rotation (or intercropping) could reduce *Microtermes* abundance and therefore damage to crops. However, there is a dearth of published information on crop rotation and termite damage/yield losses and much needs to be done to fill this gap before recommendations could be made.

4.5 CONCLUSION

The hypotheses presented for this study are re-examined :-

(1) The community structure and abundance of *Microtermes* is influenced by vegetation type and seasonal climate.

(a) There were no obvious changes in community structure with season. In newly cleared and cultivated sites, it is likely that any seasonal changes were masked by successional changes in species abundance. The absence of seasonal changes in woodland may be due several factors i.e. shading reducing changes in soil micro-climate and food type and availability.

(b) Seasonal differences were recorded in the soil abundance of *Microtermes* spp. and species. *Microtermes* were generally more abundant in the wet season compared to the dry season. Seasonal differences were more pronounced in the newly cleared and cultivated sites and more pronounced in the most abundant species (*M. subhyalinus*, *M. lepidus* and *M. grassei*).

(c) Primary woodland may be less diverse than in secondary woodland while there was a trend to higher diversity in pasture and crops than in woodland sites. There were successional changes in community structure after clearing and cultivation though the direction of these changes were dependant upon land use type, length of cropping and climate.

(d) All changes in community structure were most marked in top 25 cm though sampling would be required to 1 m to achieve an accurate assessment of species richness.

(e) *Microtermes* abundance and distribution in soil differed between cultivated and uncultivated sites. *Microtermes* were most abundant in long-term maize and more abundant in newly cleared and cultivated sites than in woodland. *M. grassei* was most abundant in secondary woodland while the remaining species were more abundant in newly cleared and cultivated sites, particularly yam and maize, than in woodland. *M. subhyalinus* was the most abundant *Microtermes* species in all vegetation types in Southern Guinea savanna except long-term cultivated maize (i.e. more than 12 years). Long term cultivation of monoculture maize leads to a decline in *Microtermes* diversity and a large increase in the abundance of *M. lepidus*, an important cereal pest.

(f) Wet season sampling proved a more accurate estimate of *Microtermes* abundance, distribution and community structure than dry season sampling, especially in the newly cleared and cultivated crops. Therefore, when considering the relative importance of species in crops, only wet season samples may be required.

(2) Changes in abundance correspond to changes in soil distribution, notably lower populations in the dry season compared to the wet season with corresponding movements down in the soil.

(a) In general, changes in total abundance of Microtermes spp. and individual species were associated with changes in soil distribution which were most marked from 0 to 50 cm. Therefore, lower dry season abundance often corresponded to movements down in the soil, though this was dependant on species and vegetation type. The most obvious changes in soil abundance and distribution were shown by the most abundant species (*M. lepidus*, *M. grassei* and *M. subhyalinus*).

(b) Changes in community structure were also most marked in the top 25 cm of the soil compared to sampling to 1 m which corresponded to the changes in soil abundance and distribution. Therefore, soil sampling from the top 25 cm should be sufficient to obtain an accurate indication of species composition and relative abundance within a vegetation type but it is not sufficient when comparing among vegetation types.

(3) Successional changes in community structure and abundance of species were identified as woodland was cleared and different crops cultivated. These changes have some predictive value in assessing populations of pest species and therefore potential yield losses.

(a) With start of maize cultivation, there was a progressive increase in *Microtermes* abundance with the greatest increases shown in the abundance of *M. lepidus* and *M. subhyalinus* (two common pest species) while long term cultivation of monoculture maize leads to a decline in *Microtermes* diversity and high populations of *M. lepidus*. Therefore, further studies which relate the cropping period of maize with *Microtermes* abundance may have use in predicting yield losses.

(b) The high populations of *Microtermes* in yam crops may be linked to the staking of yams with wooden stakes. Crops cultivated after yams may be more vulnerable to damage and yield loss due to termites. To reduce populations, wooden stakes could either be treated with a suitable pesticide or selected for resistance to termite attack.

(c) A change in crop may change species abundance and *Microtermes* community structure but these are dependant on the crops in rotation. Pest species populations may be reduced, or increases prevented, by the suitable rotation of crops; sweet potato after maize and groundnuts after yam (if non-susceptible variety or in area of low termite attack).

(d) Correct species identification is required before crop loss potential can be estimated; cultivation after clearing of woodland may result in high *Microtermes* abundance but relatively low populations of important pest species.

(e) The initial clearance and cultivation of woodland reduces *Microtermes* abundance, possibly due to disturbance by ploughing, but does not prevent further increases in the abundance of certain *Microtermes* species with continued cropping, especially *M. lepidus*.

CHAPTER FIVE

ABUNDANCE AND DISTRIBUTION OF *MICROTERMES* FUNGUS COMBS

5.1 INTRODUCTION

Fungus combs are structures found in the nests of all Macrotermitinae and are an essential element in the successful symbiosis between the termite and the fungus *Termitomyces*, except *Sphaerotermes* which builds a comb without the fungus. A fuller description of the symbiosis between *Termitomyces* and Macrotermitinae is given in the introduction in Chapter One. The fungus grows around and within the fungus comb which is constructed from fresh faecal material incorporating partly digested plant matter. The "architecture" of fungus combs varies widely with termite and ranges from small, solid sub-spheres, typically found in nests of cryptic subterranean termites, to large complex cellular and laminar constructions as seen in the mounds of *Macrotermes* (Collins, 1977; Wood & Thomas, 1989). These structures are continually being re-worked as the older portions of the comb are eaten while new faecal pellets are added, usually to the top of the fungus comb (Grassé & Noirot, 1958; Josens, 1971a). Reworking of the fungus comb with the production and consumption of fungal material is a highly developed and efficient decomposition system.

Microtermes fungus combs are found in small chambers within a diffuse network of galleries and chambers which form the nest system (Plate 5.1). The nest system is dynamic in that the nest structures and both the abundance and distribution of the termites fluctuate with changing environmental factors, i.e. food availability, soil moisture levels, predation and season.

There have been several studies on the physical and biochemical nature of the fungus comb, as reviewed in Wood & Thomas (1989). Only a few studies have examined the dynamics of the fungus comb within a subterranean nest (Bodot, 1967; Rohrmann, 1977; Josens, 1971a; Wood & Johnson, 1978).

Previous published work from the Termite Research Project in Nigeria reported an average *Microtermes* fungus comb weight of 1 g, incorporating an average of 40,000 faecal pellets. Fungus combs were distributed throughout the soil sampled to 1.5 m, with 85% of the total weight (g/m^2) found above 1 m. Food availability was suggested as a factor in seasonal fungus comb production (Wood and Johnson, 1978). In the wet season fungus combs were mainly found above 50 cm. In the dry season new fungus combs were constructed below 50 cm while those above 50 cm were consumed by the end of the dry season. Fungus comb weight was reduced by an average of 50% by the end of the dry season. Mean fungus comb weights at the end of the wet season in the top 1 m of soil were 3.3 g/m^2 in secondary woodland, 7.4 g/m^2 in short-term (1st year) maize and 8.5 g/m^2 in ranch (8 year) maize. In ranch maize, fungus comb weights were reduced to nearly zero by the end of the dry season.

Plate 5.1 Structure of *Microtermes* nest in soil from a plate nest colony of *Microtermes* nr. *lepidus* (c.f Pearce, Waite, Evans and Logan, 1991). Photograph courtesy of NRI.

key

S = soil surface
W = wood
G = galleries
FC = fungus comb in chamber
N = nursery chamber

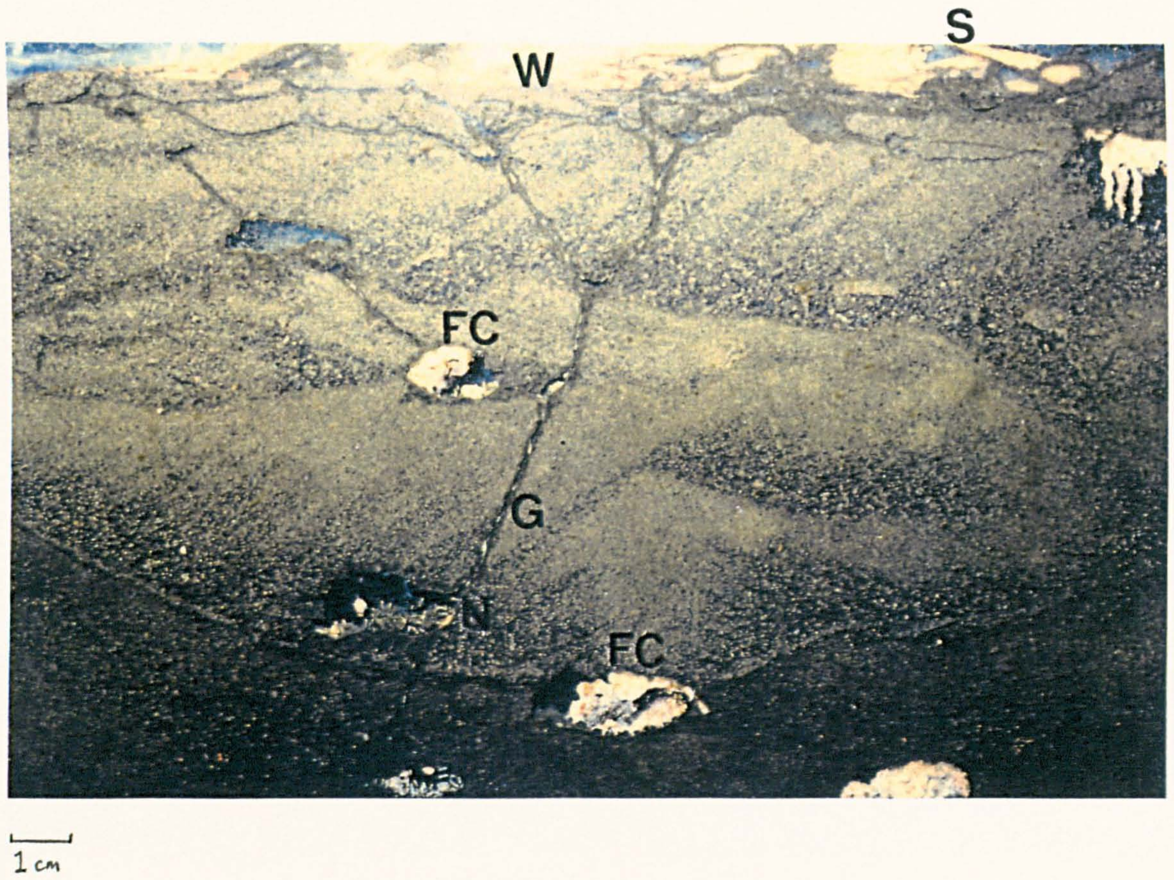

W
S
FC
G
N
FC
1 cm

Plate 5.2 Excavation of soil pits to sample *Microtermes* fungus combs at Mokwa, Nigeria. Photograph courtesy of NRI.

Studies in Sudan (El Bakri, 1986) link the mean dry weight (g) and abundance (n/m²) of fungus combs of *Microtermes sp. J.* with soil moisture levels which was itself influenced by seasonal climate and also the use of irrigation. Fungus comb dry weights and abundance were greatest in sites where soil moisture content was highest. Dry weights ranged from 3.19 g to 0.87 g and abundance from 4.2 to 10/m² with a concentration of fungus combs between 40 and 100 cm in the soil. Fungus combs of *Microtermes toumodiensis* (= *Microtermes subhyalinus* Silv.) in Guinea savanna, Côté d'Ivoire, were recorded in a range of soil types at a mean density of 0.1 to 4.8/m², with a maximum of 16.5/m² (Josens, 1971a).

These published results indicate that the abundance and dry weights of fungus combs of *Microtermes* and their distribution in the soil are influenced by seasonal climate and vegetation cover. The present study utilises field records and *Microtermes* specimens from the Termite Research Project, which includes data from Wood & Johnson (1978), to examine the following hypotheses;

(1) The abundance of fungus combs of *Microtermes* spp. and individual species will be influenced by vegetation type and seasonal climate and will correspond to changes in the community structure and abundance of *Microtermes* species.

(2) Differences in the abundance of fungus combs will correspond to changes in soil distribution, notably a movement down in the soil with a decline in weight in the dry season compared to the wet season.

These hypotheses will be examined through the following procedures;

1. Identification of *Microtermes* species sampled from fungus combs collected by the Termite Research Project and matching of identifications with available field records detailing vegetation type, sampling occasion, soil depth and fungus comb dry weights.

2. calculation of mean fungus comb abundance (n/m²), individual dry weight (g) and total dry weight (g/m²) in each vegetation type to 1 metre soil depth and at 25 cm intervals to a soil depth of 1 metre.

3. examination of fungus comb abundance, dry weight and total dry weight in relation to vegetation type, season, species and vertical distribution in soil.

4. examination of relationships among fungus comb abundance, individual dry weight and total dry weight within vegetation types.

5.2 METHODS

5.2.1 Fieldwork by Termite Research Project

Soil pits, 2 m x 1 m x 1 m deep (Plate 5.2), were dug in short-term maize, secondary woodland and long-term (ranch) maize in wet and dry seasons from 1974 to 1976 and from 1977 to 1978 in primary woodland. Normally, seven pits were excavated in each sampling occasion when the depth of each comb encountered was recorded. Combs were collected, dried and weighed and termites found on a comb were collected and stored in tubes containing 80% Ethanol for later identification. At this stage, where possible, the genus of termites from a comb was noted as other Macrotermitinae, notably *Ancistrotermes* and *Odontotermes*, also occurred in some of the sites.

5.2.2 Identification of *Microtermes* species and data analysis

In this study, species of *Microtermes* were identified as described in Chapter Four and matched with available field records which detailed sampling occasion, vegetation type, pit number and soil depth. Mean abundance ($n/m^2 \pm 1$ SE), mean individual dry weight (g ± 1 SE) and mean total dry weight ($g/m^2 \pm 1$ SE) of combs were calculated for *Microtermes* spp. and individual species in each vegetation type.

The following procedures were carried out, in accordance with Taylor's Power Law, to establish whether data transformation was required before statistical analysis. The type of transformation required was established from the value of p where $p = 1 - \frac{1}{2}b$. The value of b is calculated from the regression $\log y^{2} = \log a + b(\log \bar{x})$, when $\bar{x} = 1$. Where $p = 0$, then a logarithmic transformation should be applied and a square root transformation where $p = 0.5$ (Southwood, 1978). Twenty mean values and associated variance were calculated from sub-sets from the raw data sets for comb mean dry weights, abundance and total dry weight. Regressions were then calculated from logarithmic values of variance (y) against means (x). From the calculated values of p (Table 5.1), a square root transformation was required for comb dry weights and logarithmic transformation for comb abundance and total dry weight. Transformations were carried out on $x + 0.5$, for dry weights, and $x + 1$, for abundance and total dry weight, to allow for the occurrence of zero values (Zar, 1984). Analysis of variance was used to examine abundance, individual and total dry weight of combs with respect to vegetation, season, species and soil depth. Tukey comparisons were carried out on significant interactions; $P \leq 0.05$. Regression analysis was carried out between i. individual dry weight and abundance, ii. total dry weight and abundance, and iii. individual dry weight and total dry weight. Analysis was carried out on abundance, dry weight and total weight to a depth of 1 m and at 25 cm depth intervals to a depth of 1 m for all vegetation types and on combined groups of maize and woodland sites; to compensate for a small data set. All analyses were carried out with the aid of Statsgraphics computer software (STSC, 1989).

Table 5.1 : Regression equations from simple linear regression of variance against mean for twenty sub-sets of data from mean dry weight, abundance and total dry weight of fungus combs and p values for equation , where $x = 1$.

fungus comb variable	regression equation of variance vs mean	p where $x = 1$
dry weight (g)	$y = -0.804 + 0.99x$	0.505
abundance (n/m^2)	$y = 0.914 + 2.093x$	-0.047
total dry weight (g/m^2)	$y = 0.808 + 2.017x$	-0.009

5.3 RESULTS

Table 5.2 gives the total number of pits and fungus combs recorded for *Microtermes* in each vegetation type. Table 5.3 gives the percentage (from the total collected) of combs identified to species. Mean figures for comb values are given in parentheses in the text where appropriate.

5.3.1 Number of fungus combs identified

Not all combs could be associated with identifiable species. This was mainly due to a loss of material in the interim period of 10 years from the original study to identification at NRI. The results in this study must be considered with this in mind. However changes in species comb abundance and distribution should be highlighted in analysis as there was a high number of combs identified to species (274) with the most abundant species well represented; *M. subhyalinus*, *M. aluco* and *M. lepidus* (as identified in Chapter Four).

Table 5.2 : Number of soil pits (2 m x 2 m x 1 m) dug in each vegetation type per season and total number of *Microtermes* fungus combs collected and identified.

			Total number of fungus combs							
vegetation	season	no. of pits	M. lepidus	M. grassei	M. n.sp. C	M. subhyalinus	M. aluco	total identified	un-identified	all species
all	both	123	81	20	1	135	37	274	421	706
	dry	59	75	5	2	63	17	162	208	370
	wet	64	7	22	0	72	20	121	213	336
primary woodland	both	42	1	7	0	6	0	14	66	80
	dry	16	0	0	0	4	0	4	28	32
	wet	26	1	7	0	2	0	10	38	48
secondary woodland	both	34	5	5	1	70	19	99	99	199
	dry	20	4	4	1	48	8	65	80	145
	wet	14	1	1	0	22	11	35	19	54
short-term maize	both	40	10	15	0	55	16	96	232	330
	dry	16	5	1	1	7	7	21	76	96
	wet	24	5	14	0	48	9	76	156	234
ranch maize	dry	7	66	1	0	4	2	73	24	97

Table 5.3 : Percentage of *Microtermes* fungus combs identified to species from all collected in each vegetation type per season.

		Total number of fungus combs						
vegetation	season	M. lepidus	M. grassei	M. n.sp. C	M. subhyalinus	M. aluco	total identified	un-identified
all	both	11.47	2.83	0.14	19.12	5.24	38.81	59.63
	dry	20.27	1.35	0.54	17.03	4.59	43.78	56.22
	wet	2.08	6.55	0.00	21.43	5.95	36.01	63.39
primary woodland	both	1.25	8.75	0.00	7.50	0.00	17.50	82.50
	dry	0.00	0.00	0.00	12.50	0.00	12.50	87.50
	wet	2.08	14.58	0.00	4.17	0.00	20.83	79.17
secondary woodland	both	2.51	2.51	0.50	35.18	9.55	49.75	49.75
	dry	2.76	2.76	0.69	33.10	5.52	44.83	55.17
	wet	1.85	1.85	0.00	40.74	20.37	64.81	35.19
short-term maize	both	3.03	4.55	0.00	16.67	4.85	29.09	70.30
	dry	5.21	1.04	1.04	7.29	7.29	21.88	79.17
	wet	2.14	5.98	0.00	20.51	3.85	32.48	66.67
ranch maize	dry	68.04	1.03	0	4.12	2.06	75.26	24.74

5.3.2 Mean abundance of fungus combs

The mean abundance (n/m^2 ± 1 SE) of *Microtermes* combs to a soil depth of 1 metre and at 25 cm intervals to a depth of 1 metre in primary woodland, secondary woodland, short-term maize and long-term (ranch) maize are shown in Figures 5.3.1 and 5.3.2 respectively.

Significant interactions from analysis of variance and Tukey comparisons of abundance (n/m^2) of combs are shown in Table 5.4

5.3.2.1 Seasonal effects on abundance of fungus combs

In primary woodland (Figure 5.3.1), there were no seasonal differences in comb abundance. In secondary woodland, combs were significantly more abundant in the dry season (3.63/m^2) than in the wet (1.93/m^2) while the reverse was shown in short-term maize where combs were significantly more abundant in the wet season (4.88/m^2) than in the dry season (3.0/m^2). Significant seasonal differences in comb abundance amongst the species were found in secondary woodland and short-term maize. In both, *M. subhyalinus* combs were the most abundant and *M. n.sp. C* combs the least abundant for both seasons. In secondary woodland, *M. subhyalinus* combs were more numerous in the dry season. In the wet season *M. n.sp. C* combs were not recorded and those of *M. aluco* were more abundant than those of *M. lepidus* and *M. grassei*. In short-term maize combs of *M. subhyalinus* were significantly more abundant in the wet season (1.00/m^2) compared to the dry season (0.22/m^2). *M. grassei* produced more wet season combs than dry; 0.29 compared to 0.03/m^2.

In primary woodland, *Microtermes* combs were significantly concentrated below 75 cm in both wet and dry seasons (0.42 and 0.72/m^2) with few combs above 50 cm. However, in the wet season, there were more combs above 75 cm and fewer below 75 cm than in the dry season (Figure 5.3.2). Combs of all species recorded were more abundant below 50 cm in both seasons.

In secondary woodland, *Microtermes* combs were most abundant, in both seasons, between 25 and 75 cm. Most combs were found between 25 and 50 cm with numbers declining with increasing depth. At all depths, comb numbers were higher in the dry season than in the wet season. In the dry season, the number of combs between 0 and 25 cm (1.01/m^2) was similar to that between 25 to 50 cm (1.05/m^2) while, in the wet season, comb numbers in the top 25 cm were lower than at all other depths and markedly lower than in the dry season (0.07/m^2). In both seasons, combs of *M. subhyalinus*, *M. lepidus* and *M. aluco* were more abundant below 25 cm while combs of *M. n.sp. C* and *M. grassei* were most abundant above 25 cm.

Figure 5.3.1 : Mean abundance (n/m² ± 1 SE) of *Microtermes* fungus combs to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

KEY TO SPECIES

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

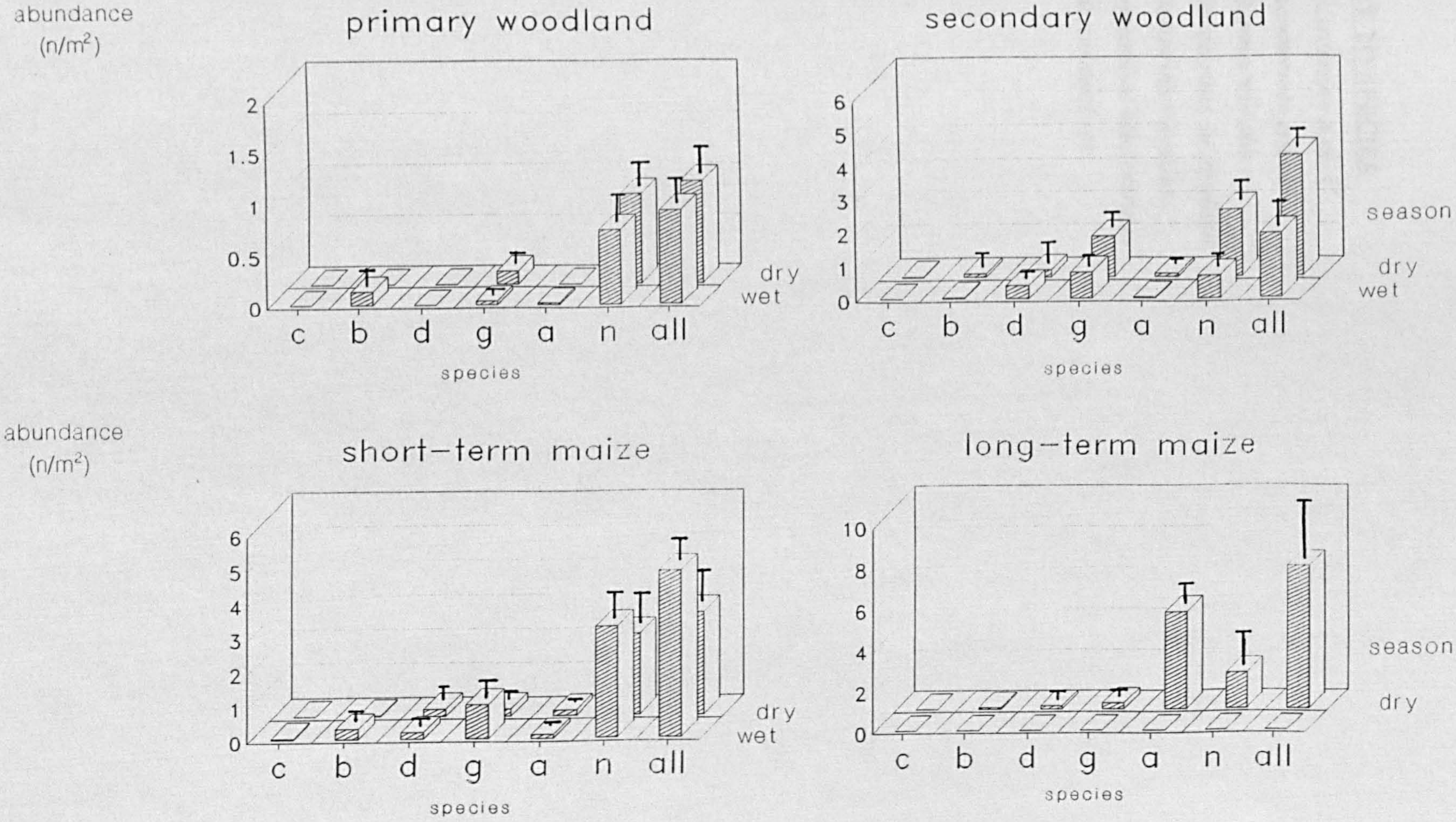
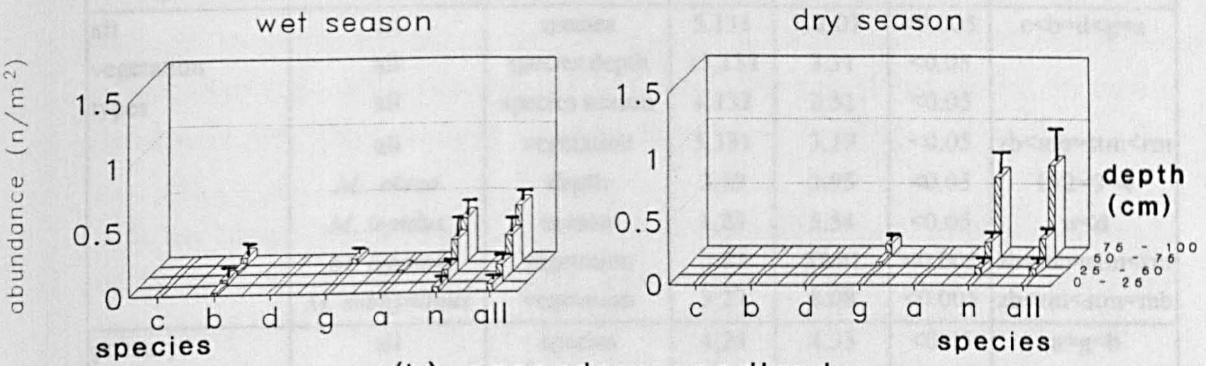

abundance
(n/m²)
primary woodland
2
1.5
1
0.5
0
c
b
d
g
a
n
all
species
dry
wet
secondary woodland
6
5
4
3
2
1
0
c
b
d
g
a
n
all
species
season
dry
wet
abundance
(n/m²)
short-term maize
6
5
4
3
2
1
0
c
b
d
g
a
n
all
species
dry
wet
long-term maize
10
8
6
4
2
0
c
b
d
g
a
n
all
species
season
dry

Figure 5.3.2 : Mean abundance (n/m² ± 1 SE) of *Microtermes* fungus combs at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

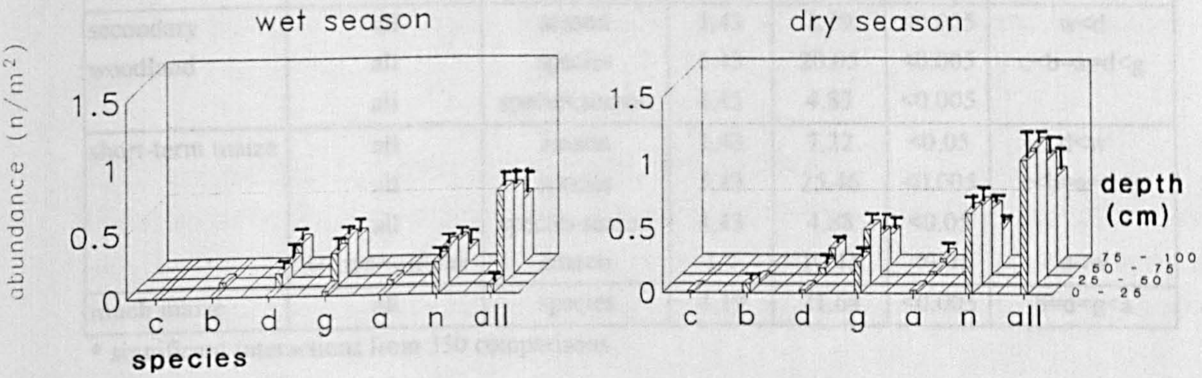
<u>KEY TO SPECIES</u>

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

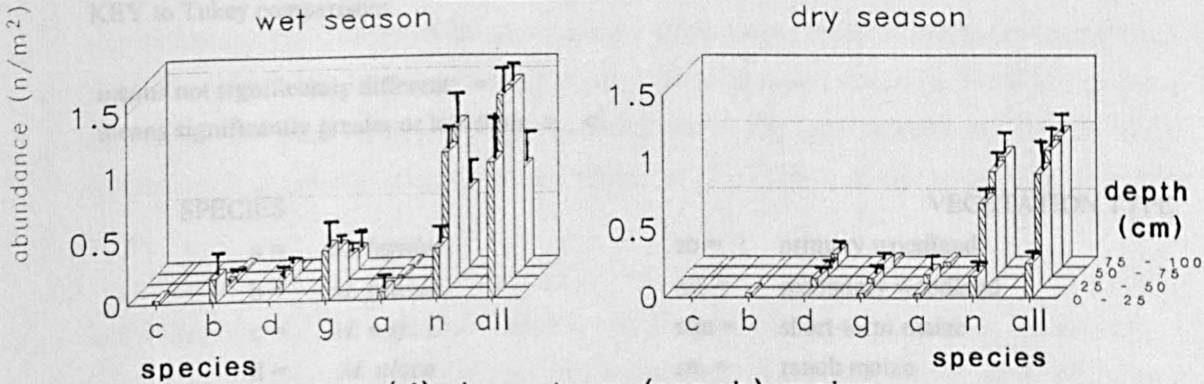
(a) primary woodland



(b) secondary woodland



(c) short-term maize



(d) long-term (ranch) maize

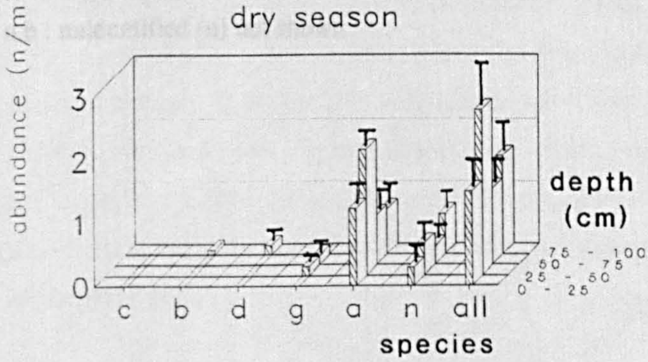


Table 5.4 : Significant interactions* from analysis of variance and Tukey comparisons of *Microtermes* fungus comb abundance (n/m^2) with species, season, depth and vegetation type.

vegetation	species	effect	d.f.	F-value	P	Tukey
all vegetation types	all	species	5,131	11.07	<0.005	c<b=d<g=a
	all	species.depth	15,131	3.31	<0.05	
	all	species.season	4,131	2.51	<0.05	
	all	vegetation	3,131	3.19	<0.05	zb<mb=stm<rm
	M.. aluco	depth	3,19	3.95	<0.05	1<2=3=4
	M. lepidus	season	1,23	5.54	<0.05	w<d
	M. lepidus	vegetation	3,23	57.91	<0.005	zb=mb=stm<rm
	M. subhyalinus	vegetation	3,27	8.08	<0.005	zb<rm<stm=mb
primary woodland	all	species	4,24	4.33	<0.05	a=g<b
	all	depth	3,24	38.73	<0.005	1=2=3<4
secondary woodland	all	season	1,43	8.19	<0.005	w<d
	all	species	5,43	20.05	<0.005	c<b=a=d<g
	all	species.season	4,43	4.83	<0.005	
short-term maize	all	season	1,43	7.22	<0.05	d<w
	all	species	5,43	25.46	<0.005	c<b=a=d<g
	all	species.season	4,43	4.88	<0.05	
	M. subhyalinus	season	1,7	10.15	<0.01	d<w
ranch maize	all	species	4,19	21.64	<0.005	b=d=g<a

* significant interactions from 350 comparisons

KEY to Tukey comparisons

means not significantly different; =
means significantly greater or less than; > , <

SPECIES
a = *M. lepidus*
b = *M. grassei*
c = *M. n.sp. C*
d = *M. aluco*
g = *M. subhyalinus*
n.b : unidentified (n) not shown

VEGETATION TYPE
zb = primary woodland
mb = secondary woodland
stm = short-term maize
rm = ranch maize

In short-term maize, the depth distribution of *Microtermes* combs did not differ significantly between the seasons. However, combs were more abundant at all depths above 75 cm in the wet season compared to the dry season, with the greatest seasonal difference shown in the top 25 cm. In the wet season, combs were concentrated above 75 cm (most between 25 and 75 cm; 1.52/m^2) while dry season combs were concentrated below 25 cm (0.84 - 0.97/m^2). In the wet season, combs of *M. grassei, M. subhyalinus* and *M. lepidus* were most abundant above 25 cm and those of *M. aluco* between 25 and 75 cm. *M. n.sp. C* combs were only found above 25 cm in the wet season.

In the dry season in ranch maize, *Microtermes* combs were most abundant between 25 and 50 cm (2.64/m^2) and least abundant between 50 and 75 cm (1.21/m^2). There was a similar number of combs in the two remaining depths (1.57 and 1.50/m^2). *M. lepidus* combs were concentrated above 50 cm while those of *M. subhyalinus* were most abundant between 25 and 75 cm. Combs of *M. grassei* and *M. aluco* were only found below 75 cm.

5.3.2.2 Vegetation cover and abundance of fungus combs

The abundance of *Microtermes* combs differed significantly amongst the vegetation types with the highest number of combs in ranch maize (6.93/m^2) followed by short-term maize (4.13/m^2) and secondary woodland (2.93/m^2) and least in primary woodland (< 1.00/m^2).

Only combs of two species were found to differ significantly in abundance amongst the vegetation types. Combs of *M. subhyalinus* were more numerous in short-term maize (0.69/m^2) and secondary woodland (1.03/m^2) than in ranch maize (0.29/m^2) or primary woodland (0.07/m^2), with primary woodland combs the least numerous. Combs of *M. lepidus* were more numerous in ranch maize (4.71/m^2) than all the remaining vegetation types.

Within the vegetation types, abundance varied significantly with species. In primary woodland, *M. grassei* combs were the most numerous (0.13/m^2) with those of the two remaining species, *M. lepidus* and *M. subhyalinus*, far less abundant (0.02/m^2 and 0.07/m^2, respectively). Combs of *M. subhyalinus* were the most numerous in secondary woodland and short-term maize. In secondary woodland, *M. aluco* combs were more numerous and *M. n.sp. C* combs less numerous than those of the remaining species, *M. grassei* and *M. lepidus*. In short-term maize, *M. n.sp. C* combs were the least numerous of all species combs. In ranch maize, combs of *M. lepidus* were much more numerous than combs of all other species.

Combs did not show significantly different soil depth distributions within individual vegetation types. Differences in comb distributions between seasons have been discussed in the previous section. However, *Microtermes* combs were generally concentrated below 25 cm, irrespective of season. *M. aluco* combs were most numerous below 25 cm with abundance increasing with depth. In maize, combs of *M. subhyalinus* were most numerous between 25 and 50 cm in the dry season and, in short-term maize, in the wet season above 50 cm. In primary woodland, combs were most numerous below 50 cm, irrespective of season while, in secondary woodland, combs were most numerous below 25 cm in the wet season and above 75 cm in the dry season. *M. grassei* combs were concentrated below 75 cm in ranch maize and primary woodland and above 25 cm in short-term maize and secondary woodland.

5.3.3 Mean individual dry weight of fungus combs

Mean individual dry weight (g ± 1 SE) of *Microtermes* combs to a soil depth of 1 metre and at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and ranch maize are shown in Figures 5.3.3 and 5.3.4, respectively.

Significant interactions from analysis of variance and Tukey comparisons of mean individual dry weights (g) of combs are shown in Table 5.5.

5.3.3.1 Seasonal effects on mean individual dry weight of fungus combs

There were no seasonal differences in *Microtermes* comb weights in primary woodland although combs were heaviest in the top 25 cm of the soil in the wet season and below 75 cm in the dry season. This was a reflection of the predominance of *M. subhyalinus* combs in the dry season and *M. grassei* combs in the wet season. Dry weights of *M. subhyalinus* combs did not vary between the seasons while *M. grassei* and *M. lepidus* combs were only present in the wet season.

In secondary woodland, *Microtermes* and *M. subhyalinus* combs were lighter in the wet season than in the dry season. Comb weights differed significantly amongst the species. For both seasons, combs of *M. n.sp. C.* were the heaviest and those of *M. subhyalinus* the lightest. Dry weights also differed amongst the species with season. In the dry season, combs of *M. n.sp. C* were the heaviest. In the wet season, when *M. n.sp. C* combs were not recorded, *M. subhyalinus* and *M. aluco* combs were heavier than those of *M. lepidus* and *M. grassei*. In the dry season, *M. lepidus*, *M. n.sp. C* and *M. grassei* combs were heaviest in the top 25 cm (Figure 5.3.4) while only light combs of *M. lepidus* and *M. grassei* were found in the wet season and no *M. n.sp. C* combs were recorded. *M. aluco* combs were heaviest below 50 cm in both seasons. However, above 75 cm, wet season combs were lighter than dry season combs. Combs of *M. subhyalinus* were lighter at all depths in the wet season than in the dry season.

Figure 5.3.3 : Mean individual dry weight (g ± 1 SE) of *Microtermes* fungus combs to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

<u>KEY TO SPECIES</u>

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

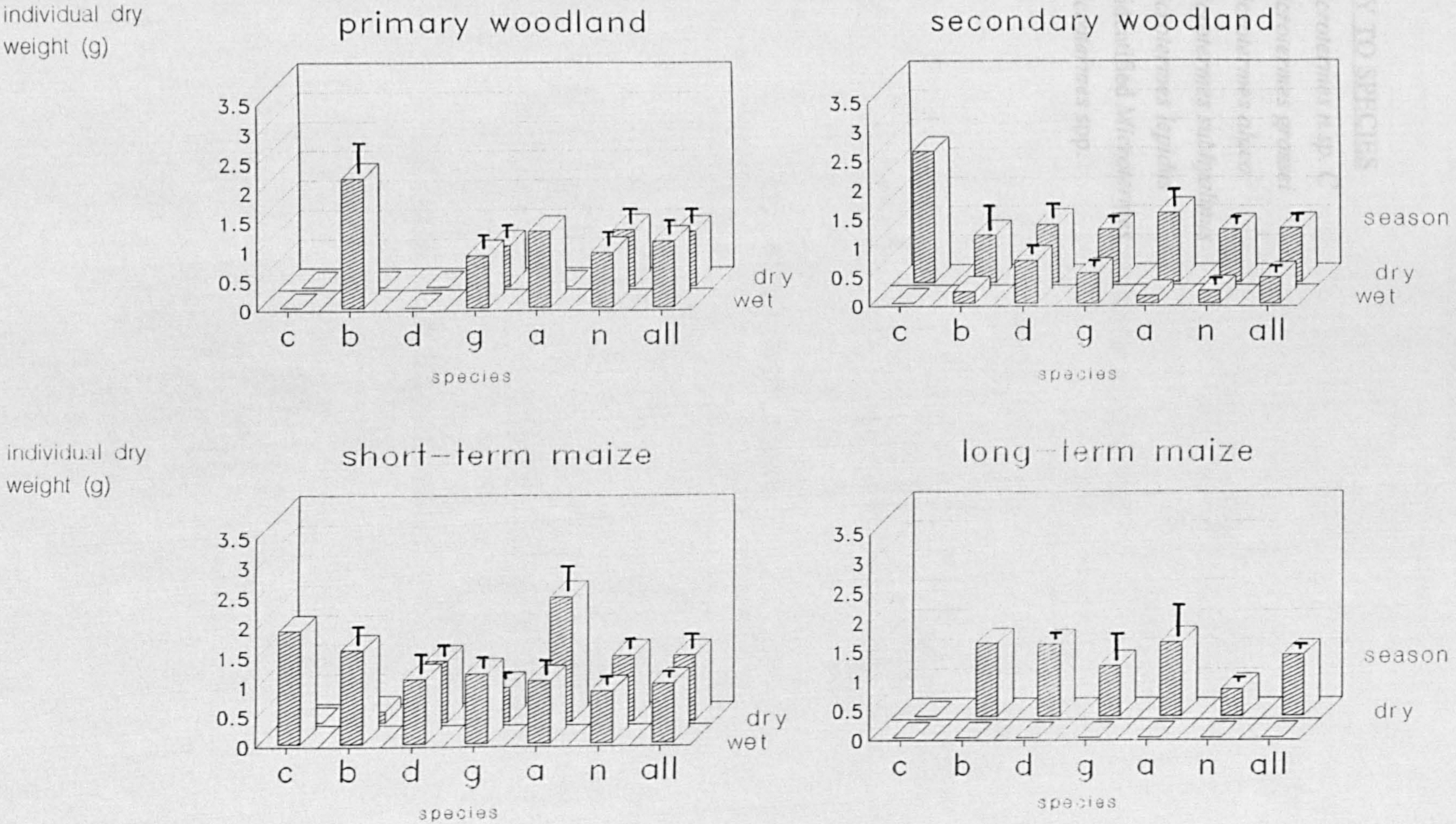

individual dry weight (g)
primary woodland
3.5
3
2.5
2
1.5
1
0.5
0
c
b
d
g
a
n
all
species
dry
wet
secondary woodland
season
dry
wet
individual dry weight (g)
short-term maize
dry
wet
long-term maize
season
dry

Figure 5.3.4 : Mean individual dry weight (g ± 1 SE) of *Microtermes* fungus combs at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

<u>KEY TO SPECIES</u>

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

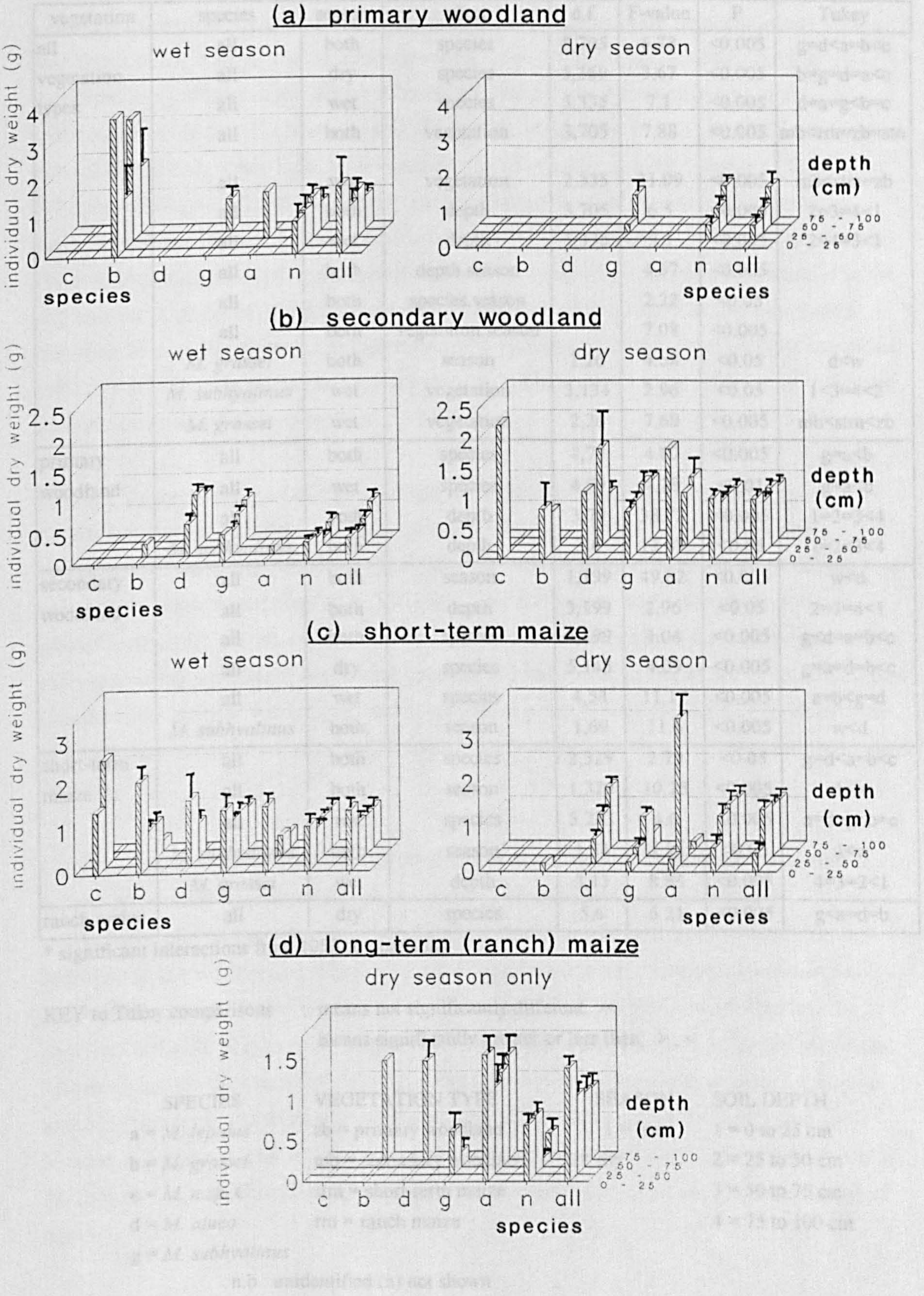

(a) primary woodland
wet season
dry season
individual dry weight (g)
0
1
2
3
4
c b d g a n all
species
depth (cm)
0 - 25
25 - 50
50 - 75
75 - 100
(b) secondary woodland
wet season
dry season
individual dry weight (g)
0
0.5
1
1.5
2
2.5
c b d g a n all
species
depth (cm)
0 - 25
25 - 50
50 - 75
75 - 100
(c) short-term maize
wet season
dry season
individual dry weight (g)
0
1
2
3
c b d g a n all
species
depth (cm)
0 - 25
25 - 50
50 - 75
75 - 100
(d) long-term (ranch) maize
dry season only
individual dry weight (g)
0
0.5
1
1.5
c b d g a n all
species
depth (cm)
0 - 25
25 - 50
50 - 75
75 - 100

Table 5.5 : Significant interactions* from analysis of variance and Tukey comparisons of mean dry weight (g) of *Microtermes* fungus combs with species, season, depth and vegetation type.

vegetation	species	season	effect	d.f.	F-value	P	Tukey
all vegetation types	all	both	species	5,705	6.78	<0.005	g=d<a=b<c
	all	dry	species	5,369	3.67	<0.005	b=g=d=a<c
	all	wet	species	5,335	7.1	<0.005	d=a=g<b=c
	all	both	vegetation	3,705	7.88	<0.005	mb<rm=zb=stm
	all	wet	vegetation	2,335	21.09	<0.005	mb<stm=zb
	all	both	depth	3,705	6.5	<0.005	2=3=4<1
	all	wet	depth	3,335	9.3	<0.005	2=4=3<1
	all	both	depth.season		4.67	<0.005	
	all	both	species.season		2.22	<0.05	
	all	both	vegetation.season		7.08	<0.005	
	M. grassei	both	season	1,26	4.58	<0.05	d<w
	M. subhyalinus	wet	vegetation	3,134	2.96	<0.05	1<3=4<2
	M. grassei	wet	vegetation	2,26	7.69	<0.005	mb<stm<zb
primary woodland	all	both	species	4,79	4.87	<0.005	g=a<b
	all	wet	species	4,79	4.28	<0.01	g=a<b
	all	both	depth	3,79	38.73	<0.005	1=2=3<4
	M. subhyalinus	both	depth	3,6	12.43	<0.05	1=2<3<4
secondary woodland	all	both	season	1,199	49.82	<0.005	w<d
	all	both	depth	3,199	2.96	<0.05	2=3=4<1
	all	both	species	5,199	4.04	<0.005	g<d=a=b<c
	all	dry	species	5,145	4.09	<0.005	g=a=d=b<c
	all	wet	species	4,53	11.17	<0.005	a=b<g=d
	M. subhyalinus	both	season	1,69	11.6	<0.005	w<d
short-term maize	all	both	species	2,329	2.79	<0.05	g=d<a=b<c
	all	both	season	1,329	10.25	<0.005	d<w
	all	wet	species	5,233	4.6	<0.005	a=d=g<b=c
	M. subhyalinus	both	season	1,54	4.33	<0.05	d<w
	M. grassei	wet	depth	3,13	8.83	<0.005	4=3=2<1
ranch maize	all	dry	species	5,6	6.21	<0.005	g<a=d=b

* significant interactions from 1050 comparisons

KEY to Tukey comparisons means not significantly different; =
means significantly greater or less than; > , <

SPECIES	VEGETATION TYPE	SEASON	SOIL DEPTH
a = *M. lepidus*	zb = primary woodland	1 = wet	1 = 0 to 25 cm
b = *M. grassei*	mb = secondary woodland	2 = dry	2 = 25 to 50 cm
c = *M. n.sp. C*	stm = short-term maize		3 = 50 to 75 cm
d = *M. aluco*	rm = ranch maize		4 = 75 to 100 cm
g = *M. subhyalinus*			

n.b : unidentified (n) not shown

In short-term maize, only *M. subhyalinus* combs weights differed significantly with season; dry season combs were lighter than wet season combs. For both seasons, weights of *Microtermes* combs were similar at all depths below 25 cm. In the top 25 cm, wet season combs were heavier and dry season combs lighter than at other depths. Wet season combs of *M. lepidus*, *M. subhyalinus* and *M. grassei* were heaviest above 25 cm and those of *M. n.sp. C* and *M. aluco* heaviest from 25 to 50 cm. Combs of *M. grassei* exhibited a significant depth distribution of dry weight; the heaviest combs were distributed in the top 25 cm of the soil. In the dry season, *M. n.sp. C* combs were not recorded and only a few light *M. grassei* combs above 25 cm were recorded. Combs of *M. subhyalinus* were lighter in the dry season than in the wet season at all depths, especially above 25 cm. Combs of *M. lepidus* were also lighter in the dry season than in the wet season at all depths, except between 25 - 50 cm where combs were heavier in the dry season. Combs of *M. aluco* in the dry season were lighter than in the wet season between 25 and 50 cm, with the lightest combs between 25 and 50 cm; weights increased with depth in the dry season so that dry season combs below 75 cm were equal in weight to wet season combs between 25 and 50 cm.

5.3.3.2 Vegetation cover effects on mean individual dry weight of fungus combs

Comb weights ranged from 1.13 g, in primary woodland to 0.45 g, in secondary woodland. Combs were significantly lighter for both seasons in secondary woodland than in other vegetation types (mean = 0.801 g). This difference was a wet season phenomenon with combs significantly heavier in primary woodland and short-term maize than secondary woodland; dry season weights did not differ amongst the vegetation types. Combs of *M. grassei* were significantly heavier in primary woodland (2.21 g) than those in short-term maize (1.49 g) which in turn were heavier than those in secondary woodland (0.20 g).

Comb weights were significantly different amongst the species within each vegetation types. In primary woodland, *M. grassei* combs were heavier than those of *M. subhyalinus* and *M. lepidus*. In secondary woodland, *M. n.sp. C* combs were the heaviest; in the wet season, when *M. n.sp. C* combs were not recorded, combs of *M. subhyalinus* and *M. aluco* were heavier than those of *M. grassei* and *M. lepidus*. In short-term maize, combs of *M. n.sp. C* were heaviest with combs of *M. subhyalinus* and *M. aluco* lighter than those of *M. grassei* and *M. lepidus*, in the wet season, *M. n.sp. C* and *M. grassei* combs were heavier than those of *M. subhyalinus*, *M. aluco* and *M. lepidus*. In ranch maize, dry season combs of *M. subhyalinus* were lighter than those of *M. lepidus*, *M. aluco* and *M. grassei*, all of which were similar in weight irrespective of depth.

5.3.4 Mean total dry weight of fungus combs

The mean total dry weight (g/m² ± 1 SE) of *Microtermes* fungus combs to a soil depth of 1 metre and at 25 cm intervals to 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and ranch maize are shown in Figures 5.3.5 and 5.3.6, respectively.

Significant interactions from analysis of variance and Tukey comparisons of total dry weight (g/m²) of combs are shown in Table 5.6.

5.3.4.1 Seasonal effects on total dry weight of fungus combs

In primary woodland, the total dry weight of *Microtermes* fungus combs did not differ between the seasons. Total dry weight of combs was concentrated below 50 cm in both seasons and declined with decreasing depth with total dry weights less in the wet season than in the dry season below 75 cm and greater than in the dry season above 50 cm.

In secondary woodland, total dry weight for *Microtermes* combs was greater in the dry season than in the wet season (3.32 g/m² compared to 0.78 g/m²) with total dry weight greatest above 25 cm and declining with increasing depth. In the wet season, total dry weight was lowest between 0 and 25 cm and similar at all depth intervals below 25 cm . Total dry weight of *M. subhyalinus* combs in the wet season was significantly less than in the dry season (0.41 g/m² compared to 1.10 g/m²) and lower than in the dry season at all depths, particularly between 0 and 25 cm. There were no seasonal differences in the total dry weight for combs of the remaining species.

In short-term maize, total dry weight for *Microtermes* combs was significantly lower in the dry season than in the wet season (4.72 g/m² compared to 3.18 g/m²), with total dry weight greater in the wet than dry season at all depths above 75 cm, especially between 0 and 25 cm. Total dry weight of *Microtermes* combs was distributed equally at depths below 25 cm in the dry season and above 75 cm in the wet season, with low total dry weight above 25 cm and below 75 cm, respectively, in each season. In the wet season, total dry weight of *M. subhyalinus* combs was significantly greater than for the dry season (1.17 g/m² compared to 0.13 g/m²). In the wet season, there was a decline in total dry weight with increasing depth while in the dry season, total dry weight was concentrated between 50 and 75 cm and less than in the wet season at each depth, particularly in the top 25 cm. Total dry weight of *M. aluco* combs in the wet season was concentrated between 25 and 75 cm and that of all other species above 25 cm. In the dry season, total dry weight of *M. lepidus* combs was concentrated between 25 and 50 cm and that of *M. aluco* concentrated below 25 cm, with the highest total dry weight below 75 cm.

Figure 5.3.5 : Mean total dry weight (g/m² ± 1 SE) of *Microtermes* fungus combs to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

KEY TO SPECIES

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

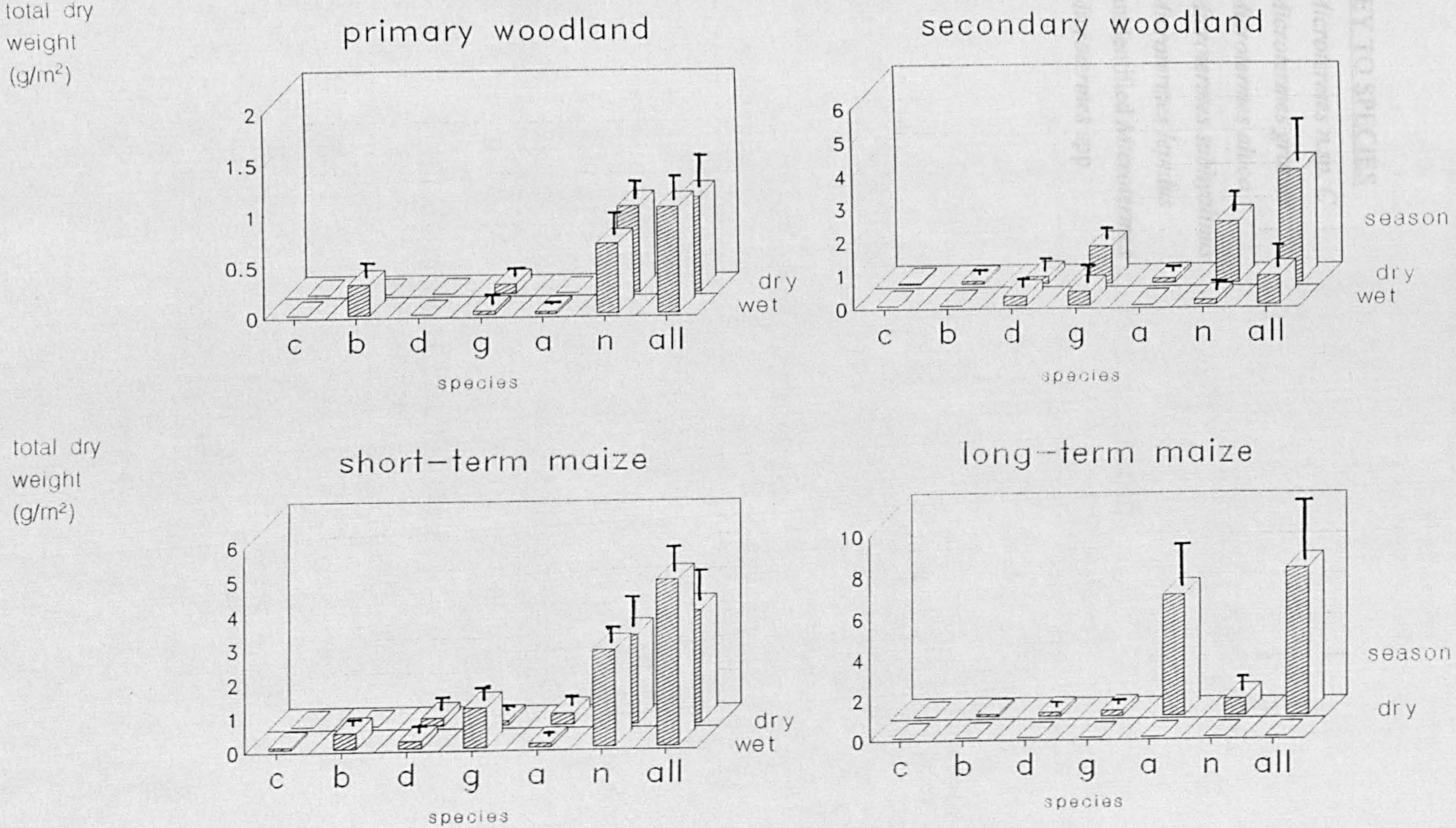


Figure 5.3.6 : Mean total dry weight ($g/m^2 \pm 1$ SE) of *Microtermes* combs at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

KEY TO SPECIES

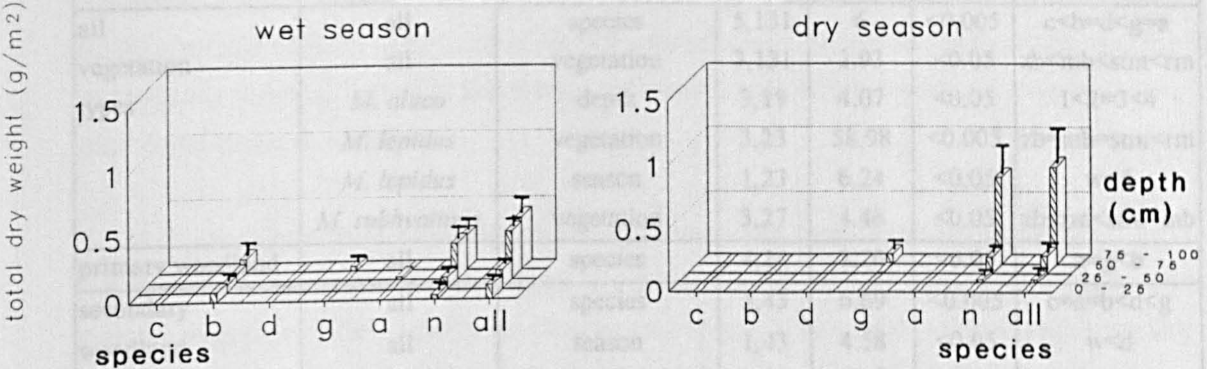
c = *Microtermes* n.sp. C
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp

Figure 5.3.6 : Mean total dry weight (g/m² ± 1 SE) of *Microtermes* combs at 25 cm intervals to a soil depth of 1 metre for wet and dry seasons in primary woodland, secondary woodland, short-term maize and dry seasons only in long-term (ranch) maize.

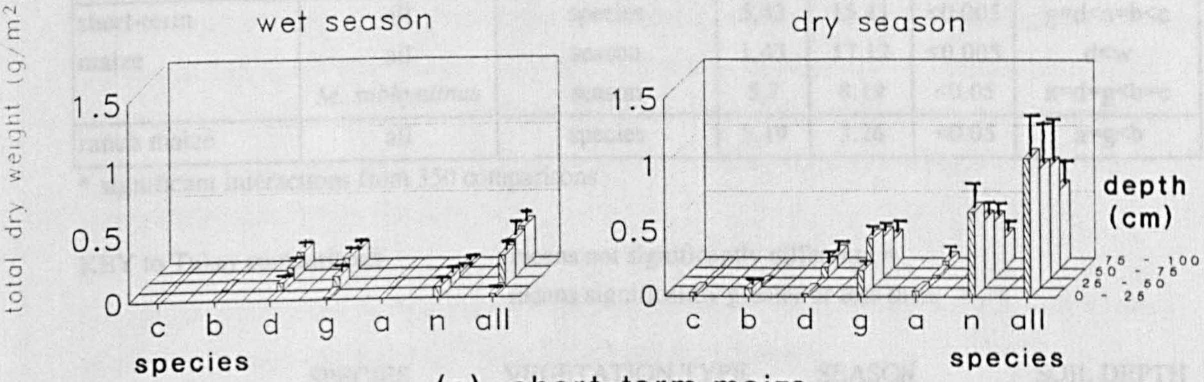
<u>KEY TO SPECIES</u>

c = *Microtermes n.sp. C*
b = *Microtermes grassei*
d = *Microtermes aluco*
g = *Microtermes subhyalinus*
a = *Microtermes lepidus*
n = unidentified *Microtermes*
all = *Microtermes* spp.

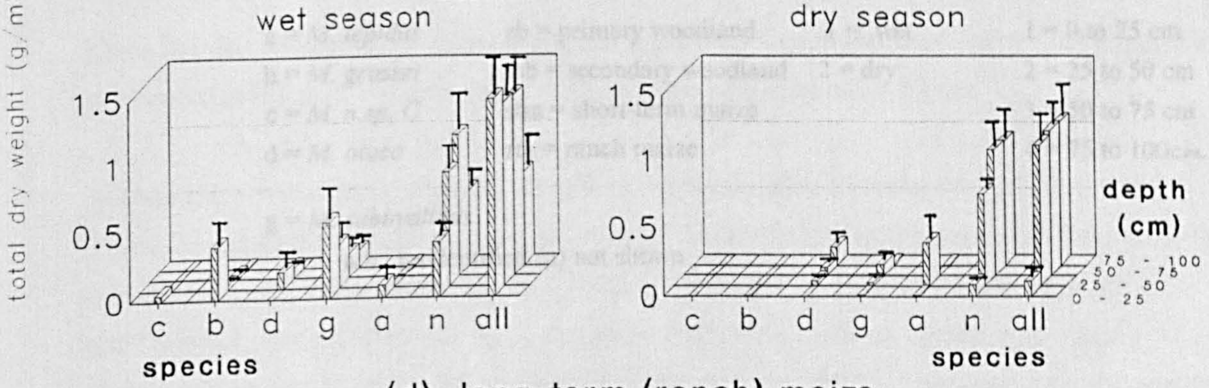
(a) primary woodland



(b) secondary woodland



(c) short-term maize



(d) long-term (ranch) maize

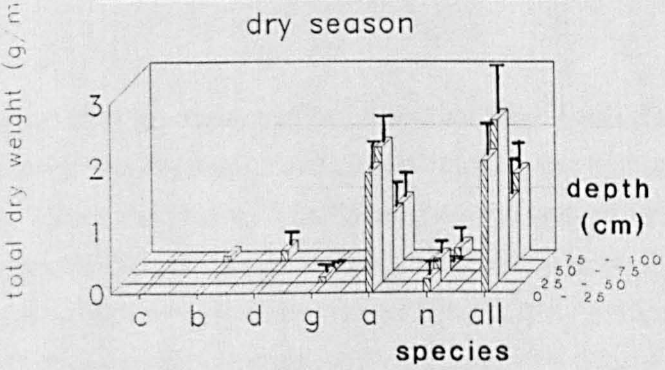


Table 5.6 : Significant interactions* from analysis of variance and Tukey comparisons of mean total dry weight (g) of *Microtermes* fungus comb with species, season, depth and vegetation type.

vegetation	species	effect	d.f.	F-value	P	Tukey
all vegetation types	all	species	5,131	6	<0.005	c<b=d<g=a
	all	vegetation	3,131	2.93	<0.05	zb<mb<stm<rm
	M. aluco	depth	3,19	4.07	<0.05	1<2=3<4
	M. lepidus	vegetation	3,23	58.98	<0.005	zb=mb=stm<rm
	M. lepidus	season	1,23	6.24	<0.05	w<d
	M. subhyalinus	vegetation	3,27	4.46	<0.05	zb<rm<stm=mb
primary woodland	all	species	4,24	3.26	<0.05	a=g<b
secondary woodland	all	species	5,43	6.69	<0.005	c=a=b<d<g
	all	season	1,43	4.58	<0.05	w<d
	M. subhyalinus	species	1,15	11.7	<0.05	w<d
short-term maize	all	species	5,43	15.41	<0.005	g=d<a=b<c
	all	season	1,43	17.12	<0.005	d<w
	M. subhyalinus	season	5,7	8.19	<0.05	a=d=g<b=c
ranch maize	all	species	5,19	3.26	<0.05	a=g<b

* significant interactions from 350 comparisons

KEY to Tukey comparisons
means not significantly different; =
means significantly greater or less than; > , <

SPECIES	VEGETATION TYPE	SEASON	SOIL DEPTH
a = *M. lepidus*	zb = primary woodland	1 = wet	1 = 0 to 25 cm
b = *M. grassei*	mb = secondary woodland	2 = dry	2 = 25 to 50 cm
c = *M. n.sp. C*	stm = short-term maize		3 = 50 to 75 cm
d = *M. aluco*	rm = ranch maize		4 = 75 to 100cm
g = *M. subhyalinus*			

n.b : unidentified (n) not shown

5.4.3.2 Vegetation cover effects on total dry weight of fungus combs

Total dry weight of combs differed significantly with vegetation cover. Total dry weight of *Microtermes* combs was higher in maize sites than in woodland sites for both seasons. Ranch maize exhibited the highest total dry weight (7.19 g/m^2) followed by short-term maize (4.25 g/m^2) then secondary woodland (2.34 g/m^2) and finally primary woodland (1.00 g/m^2). Total dry weight of *M. lepidus* combs was highest in ranch maize and for *M. subhyalinus* combs, higher in short-term maize and secondary woodland than in ranch maize and primary woodland.

Total dry weight also differed significantly amongst the species within individual vegetation types. In ranch maize, total dry weight of *M. lepidus* combs (5.89 g/m^2) was greater than that of the remaining *Microtermes* species. In primary woodland, total dry weight of *M. grassei* combs (0.18 g/m^2) was greater than that of *M. lepidus* and *M. subhyalinus* combs. Total dry weight of *M. subhyalinus* combs was the highest amongst the species in short-term maize (0.75 g/m^2) and secondary woodland (0.82 g/m^2). In secondary woodland, total dry weight of *M. aluco* combs (0.24 g/m^2) was greater than that of the remaining species while in short-term maize total dry weight of *M. n.sp. C* comb (0.06 g/m^2) was the lowest.

Although there were no significant depth distributions of total dry weight, some trends within each vegetation type (Figure 5.3.6) are noted below.

The total dry weight of *M. grassei* combs in primary woodland was distributed equally at all depths and that of the remaining species concentrated below 50 cm.

In secondary woodland, total dry weight of *M. subhyalinus* combs was concentrated below 25 cm in both seasons and greater at all in depths in the dry season compared to the wet season, especially above 25 cm. Total dry weights of *M. grassei* and *M. n.sp. C* combs were concentrated above 25 cm while that of *M. lepidus* combs was equally distributed at depths above 25 and below 50 cm and that of *M. aluco* combs concentrated below 50 cm.

In short-term maize, total dry weight of *Microtermes* combs was distributed equally at all depths below 25 cm in the dry season and above 75 cm in the wet season with low total dry weight above 25 cm and below 75 cm in each season respectively; total dry weight in wet season was greater than in the dry season at all depths above 75 cm. In the wet season, total dry weight of *M. aluco* combs was concentrated between 25 and 75 cm and that of all other species concentrated above 25 cm; total dry weight of *M. subhyalinus* combs declined gradually with increasing depth. In the dry season, total dry weight of *M. lepidus* combs was concentrated between 25 and 50 cm, that of *M. aluco* and *M.*

subhyalinus below 25 cm; the former below 75 cm and the latter between 50 and 75 cm. total dry weight of *M. subhyalinus* combs in the dry season was less than in the wet season at all depths, particularly in top 25 cm.

In ranch maize, total dry weight was concentrated above 50 cm for *Microtermes* spp. and *M. lepidus*, below 75 cm for *M. aluco* and *M. grassei* and between 25 and 50 cm for *M. subhyalinus*.

5.3.5 Correlation of abundance, individual dry weight and total dry weight of fungus combs

Table 5.7 gives significant results from correlation analysis and coefficients of determination (r^2). When results for individual species are not given, this was due either to non-significant results (short-term maize and secondary woodland) or too few comparisons to carry out the analysis (primary woodland and ranch maize). All significant regressions showed positive relationships between comb abundance, weights or total dry weight.

For all vegetation types, total dry weight of combs of *Microtermes* spp., all species and individual species, except *M. n.sp. C*, were closely correlated to abundance, especially for *M. subhyalinus* and *M. lepidus*. Total dry weight of *M. grassei* combs showed similar correlation with individual dry weight.

In primary woodland, total dry weight of *Microtermes* combs correlated significantly, but poorly, with abundance and individual dry weight. In secondary woodland, total dry weight correlated highly with abundance and poorly with individual dry weight for both *Microtermes* and *M. subhyalinus* combs. In short-term maize, total dry weight for *Microtermes*, *M. subhyalinus* and *M. aluco* comb correlated highly with abundance while total dry weight for *M. grassei* combs correlated highly with both abundance and individual dry weight. In ranch maize, total dry weight of *Microtermes* and *M. lepidus* combs correlated highly with both abundance and individual dry weight while individual dry weight also correlated with abundance of *Microtermes* and *M. lepidus* combs.

Table 5.7 : Significant interactions* from correlation analysis of *Microtermes* fungus combs total dry weight (g/m^2) against dry weight (g); total dry weight against abundance (n/m^2) and dry weight against abundance.

vegetation	species	independent variable	dependent variable	r2	F-value	P	n
all	total	IDW	T	42.06	69.69	<0.005	98
	total	N	T	79.47	371.51	<0.005	98
	total	N	IDW	7.85	8.18	<0.01	98
	all species	IDW	T	26.65	28.7	<0.005	81
	all species	N	T	79.18	300.43	<0.005	81
	M. grassei	IDW	T	41.92	7.22	<0.05	12
	M.aluco	N	T	58.23	23.7	<0.005	19
	M.grassei	N	T	77.71	34.86	<0.005	12
	M.grassei	N	IDW	77.74	34.32	<0.005	12
	M.lepidus	IDW	T	41.07	8.36	<0.05	14
	M.lepidus	N	T	84.28	64.35	<0.005	14
	M.subhyalinus	IDW	T	81.33	135.04	<0.005	33
	M.subhyalinus	N	T	36.33	17.69	<0.005	33
primary woodland	total	IDW	T	32.7	9.72	<0.01	22
	total	N	T	53.91	23.39	<0.005	22
secondary woodland	total	IDW	T	53.48	28.74	<0.005	27
	total	N	T	82.37	56.43	<0.005	27
	total	N	IDW	19.11	5.9	<0.05	27
	all species	IDW	T	26.63	11.98	<0.005	35
	all species	N	T	71.88	84.38	<0.005	35
	M.subhyalinus	IDW	T	42.38	11.77	<0.005	18
	M.subhyalinus	N	T	77.19	54.15	<0.005	18
short-term maize	total	IDW	T	33.62	17.22	<0.005	36
	total	N	T	85.95	207.97	<0.005	36
	all species	IDW	T	28.36	13.46	<0.005	30
	all species	N	T	79.18	129.33	<0.005	30
	M.aluco	N	T	91.66	76.98	<0.005	7
	M.grassei	IDW	T	73.45	13.83	<0.01	7
	M.grassei	N	T	87.16	33.93	<0.005	7
	M.subhyalinus	IDW	T	34.09	6.21	<0.05	14
	M.subhyalinus	N	T	86.58	77.4	<0.005	14
ranch maize	total	IDW	T	94.92	205.48	<0.005	13
	total	N	T	87.47	76.78	<0.005	13
	total	N	IDW	77.63	38.18	<0.005	13
	all species	N	T	83.02	39.12	<0.005	10
	M.lepidus	IDW	T	76.05	15.88	<0.01	7
	M.lepidus	N	T	73.57	13.92	<0.05	7

* significant results from 105 comparisons

key

IDW = individual dry weight

T = total dry weight

N = abundance

5.4 DISCUSSION

Since only a proportion of the combs could be associated with individual species, conclusions as to the influence of vegetation type, season and soil depth on the abundance and distribution of combs of these individual species must be treated with caution. Only further research can substantiate any conclusions presented in this study. The discussion makes use of the data presented in Chapter Four on the soil abundance and distribution of Microtermes to aid in the interpretation of results.

5.4.1 Seasonal effects on abundance, individual dry weight and total dry weight of fungus combs

Primary woodland : The lack of seasonal change in the abundance, total dry weight or dry weight of *Microtermes* combs and their concentration below 75 cm may reflect the presence of other termites, especially wood and litter feeders, which are known to be more abundant in primary woodland that in other vegetation types in Southern Guinea savanna (Wood et al, 1977b). Other termites which also colonise the upper soil region may restrict the build up of *Microtermes* combs either through competition for food resources or for nesting sites.

An increase in numbers of species constructing combs higher up in the soil in the wet season corresponds to an increase in foraging activity as a response to food availability and the soil micro-climate. This corresponds to the higher wet than dry season abundance of species in the top 25 cm of the soil. The absence of *M. lepidus* and *M. grassei* combs in the dry season can be attributed to construction below the maximum sampling depth (1 m) as both soil sampling to a depth of 1 m recorded both these species in the dry season though at much lower abundance than in the wet season.

Unfortunately there was no data available for *Microtermes* soil abundance for this study period. However, population data available from 1974 to 1976, show that there were no seasonal differences in the abundance of *Microtermes* spp. while *M. grassei* and *M. subhyalinus* were the most abundant species in primary woodland. These parallel the lack of seasonal differences in *Microtermes* spp. combs and relative abundance of combs of these two species.

Secondary woodland : *Microtermes* constructed fewer lighter combs and hence lower total dry weight in the wet season than in the dry season, particularly above 25 cm. These results differ from those of Wood and Johnson (1978) who noted lower dry season total dry weight (referred to as "comb weights", g/m^2) and total dry weight which was always lowest above 25 cm, irrespective of season. However their study dealt solely with combs sampled at the end of each season while secondary woodland combs for this study were collected earlier in each season. It is probable that this study shows intermediate stages in the cycle of comb formation and destruction from season to season. Thus, this study would still support the previous results which suggest that *Microtermes* comb total dry weight is increased in the wet season and utilised in the dry season when food resources are more limited and the upper soil environment less hospitable i.e. drier and warmer (Wood & Johnson, 1978). The differences in total dry weight above 25 cm may be the result of sampling error or, more likely, due to differing environmental conditions: soil moisture, soil temperature and food availability. The results from this study also suggest that comb total dry weight in the top 1 metre of soil can drop to much lower levels (0.8 g/m^2) than previously recorded in this area.

Differing soil environments between seasons would affect comb dry weight, abundance and total dry weight. Several factors may be influencing the soil environment; air temperature, rainfall, reduction in forage, interactions among the *Microtermes* species themselves, food site preferences or competition for resources with other termites/soil organisms. The relative importance of these factors cannot be determined from this study. However, it can be stated that these factors are most influential on combs in the top 25 cm of the soil.

The predominance of *M. subhyalinus* combs above 25 cm suggests that this species was the main element in differences in *Microtermes* comb abundance and total dry weight while all species exhibited slightly heavier dry season combs, at all depths, accounting for the seasonal difference in *Microtermes* comb weights. This corresponds with results from soil abundance and distribution, where *M. subhyalinus* was the predominant species in secondary woodland with greater abundance in the wet compared to dry season, particularly in the top 25 cm of the soil.

Short-term maize : Results concur with those of Wood and Johnson (1978) for total dry weight of *Microtermes* combs in one - year old maize, although their study showed total dry weight to be lower in both seasons. Seasonal differences in *Microtermes* comb abundance and total dry weight were most noticeable as a "swap" from the two depth levels, 0 to 25 cm and 75 to 100 cm; abundance and total dry weight were greater in the wet season than in dry season above 25 cm and lower than in the dry season below 75 cm while dry weights were only greater in the wet season compared to the dry season above 25 cm. These results may be explained by the greater number of wet season combs of *M. subhyalinus* and, to a lesser extent, *M. grassei* above 25 cm with fewer wet season combs of *M. subhyalinus*, *M. aluco* and *M. lepidus* below 75 cm compared to the dry season. Soil abundance data show that the most abundant species in short-term maize was *M. subhyalinus* which would explain, in part, the dynamics of *Microtermes* spp. and *M. subhyalinus* fungus combs as this species was more abundant in the wet season compared to the dry season, especially above 50 cm.

It is assumed that, in the dry season, species consumed combs in the upper regions of the soil and constructed new combs at lower depths (Wood & Johnson, 1978; Josens, 1971a & b). Results from this study agree, in part, with this assumption; fewer combs of lighter weight in the top 75 cm in the dry season, especially from 0 to 25 cm, suggest that these combs have been consumed. However, if new combs were constructed at lower depths, then this occurred below 1 m; comb numbers, dry weights and hence total dry weight were little different between the seasons from 75 to 100 cm although they were relatively more abundant in the dry season at this depth that at any other. The reduction in comb numbers, dry weights and total dry weight in the top 1 m is mainly due to an inability to replenish combs due, either, to lack of food or an inhospitable soil environment. The soil surface would be exposed after harvest and therefore more prone to soil moisture losses and higher soil temperatures and it is well documented that termites, including *Microtermes*, move down in the soil to escape desiccation (Bodot, 1967; Lepage, 1974). In addition, foraging activity would be reduced with the reduction in surface food available after harvest.

Comparisons with the population data from Chapter Four, indicate that the seasonal change in fungus comb factors relate to a reduction in *Microtermes* populations above 50 cm from wet to dry seasons. The predominance of combs of *M. subhyalinus* corresponds to the predominant abundance of this species. Unusually, *M. lepidus* was abundant in maize but few combs were found. Fungus combs of this species may be lower in soil (below the 1 m sampling depth) or may form part of the unidentified samples.

5.4.2 Vegetation cover effects on abundance, individual dry weights and total dry weight of fungus combs

Differences in *Microtermes* comb abundance, dry weight and total dry weight were mainly due to *M. subhyalinus* and *M. lepidus*. *M. n.sp. C* combs were rare and only encountered on a few occasions in secondary woodland and short-term maize where this species produced the heaviest combs; this corresponds with the low soil abundance and rare occurrence of this species in all vegetation types. *M. aluco* combs were not present in primary woodland and this, combined with a low soil abundance and occurrence, may indicate that *M. aluco* not be common in this vegetation type. *M. grassei* combs maintained similar abundance and total dry weight in all vegetation types but its combs were heaviest in primary woodland. This concurs with previous published work which records *M. grassei* as a woodland species (Wood, 1981) and with results from soil abundance which showed that *M. grassei* was more abundant in both woodland sites, particularly in secondary woodland, than in the remaining vegetation types. These factors indicate that this species may not increase fungus comb numbers with food availability or type, as shown by other species, but rather concentrates on a limited number of combs.

Higher weights of combs in secondary woodland indicate that either food type or competition was less limiting in this vegetation type.

Primary woodland supported combs of only three species (*M. lepidus*, *M. subhyalinus* and *M. grassei*) at low abundance in the top 1 metre of soil. Species identification from the total number of combs collected was the lowest for the four vegetation types and it is possible that combs of other species were present but not recorded (*M. aluco* and *M. n.sp. C*). However, the abundance of fungus combs did reflect the soil abundance of each species; *M. lepidus*, *M. subhyalinus* and *M. grassei* were the most abundant species recorded in primary woodland while *M. aluco* and *M. n.sp. C* exhibited low abundance. As previously suggested, competition with other termites for resources may be important in comb abundance and distribution in woodland.

The differences in *Microtermes* comb abundance and depth distribution between the two woodland sites is quite marked. There are certain elements which may be relevant but their importance cannot be determined from this study. The first, as above, is competition from other termites which are known to be more abundant in primary woodland that in other vegetation types in Southern Guinea savanna. The second was a difference in sampling dates between the two vegetation types which would have obvious consequences when studying dynamic systems.

The results further confirm that cultivation of maize results in a build up in *Microtermes* comb numbers and hence total dry weight (Wood & Johnson, 1978). It further suggests that, following initial cultivation of maize, combs occur at similar abundance levels and species composition to that found in secondary woodland, although heavier combs may be produced, especially above 25 cm in the soil. However, prolonged cultivation of maize leads to an increase in the numbers and total dry weight of *M. lepidus* combs at all depths, in particular above 25 cm. This corresponds to the increase in the soil abundance of *M. lepidus* in short-maize, especially above 50 cm, and the high abundance and concentration in the top 25 cm exhibited by this species in both long-term maize sites. The remaining species maintain similar numbers of combs compared with short-term maize but these are only found below 25 cm but these support much lower populations of each species compared to short-term maize.

5.4.3 Total dry weight of fungus combs as a product of individual dry weight and abundance.

Total dry weight of combs of total and individual species, except *M. n.sp. C* and *M. grassei*, were mainly a product of comb abundance in all vegetation types, except long-term cultivated maize; total dry weight increased as abundance increased. The best relationships between total dry weight and abundance were shown in secondary woodland

and short-term maize where comb numbers were higher than compared to primary woodland. The results also show that, in primary woodland, secondary woodland and short-term maize, individual dry weight did not increase with increasing abundance. *M. n.sp. C* combs were too few to carry out analysis while total dry weight of *M. grassei* combs was equally a product of individual dry weight and abundance.

In long-term (ranch) maize, total dry weight of *Microtermes* and *M. lepidus* combs increased with both abundance and individual dry weight while individual dry weight of *Microtermes* combs increased as abundance increased. Differences shown between the vegetation types could be due to differing levels of competition for both food and space. Heavier and more abundant of *M. lepidus* combs in long-term maize combs compared to other vegetation types may be as a result of reduced competition for resources from other termites, especially other *Microtermes* species.

5.5 CONCLUSION

The hypotheses presented in this study are re-examined:

(1) The abundance of fungus combs of *Microtermes* spp. and individual species will be influenced by vegetation type and seasonal climate and will correspond to changes in the community structure and abundance of *Microtermes* species.

(a) The abundance and distribution of combs continually change, with seasonal differences in dry weight, abundance and total dry weight. Therefore, sampling over seasons should be carried out on similar dates in and between sites.

(b) Vegetation cover has a major influence on seasonal changes in the abundance, dry weights and total dry weight of *Microtermes* species combs. This may be a reflection of food availability and soil conditions.

(c) In primary woodland, species composition of combs differed between seasons

(d) Changes in the total dry weight of fungus combs were generally a result of changes in comb abundance, except in long-term maize.

(e) *Microtermes* fungus combs increased in both total dry weight and individual dry weight with increased abundance in long-term maize and this was probably due to reduced competition from other termite species.

(f) From the results of Wood and Johnson (1978), it was expected that seasonal fluctuations in *Microtermes* comb abundance and distribution would be greater in short-term maize than in secondary woodland. Differences in seasonal food availability and soil conditions would be more pronounced in the dry season in maize when only residues are left after harvest and the soil is more exposed while food would be available throughout the year in woodland. However, there was little difference in comb abundance and total dry weight in the dry season between the two vegetation types in this study. The short period of cultivation of maize may not have been sufficient to produce the previously recorded seasonal differences and the presence of residual woodland roots and litter providing supplementary food sources in maize. There was, however, a greater change in the soil depth distribution of combs between seasons in short-term maize than in the other vegetation types.

(g) Of all species, *M. subhyalinus* showed the greatest seasonal fluctuations in abundance and distribution in secondary woodland and short-term maize and also had the most abundant combs.

(h) Dynamics of *Microtermes* spp. and individual species fungus combs can be compared with soil abundance and distribution.

(2) Differences in the abundance of fungus combs will correspond to changes in soil distribution, notably a movement down in the soil with a decline in weight in the dry season compared to the wet season.

(a) In secondary woodland, seasonal differences related to changes in abundance and weights of species combs above 25 cm and below 75 cm in the soil.

(b) In short-term maize, seasonal differences were due to changes in species comb abundance throughout the top 1 m of soil.

(c) Of all species, *M. subhyalinus* showed the greatest seasonal fluctuations in abundance and distribution in secondary woodland and short-term maize and also had the most abundant combs.

(d) With the cultivation of maize, combs increased in abundance in the top 50 cm of the soil and were not adversely effected by ploughing, which was carried out when there were few combs at this soil depth.

(e) Future studies could examine the effect of ploughing at the end of the wet season and determine whether combs would be re-constructed to the same extent if the dry season food source was reduced.

CHAPTER SIX

FORAGING BY *MICROTERMES* ON SURFACE LAID BAITS

6.1 INTRODUCTION

Foraging by termites on wood baits has been widely used as a method of studying the susceptibility of various timbers to termite damage and the efficacy of soil treatments in termite control (Harris, 1969). These techniques were modified by the Termite Research Project (Wood et al., 1977a) to examine foraging activity of wood and litter feeding termites at Mokwa and, primarily, to study the relationship between foraging activity and abundance of *Microtermes*, which was the dominant termite genus in cultivated plots. The TRP study had a practical objective to determine whether measurements of foraging at baits could be related to population density. This aspect of the use of baits will be examined in Chapter Seven.

In a study of reproductive isolating mechanisms among *Microtermes* species found at Mokwa, Wood (1981) examined spatial distribution on baits and in soil samples in a secondary woodland plot. His results indicated that *Microtermes* species often foraged simultaneously on the same baits but this co-occurrence could be explained by random occurrence i.e. there was no association amongst the species.

At the time of the fieldwork in Nigeria, there were no previous studies to indicate the suitability of bait materials, optimum size or spacing of baits. Subsequently, methods of baiting have been evaluated by several authors, as discussed below.

In Africa, in addition to that of the Termite Research Project, four field baiting studies have been carried out to study termite foraging activity and species composition.

In Ghana, Usher (1975) carried out a study to investigate the effects of farm scrub clearance on a wood feeding termite community. Partially buried sapwood was used in a baiting programme to determine differences in termite communities in a cleared area of farm scrub and an undisturbed area of farm scrub. The results showed that many termite species were not randomly distributed on the cleared farm scrub area. Clearance affected the species occurring on baits with an increase in some species, in particular *Microtermes subhyalinus*.

Buxton (1981), in Kenya, used baits (10 - 20 cm x 1 - 4 cm) from branches of indigenous *Commiphora* spp. timber. Thirty baits were placed at intervals of 5 m along a transect and examined once a month. From the distinctive foraging galleries of each species, Buxton was able to identify the different species of Termitinae and Macrotermitinae, even in the absence of termites. The study showed that foraging and consumption increased during the wetter periods.

In the northern Transvaal of Southern Africa, Ferrar (1981a, b & c) utilised the baiting method of La Fage, Nutting and Haverty (1973), which is discussed below. He showed that *Microtermes* foraged on more baits than all other termites with greatest foraging intensity during the wettest periods of the year, ranging from 3% of all baits in burnt areas to 59% in *Acacia* woodland. Foraging was rare in the dry season.

In northern Sudan, El Bakri (1986) monitored foraging by *Microtermes* species in three experiments as occurrence on baits. The first of these examined seasonal foraging on surface laid wooden baits (10 x 2.5 x 2 cm) in sugar-cane stubble. Baits were laid out at 3 m x 3 m intervals in two irrigated and two rain-fed plots; each approximately 2.3 ha. Baits were examined every three weeks for 26 months; two rainy and two dry seasons. Three species were recorded foraging on baits; *M. lepidus*, *M. sp. J* and *M. tragardhi*. *Microtermes* foraging on baits ranged from 1.96% of all baits laid in the dry season to 33.96% in the rainy season, with foraging by *M. sp. J* the most intense and the least by *M. tragardhi*. In all plots foraging was lowest in the dry season and highest three months into the rainy season. Foraging was higher in irrigated plots than in the rain-fed plots.

The second experiment examined the effect of shade on foraging by *Microtermes*. Baits (3 m x 3 m grid) were laid out in shaded and exposed areas of plots in a rain-fed orchard (plots 39 m x 48 m). Seasonal variations in foraging, similar to the first experiment, was shown by the two species present, *M. sp. J* and *M. lepidus*, with low foraging in the dry season (< 5% attack). In the rainy season, *M. sp. J* foraging on baits was higher in the shaded areas (23.24 - 23.63%) than in exposed areas (9.64 - 14.41%).

The third experiment examined diurnal foraging on cardboard discs (10 diameter and 0.7 cm thickness) on an irrigated lawn of *Cynodon dactylon* and a rain-fed bush area. Fifty baits were monitored every 3 hours over 24 hours at weekly intervals for two months. During the rainy season on the irrigated lawn, *M. sp. J* and *M. lepidus* foraging activity was lowest in the mid afternoon when the air temperature was highest and peaked in the early morning and evening when air temperature was lowest. Foraging was, again, lower in the dry season for both species. There were no diurnal patterns in the rain-fed area where only low levels of foraging were noted.

In the Arabian Peninsula, several studies have been made of termite foraging activity on baits (Abou Ghadi and Khalifa, 1982; Ali, Abu Ghadir and Abel Hafez, 1982; Badawi, Faragalla and Dabbour 1984; Abushama and Al-Houty, 1981). All these studies identified that termite foraging was related to available soil moisture and soil temperature.

Extensive baiting studies have been carried out in desert regions of the Neotropical region. La Fage et al. (1973) presented a modification of the bait-sampling method using toilet rolls as a food source to attract termites to the surface. Baits were placed on the ground at 1 m x 1 m intervals in plots of 10 m x 10 m; a total of 100 baits per plot. Baits were examined at weekly intervals. This method was used in the desert grassland ecosystem of the Arizona desert to provide information on the spatial distribution and surface foraging behaviour of two subterranean termites; *Gnathamitermes perplexus* (Banks) and *Heterotermes aureus* (Snyder). Identification of species was aided by their characteristic mode of attack and gallery formation. Results showed that soil temperature and soil moisture influenced foraging activity while each species showed characteristic foraging gallery patterns within and around the toilet rolls.

This baiting method was used by Haverty et al. (1974, 1975) and Jones, Trosset and Nutting (1987) to further examine relationships between species foraging and environmental factors in the Arizona desert. In both studies, baits were examined over a 24 h period once a week. Foraging intensity was categorised from gallery formation and the number of species present. Foraging by the subterranean termite *Heterotermes aureus* was greatest where vegetation cover was most dense and foraging activity increased as soil temperature and moisture content increased. Jones and Trosset (1991) examined the patterns of food resource use by *G. perplexus* and *H. aureus* with toilet roll baits. The authors concluded that patterns of co-occurrence on baits indicated that the two species were separated both spatially and temporally with interspecific interference competition affecting species spatial and temporal distribution.

Abensperg-Traun (1993) carried out a comparative study of baiting methods for sampling wood feeding subterranean termites in Western Australia. Undecayed/untreated wooden stakes of five timber species (two indigenous and three exotic), toilet rolls and sawdust baits were used to examine foraging activity and bait consumption every four weeks over a twelve month period. Species richness of the termite assemblage was highest on the wooden baits while the frequency of occurrence of individual species differed amongst the baits. Bait consumption was greatest on wooden baits from two exotic tree species and toilet rolls. The author concluded that a composite sampling strategy is required to adequately sample an assemblage of wood-feeding termites where there are different feeding preferences and strategies.

The studies described above have established that termite foraging on baits exhibits diurnal patterns and seasonal differences, which can be related to seasonal weather conditions affecting soil temperature and moisture. Foraging activity is often effected by vegetation cover with activity often higher in more shaded areas. Studies of termite communities show that species composition alters after clearing and cultivation with *Microtermes* increasing in activity on baits. There are differing results on the co-occurrence of species on baits with one record of random distribution (Wood, 1981) and two records of non-random distribution (Jones and Trosset, 1991; Usher 1975).

This study will examine seasonal, temporal and vegetation cover effects on foraging by *Microtermes* spp. and individual species on baits in cultivated and uncultivated sites at Mokwa to test the following hypotheses:

(1) The community structure and foraging activity of *Microtermes* will be influenced by vegetation type and seasonal climate, notably reduced foraging in the dry season compared to the wet season, with successional changes identified as woodland is cleared and different crops cultivated.

(2) Spatial distribution of species can be detected from foraging activity.

These hypotheses will be examined through the following procedures:

1. Identification of *Microtermes* species collected from baits by the Termite Research Project and matching of identifications with available field records from TRP.
2. Examination of foraging activity of *Microtermes* in uncultivated and cultivated sites with season and year.
3. Examination of the spatial distribution and association of *Microtermes* species on baits in each vegetation type.

6.2 METHODS

6.2.1 Fieldwork carried out by the Termite Research Project

Surface-laid softwood baits (15.2 cm x 2.54 cm x 2.54 cm) were placed at 4 m x 3.5 m intervals on each plot where soil sampling was being carried out to quantify *Microtermes* abundance. There were a total of 297 baits (11 x 27) per plot per sampling occasion. Figure 6.1 shows the bait layout on the plots. There were a total of thirty nine plots for nine different vegetation types. There were nine vegetation types; primary (undisturbed) woodland, twelve and twenty-six years of continuous maize cultivation, secondary (regenerated) woodland and the following which were established from newly cleared secondary woodland: pasture, sweet potato, groundnuts, yam and (short-term) maize. Full descriptions of the plot layouts and cultivation methods are given in Chapter Three.

Baits were left for periods ranging from 4 to 8 weeks, with most sampling carried out at 4 weekly intervals when all available baits remaining were collected. Termites present on baits were collected and preserved in 70% Ethanol for identification. Each tube was labelled with a plot and bait number which could be used at a later date to reconstruct the foraging pattern of species in each plot.

6.2.2 Identification of *Microtermes* species and analysis of data

The collections were identified during the course of this study using a key developed at the Natural Resources Institute (NRI) (Appendix 1). The number of bait sampling occasions for each vegetation type are given in Table 6.1. The total number of baits from which *Microtermes* spp. were collected (T) and the total number of baits from which individual species were collected (n) were calculated for each plot.

6.2.3 Foraging activity of *Microtermes* on baits

The following measures of diversity were calculated to examine community structure for each vegetation type in wet and dry seasons. These methods are described in greater detail in Chapter Four and formulae are given in the Appendix.

(i) Species richness
(ii) Shannon-Wiener diversity index (H')
(iii) Evenness index (J')

The data were used to calculate the occurrence of *Microtermes* on baits (B_a) as a percentage of the total number of baits laid; ($B_a = T/297 \times 100$). Two estimates of the percentage occurrence on baits were calculated for individual species. The first ($B_{\%l}$) was the occurrence of each species on baits (n) as a percentage of the number of baits laid ($B_{\%l} = n/297 \times 100$) and the second ($B_{\%a}$) the occurrence of each species on baits (n) as a percentage of the total occurrence of *Microtermes* on baits ($B_{\%a} = n/T \times 100$).

Figure 6.1 : Experimental design for the layout of softwood baits in uncultivated and cultivated plots at Mokwa in the Southern Guinea savanna vegetation zone of Nigeria.

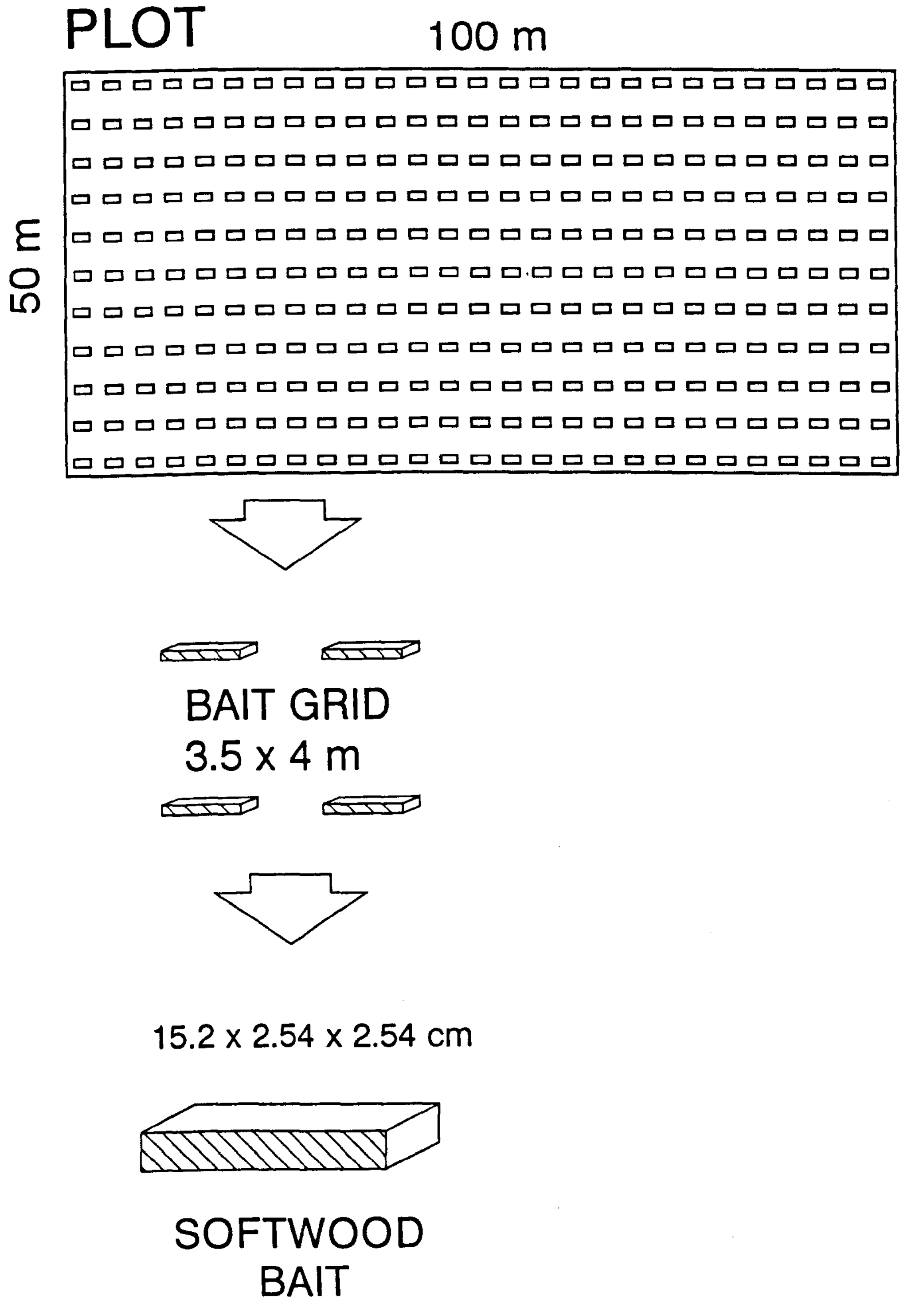

PLOT
100 m
50 m
BAIT GRID
3.5 x 4 m
15.2 x 2.54 x 2.54 cm
SOFTWOOD
BAIT

Table 6.1 : The number of sampling occasions from 297 softwood baits in each vegetation type for two wet seasons and one dry season from 1974 to 1975.

vegetation type	plot no.	season		
		wet	dry	wet
primary woodland	13	-	-	1
secondary woodland	1+12		2	3
pasture	4+5	1	1	2
groundnuts	2+11	2	2	2
sweet potato	8+10	2	1	2
yam	3+6	2	3	2
short-term maize	7+9	1	2	4
ranch maize	19	-	-	1
farm maize	20+21	1	-	1

Corrigenda

It is incorrect to carry out goodness-of-fit testing to examine the co-occurrence of *Microtermes* species on baits under the assumption that there is equal likelihood of each species occurring. Therefore, the results for this section should be disregarded.

Corrections for non-normality of the data were carried out before further analysis. Square root transformation ($X' = \sqrt{(X + 0.5)}$) was used on the counts of *Microtermes* on baits. Arcsine transformation ($p' = \arcsin \sqrt{p}$) was used on percentages of *Microtermes* on baits (p). When percentages were 0% then $p = 1/4n$ and when percentages were 100% then $p = 1 - 1/4n$ (Zar, 1984).

Statistical analysis of the data was carried out with the aid of a computer software programme Statsgraphics version 4.0 (STSC, 1989). Analysis of variance was used to examine foraging in relation to seasons, years and vegetation. Significant interactions were further examined using the Tukey multiple comparison procedure (Zar, 1984). As samples were lost during storage, foraging of individual species could only be examined within vegetation groups which were formed on the basis of 1. uncultivated + cleared only, 2. all newly cultivated crops, 3. "root" crops (sweet potato, groundnuts and yam), 4. maize, 5. short-term maize and yam and 6. groundnuts and sweet potato. The last two groups are crops which showed similar *Microtermes* spp. abundance from Chapter Four.

The data were used to construct diagrams of species distribution on baits for vegetation types where field plot layouts were available. Table 6.2 lists the plots available and relevant Appendices. Co-occurrence on baits of *Microtermes* species was examined for the above plots using goodness-of-fit testing by the log-likelihood statistic (G) with the use of Yates correction factor (Zar, 1984). Observed frequencies of 0 to 5 species on baits were compared with expected binomial frequencies to test the null hypothesis that there were no species interactions i.e. foraging by species was random. Expected frequencies were calculated assuming equal likelihood of species occurring on baits which may over-estimate the co-occurrence of rarer species. To examine this problem, goodness-of-fit testing was attempted by calculating the probability of each species occurring on baits for levels 1, 2, 3, 4 and 5 using the relative occurrence of each species on baits. G statistic could not be tested as degrees of freedom were insufficient.

The distribution of *Microtermes* spp. and, where possible, individual species on baits were examined by goodness-of-fit testing of the log-likelihood statistic (G). Plots were sub-divided into 4 x 8 quadrats; each 12.5 x 12.5 m (c.f. Pielou, 1978). The numbers of baits where *Microtermes* spp. and individual species occurred were counted in each quadrat. These observed frequencies were compared with expected Poisson frequencies to test the null hypothesis that distribution on baits was random. The co-occurrence of species were recorded from each plot and two by two contingency tables were constructed for each possible species association. Species associations were examined from these tables by goodness-of-fit testing using the log-likelihood statistic (G), with Yates correction. The degree of association was calculated from the Cramer contingency coefficient which ranges from +1 to -1, with +1 indicating complete association.

Table 6.2 : Available spatial distributions of *Microtermes* species foraging on baits for uncultivated and cultivated vegetation types in two wet seasons and one dry season from 1974 to 1975.

vegetation type	plot number	season/ year	month	Appendix page
secondary woodland	12	wet 1	June	239
	12	dry 1	December	239
	12	wet 2	August	240
	12	wet 2	June	240
	1	dry 1	February	241
	1	wet 2	May	241
pasture	4	dry 1	February	242
	4	wet 2	July	242
	5	wet 2	July	243
sweet potato	8	wet 1	July	243
	8	wet 2	July	244
	10	wet 1	October	244
	10	dry 1	April	245
	10	wet 2	July	245
groundnuts	2	dry 1	February	246
	2	wet 2	June	246
	11	wet 1	June	247
	11	wet 1	August	247
	11	dry 1	January	248
	11	wet 2	June	248
yam	3	wet 1	October	249
	3	dry 1	April	249
	3	wet 2	June	250
	6	wet 1	August	250
	6	dry 1	December	251
	6	dry 1	February	251
	6	wet 2	June	252
short-term maize	7	wet 1	August	252
	7	dry 1	April	253
	7	wet 2	May	253
	7	wet 2	August	254
	9	dry 1	February	254
	9	wet 2	June	255
	9	wet 2	August	255

6.3 RESULTS

6.3.1 Community structure of *Microtermes* foraging on baits

Species richness, Shannon-Wiener diversity (H') and Evenness (J') indices for *Microtermes* foraging on baits are shown in Figure 6.2. In the results section the term, *diversity*, refers to the Shannon-Wiener index of diversity.

Species richness ranged from one to five. Three or more species were recorded in all vegetation types, except farm maize in the second wet season when only *M. lepidus* was recorded. Seasonal comparisons show that species richness in secondary woodland, pasture and sweet potato was higher in both wet seasons compared to the dry season. In sweet potato, species richness was lower in the wet season than in secondary woodland and pasture. In short-term maize and groundnuts, species richness increased from the first wet to dry season and in groundnuts, further increased from the dry to second wet season. There were no seasonal difference in species richness in yam.

Seasonal comparisons of diversity showed different trends (Figure 6.2). Dry season diversity was higher in secondary woodland, groundnuts, yam and short-term maize and lower in pasture and, to a lesser extent, sweet potato than in to both wet seasons. In yam and short-term maize, diversity increased from the first to second wet season. Seasonal differences in evenness reflected those for diversity in all vegetation types except sweet potato where evenness was higher in the dry season compared to wet seasons.

Comparisons of species richness amongst the vegetation types (Figure 6.2) show that species richness in the first wet season was similar amongst secondary woodland, pasture and yam and amongst sweet potato, groundnuts, short-term maize and long-term farm maize. Species richness was greatest in the former; five species compared to four. In the dry season, species richness was greatest in short-term maize (5 spp.), similar amongst secondary woodland, groundnuts and yam (4.5 spp.) and between sweet potato and pasture (4 spp.). In the second wet season, species richness was similar amongst secondary woodland, pasture, groundnuts and short-term maize and between yam and sweet potato with the former greater than the later. Species richness was lowest in both long-term maize sites (1 to 4 spp.).

In both wet seasons, diversity was lower in the long-term maize sites compared to the remaining vegetation types (0 to 1.089). In the first wet season, there was little difference in diversity amongst the vegetation types, except long-term farm maize, as previously mentioned. In the dry season, diversity was greatest in short-term maize (1.573) and lowest in pasture and sweet potato (1.321). Diversity was similar amongst secondary woodland, groundnuts and yam (1.463 - 1.472).

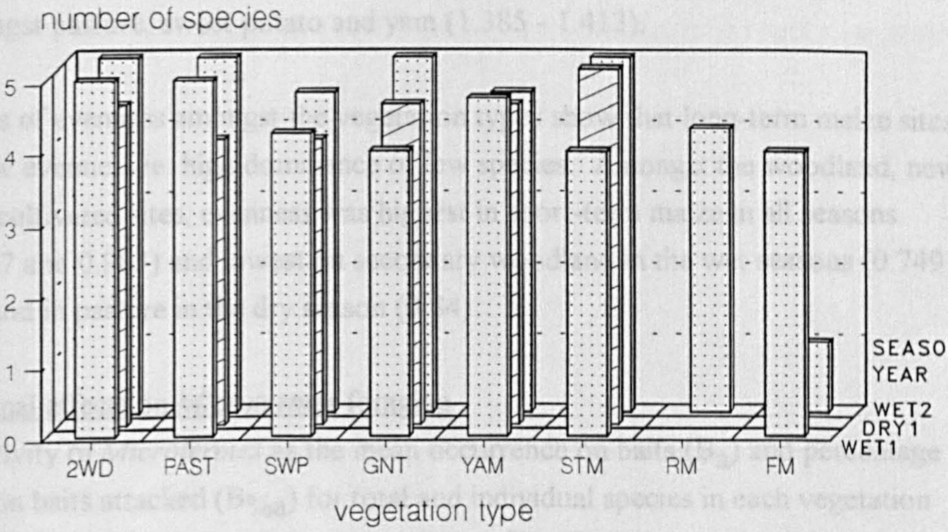
Figure 6.2 : Species richness, Shannon-Wiener diversity index (H') and Evenness index (J') of *Microtermes* foraging on baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

KEY

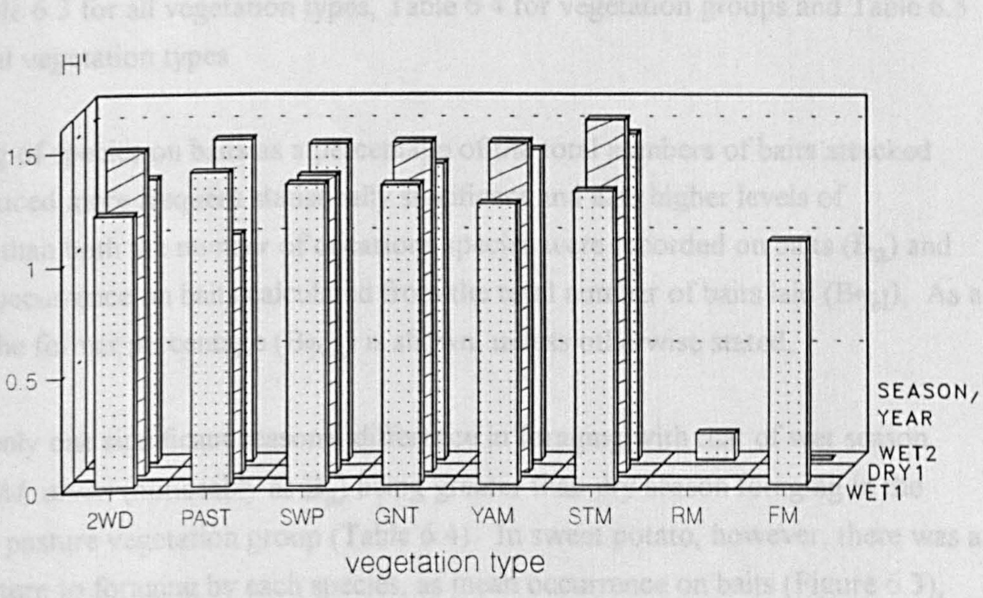
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

WET1 = wet season 1, year 1 (1974)
DRY1 = dry season 1, year 1 (1974/75)
WET2 = wet season 2, year 2 (1975)

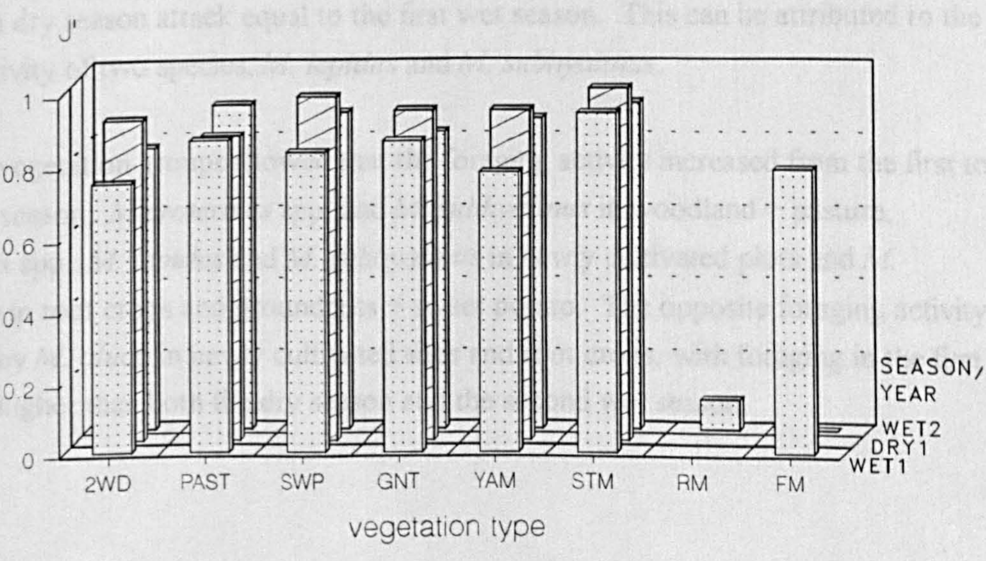
(a) Species richness



(b) Shannon-Wiener diversity (H')



(c) Evenness (J')



In the second wet season, diversity was greatest in short-term maize (1.453) and lowest in the long-term maize sites, followed by secondary woodland (1.258). Diversity was similar amongst pasture, sweet potato and yam (1.385 - 1.413).

Comparisons of evenness amongst the vegetation types show that long-term maize sites exhibited low evenness ie. high dominance of few species. Amongst the woodland, newly cleared and cultivated sites, evenness was highest in short-term maize in all seasons (0.941, 0.977 and 0.903) and lowest on secondary woodland in the wet seasons (0.749 and 0.781) and in pasture in the dry season (0.84).

6.3.2 Seasonal effects on *Microtermes* foraging

Foraging activity of *Microtermes* as the mean occurrence on baits (B_a) and percentage occurrence on baits attacked ($B_{\%a}$) for total and individual species in each vegetation type are shown in Figures 6.3 and 6.4 respectively. Significant interactions from analysis of variance and significant differences from Tukey multiple comparisons of means are given in Table 6.3 for all vegetation types, Table 6.4 for vegetation groups and Table 6.5 for individual vegetation types.

The foraging of species on baits as a percentage of the total numbers of baits attacked ($B_{\%a}$) produced more frequent statistically significant and also higher levels of significance than both the number of occasions species were recorded on baits (B_a) and percentage occurrence on baits calculated from the total number of baits laid ($B_{\%l}$). As a result only the former percentage ($B_{\%a}$) is shown, unless otherwise stated.

There was only one significant seasonal difference in foraging with that of wet season foraging by *M. aluco* (noticeably as B_a) being greater than dry season foraging in the woodland + pasture vegetation group (Table 6.4). In sweet potato, however, there was a seasonal pattern to foraging by each species, as mean occurrence on baits (Figure 6.3), except for *M. n.sp. C*. Analysis of *Microtermes* foraging over all vegetation types (Table 6.3) showed that foraging was greater in the second wet season compared to the first wet season, with dry season attack equal to the first wet season. This can be attributed to the foraging activity of two species; *M. lepidus* and *M. subhyalinus*.

Analysis of vegetation groups showed that the foraging activity increased from the first to second wet season; *Microtermes* spp. and *M. subhyalinus* in woodland + pasture, *Microtermes* spp., *M. lepidus* and *M. subhyalinus* in newly cultivated plots and *M. subhyalinus* in root crops and groundnuts + sweet potato. The opposite foraging activity was shown by *M. aluco* in newly cultivated sites and root crops, with foraging in the first wet season higher than both the dry season and the second wet season.

Figure 6.3 : Foraging activity of *Microtermes* on softwood baits as mean occurrence on baits (B_a ± 1 SE) in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria.

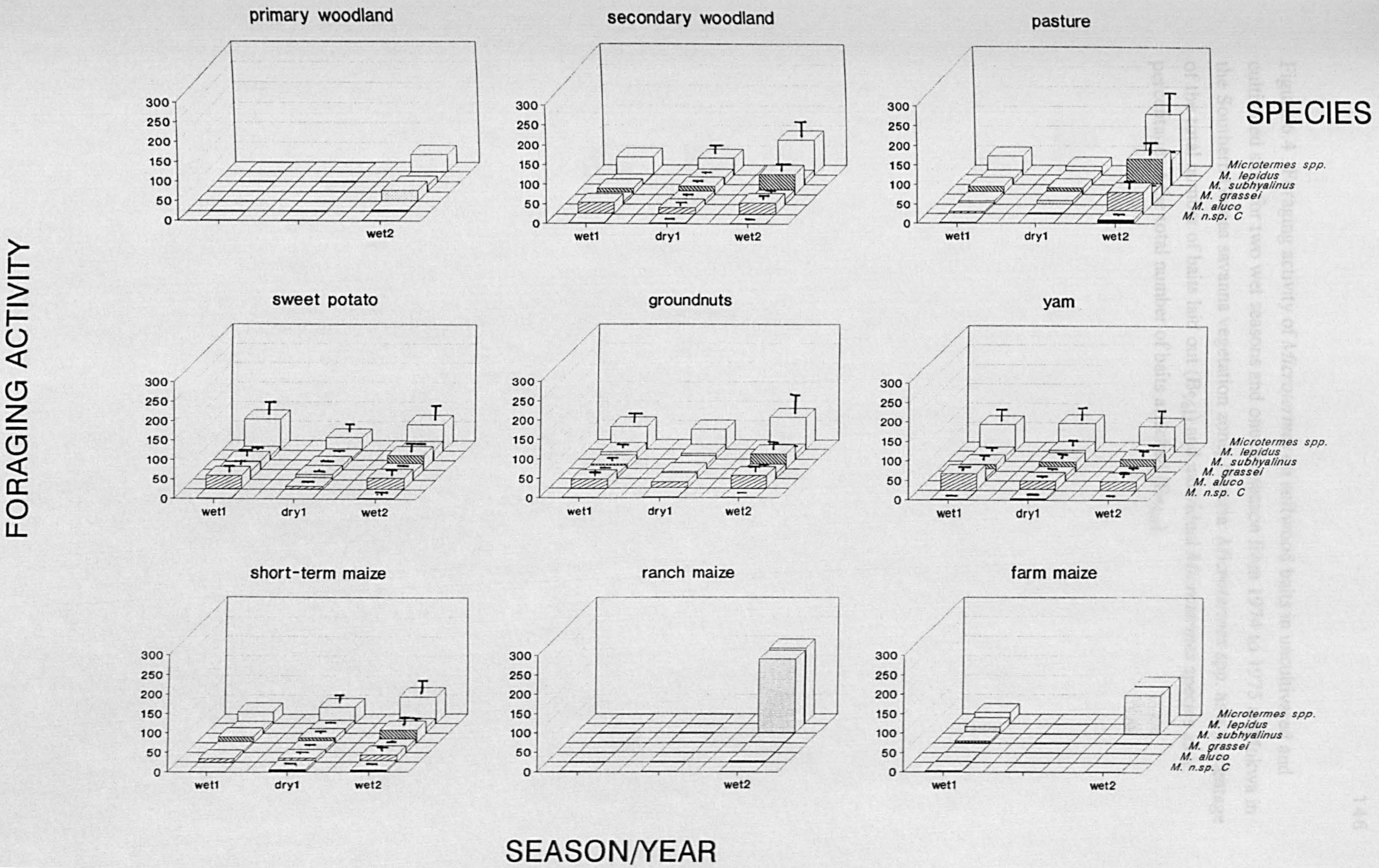
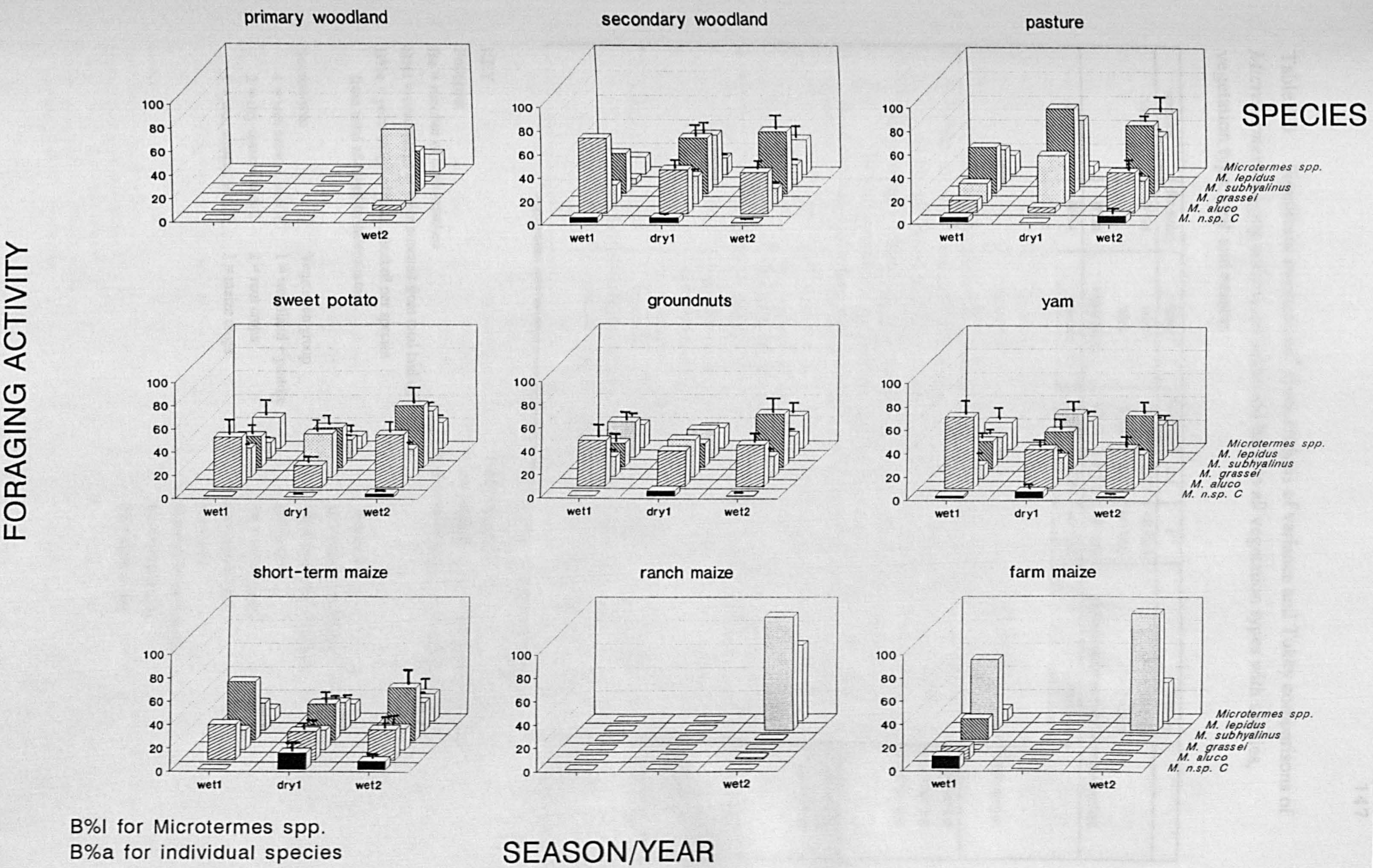

FORAGING ACTIVITY
SEASON/YEAR
SPECIES
primary woodland
secondary woodland
pasture
sweet potato
groundnuts
yam
short-term maize
ranch maize
farm maize
0
50
100
150
200
250
300
wet1
dry1
wet2
Microtermes spp.
M. lepidus
M. subhyalinus
M. grassei
M. aluco
M. n.sp. C

Figure 6.4 : Foraging activity of *Microtermes* on softwood baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa in the Southern Guinea savanna vegetation zone, Nigeria: *Microtermes* spp. as a percentage of the total number of baits laid out ($\mathrm{B}\%_{l}$) and individual *Microtermes* species as a percentage of the total number of baits attacked ($\mathrm{B}\%_{a}$).



B%I for Microtermes spp.
B%a for individual species

Corrigenda

In Tables 6.3, 6.4 and 6.5, the three foraging activities of *Microtermes*, Ba, B%l and B%a, are not independent as they are derived from the same field data. As a consequence, the significance levels should be interpreted with caution, and are best taken as guides for exploring the data. In particular they can be used to indicate which measure of activity (Ba, B%l or B%a) is most appropriate, and which factors have the most biological relevance.

Problems with multiple comparisons can be minimised by restricting attention to the following analyses which appear to be the most informative:

B%l and B%a only, at levels
- year + vegetation (Table 6.3),
- species + year or year + vegetation (Table 6.4)
- species + year (Table 6.5)

Table 6.3 : Significant interactions* from analysis of variance and Tukey comparisons of *Microtermes* foraging activity on softwood baits in all vegetation types with species, vegetation type, year and season.

species	foraging	level	F-value	d.f.	P	Tukey
total	B%a	year	8.66	2,27	<0.005	2=1<3
	Ba	year	8.56	2,27	<0.005	2=1<3
	B%a	vegetation	12.01	8,21	<0.005	zb<mb=stm=sw=gn=ym=gr<fm<rm
all	B%a	species	27.76	4,145	<0.005	c<b=d<a=g
	B%l	species	17.22	4,145	<0.005	c<b=d<a=g
	Ba	species	7.26	4,145	<0.005	c<b=d=a=g
	Ba	vegetation	7.12	8,141	<0.005	zb<mb<fm=stm=gr=sw=gn=rm=ym
	Ba	year	8.39	2,147	<0.005	2=1<3
M. lepidus	B%a	vegetation	21.92	8,21	<0.005	zb<mb=sw=gn=stm=ym=gr<fm<rm
	B%l	vegetation	10.03	8,21	<0.005	zb<mb=sw=gn=stm=ym=gr<fm<rm
	Ba	vegetation	14.43	8,21	<0.005	zb<mb=stm=sw=gn=ym=gr=fm<rm
	B%a	vegetation group	5.38	2,27	<0.05	3=2<1
	B%l	year	8.85	2,27	<0.05	1=2<3
M. grassei	B%a	vegetation	10.42	8,21	<0.005	fm=rm<mb=ym=stm=gn=gr=sw<zb
	B%l	vegetation	8.91	8,21	<0.01	fm=rm<mb=ym=stm=gn=gr=sw=zb
	B%a	vegetation group	6.28	2,27	<0.01	1<2=3
	B%l	vegetation group	3.38	2,27	<0.05	1<2=3
M. aluco	B%a	vegetation	5.02	8,21	<0.005	rm=fm=zb<gr=stm=sw=gn=mb=ym
	B%a	vegetation group	5.29	2,27	<0.01	1<3=2
	B%l	vegetation group	4.97	2,27	<0.05	1<3=2
	Ba	vegetation group	3.71	2,27	<0.05	1<3=2
M. subhyalinus	B%a	vegetation	8.95	8,21	<0.005	rm=fm<ym=sw=gn=zb=mb=stm=gr
	B%a	vegetation group	3.98	2,27	<0.05	1<2=3
	B%l	vegetation group	3.91	2,27	<0.05	1<2=3
	Ba	year	4.23	2,27	<0.05	1=2<3

* significant interactions from 56 comparisons.

KEY

Foraging

Ba = number of baits attacked

B%l = percentage of baits attacked from total laid out

B%a = percentage of baits attacked per species
from total attacked by Microtermes.

Season/year :

1 = wet season, year 1
2 = dry season, year 2
3 = wet season, year 3

Vegetation group :

1 = woodland + pasture
2 = root crops
3 = maize crops

Tukey comparisons

= ; no significant difference between means
\> or < ; mean significantly greater or less than

Vegetation :

zb = primary woodland
mb = secondary woodland
gr = pasture
sw = sweet potato
gn = groundnuts
ym = yam
stm = short-term maize
rm = ranch maize
fm = farm maize

Table 6.4 : Significant interactions* from analysis of variance and Tukey comparisons of *Microtermes* foraging activity on softwood baits in vegetation groups with species, vegetation type, year and season.

season	vegetation	species	foraging	level	F	d.f.	P	Tukey
both	maize	all	B%a	species	5.34	4,30	<0.005	*c<b=d=g<a*
both		all	B%l	species	4.13	4,30	<0.01	*c=b=d=g<a*
both		*M. aluco*	B%a	vegetation	11.2	2,4	<0.05	rm<fm<stm
both		*M. lepidus*	B%a	vegetation	141	2,4	<0.005	stm<fm<rm
both		*M. lepidus*	Ba	vegetation	21.5	2,4	<0.01	stm<fm<rm
both		*M. subhyalinus*	B%a	vegetation	9.79	2,4	<0.05	rm<fm<stm
both	root crops	all	B%a	species	54.3	4,80	<0.005	*c<b<a=g<d*
both		all	B%l	species	33.8	4,80	<0.005	*c<b<a=g<d*
both		all	Ba	species	18.4	4,80	<0.005	*c<b<a=g<d*
both		*M. aluco*	B%a	year	6.84	2,10	<0.05	2=3<1
both		*M. subhyalinus*	B%a	year	11.5	2,10	<0.05	2=1<3
both		*M. subhyalinus*	B%l	year	4.96	2,10	<0.05	2=1<3
both		*M. subhyalinus*	Ba	year	4.68	2,10	<0.05	2=1<3
both	woodland+pasture	all	B%a	species	14.2	4,45	<0.005	*c<a=b=d<g*
both		all	B%l	species	8.17	4,45	<0.005	*c<=b=a=d=g*
both		all	Ba	species	3.68	4,45	<0.01	*c<b=a=d=g*
both		all	B%l	year	8.41	2,47	<0.005	1=2<3
both		all	Ba	year	9.51	2,47	<0.005	1=2<3
both		*M. aluco*	Ba	year	6.01	2,7	<0.05	2<1<3
both		*M. grassei*	B%a	vegetation	18.3	2,7	<0.05	mb<gr<zb
both		*M. subhyalinus*	B%l	year	7.65	2,7	<0.05	1=2<3
both		*M. subhyalinus*	Ba	year	6.99	2,7	<0.05	1=2<3
both		*Microtermes spp.*	B%l	year	9.16	2,7	<0.05	1=2<3
both		*Microtermes spp.*	Ba	year	8.26	2,7	<0.05	1=2<3
both	newly cultivated	all	B%a	species	58.9	4,84	<0.005	*c<b=a<d=g*
both		all	B%l	species	33.1	4,84	<0.005	*c<b<a<d=g*
both		all	Ba	vegetation	17.9	3,81	<0.005	stm<sw=gn=ym
both		*M. aluco*	B%a	year	6.58	2,14	<0.05	2=3<1
wet		*M. aluco*	B%a	year	8.69	1,12	<0.05	3<1
wet		*M. lepidus*	B%l	year	8.02	1,12	<0.05	1<3
wet		*M. lepidus*	Ba	year	7.33	1,12	<0.05	1<3
both		*M. subhyalinus*	B%a	year	4.57	2,14	<0.05	2=1<3
both		*M. subhyalinus*	Ba	year	5.8	2.14	<0.05	2=1<3
wet		*M. subhyalinus*	B%a	year	8.04	1,12	<0.05	1<3
wet		*M. subhyalinus*	B%l	year	7.95	1,12	<0.05	1<3
wet		*M. subhyalinus*	Ba	year	7.47	1,12	<0.05	1<3
both	groundnut + sweet potato	all	B%a	species	42	4,35	<0.005	*c<b<a=g=d*
both		all	B%l	species	19	4,35	<0.005	*c<b=a=g=d*
wet		*M. aluco*	B%a	year	8.69	1,5	<0.05	3<1
wet		*M. subhyalinus*	B%a	year	10.1	1,5	<0.05	1<3
both	short-term maize+yam	all	Ba	vegetation	5.84	1,7	<0.05	stm<ym

* significant interactions from 378 comparisons.

KEY

Tukey comparisons

= ; no significant difference between means

> or < : mean significantly greater or less than

Foraging

Ba = number of baits attacked

B%l = percentage of baits attacked from total laid out

B%a = percentage of baits attacked per species from total attacked by Microtermes

Vegetation :

zb = primary woodland

mb = secondary woodland

gr = pasture

sw = sweet potato

gn = groundnuts

ym = yam

stm = short-term maize

rm = ranch maize

fm = farm maize

Species :

c = *Microtermes n.sp. C*

b = *Microtermes grassei*

d = *Microtermes aluco*

g = *Microtermes subhyalinus*

a = *Microtermes lepidus*

Season/year :

1 = wet season, year 1

2 = dry season, year 2

3 = wet season, year 3

Table 6.5 : Significant interactions* from analysis of variance and Tukey comparisons of *Microtermes* foraging activity on softwood baits within vegetation types with species, year and season.

season	vegetation	foraging	level	F-value	d.f.	P	Tukey
both	secondary woodland	B%a	species	13.73	4,20	<0.005	*c<b<a=d=g*
both		B%l	species	7.28	4,20	<0.01	*c<b<a=d=g*
both	pasture	B%a	species	18.06	4,15	<0.005	*c<d=b<a=g*
both		B%l	year	8.52	2,17	<0.005	2=1<3
both		Ba	year	5.48	2,17	<0.005	2=1<3
both	sweet potato	B%a	species	21.94	4,20	<0.005	*c<b=a=g=d*
both		B%l	species	8.59	4,20	<0.005	*c<b=a=g=d*
wet	groundnut	B%a	species	16.83	4,10	<0.005	*c<b=a=d=g*
wet		B%l	species	9.41	4,10	<0.005	*c<b=a=d=g*
both	yam	B%a	species	15.51	4,20	<0.005	*c<b<a=g=d*
both		B%l	species	14.66	4,20	<0.005	*c<b<a=g=d*
both		Ba	species	14.58	4,20	<0.005	*c<b<a=g=d*
both	short-term maize	B%a	species	12.95	4,15	<0.005	*c<b<a=d=g*
both		B%l	species	4.35	4,15	<0.05	*c<b=a=d=g*
wet	long-term maize	B%a	species	23.06	4,10	<0.005	*b=c=d=g<a*
wet		B%l	species	9.28	4,10	<0.005	*b=c=d=g<a*
wet	.	Ba	species	11.06	4,10	<0.005	*b=c=d=g<a*

* significant interactions from 48 comparisons.

KEY

Foraging
Ba = number of baits attacked
B%l = percentage of baits attacked from total laid out
B%a = percentage of baits attacked per species
from total attacked by Microtermes.

Tukey comparisons
= ; no significant difference between means
> or < ; mean significantly greater or less than

Season/year :
1 = wet season, year 1
2 = dry season, year 2
3 = wet season, year 3

Species :
c = Microtermes n.sp. C
b = Microtermes grassei
d = Microtermes aluco
g = Microtermes subhyalinus
a = Microtermes lepidus

As stated above, it was not possible to examine seasonal effects on species foraging in each vegetation type. However, from Figure 6.4, it can be shown that, in sweet potato, pasture and groundnuts, foraging in the wet season by *Microtermes* spp., *M. aluco*, *M. subhyalinus*, *M. grassei* and *M. lepidus*, except *M. grassei* in groundnuts, and *M. aluco* in secondary woodland was greater than in the dry season.

Figure 6. 4 also show that *Microtermes* spp. foraging activity (B_a) in secondary woodland, pasture, farm maize, short-term maize and groundnuts was higher in the second wet season compared to the first wet season. This pattern of foraging activity was shown by *M. subhyalinus* in secondary woodland, yam and groundnuts, by each species in pasture, in particular, *M. subhyalinus*, *M. lepidus* and *M. grassei* and by *M. lepidus* in sweet potato and farm maize.

6.3.3 Vegetation cover effects on *Microtermes* foraging

Microtermes spp. were recorded on 22 to 194 baits (rarely over 100) from a total 297 while individual species were rarely recorded from more than 50 baits. Foraging activity was significantly different amongst the vegetation types (Table 6.3). Foraging by *Microtermes* spp. (B_a) was significantly lower in primary woodland and higher in both long-term maize sites than in the remaining vegetation types while the foraging of all individual species (again, B_a) was significantly lower in primary woodland followed by secondary woodland than in other vegetation types.

The foraging activity of individual species also differed amongst the vegetation types (Table 6.3). Foraging by *M. lepidus* was highest in ranch maize followed by farm maize and lowest in primary woodland. Foraging by *M. subhyalinus* and *M. grassei* was lowest in both long-term maize sites and highest for *M. grassei* in primary woodland. Foraging by *M. aluco* was least in long-term maize and primary woodland. There were no further significant differences in foraging by these species among the remaining vegetation types. *M. n.sp. C* foraging activity was low and did not differ with vegetation type.

Foraging differences within vegetation groups (Table 6.4) agreed, in general, with previous results and highlighted additional vegetation type differences. In the maize group, foraging by *M. aluco* and *M. subhyalinus* was greatest in short-term maize and least in ranch maize while foraging by *M. lepidus* showed the opposite pattern. In the woodland + pasture group, *M. grassei* foraging was highest in primary woodland and least in secondary woodland. In newly cultivated plots, foraging by all individual species (B_a) was lowest in short-term maize; this difference was not shown from analysis of all vegetation types. Analysis of all vegetation types (Table 6.3) showed that foraging activity ($B\%_a$) was significantly different amongst the species; *M. subhyalinus* and *M.*

lepidus foraging activity was higher and *M. n.sp. C* foraging lower than that of *M. grassei* and *M. aluco*.

Foraging amongst species also differed within vegetation groups (Table 6.4). In the maize group, foraging by *M. lepidus* was the most active, followed by that of *M. aluco*, *M. grassei* and *M. subhyalinus* with *M. n.sp. C* foraging the lowest. In woodland + pasture, *M. subhyalinus* showed the highest and *M. n.sp. C* the lowest foraging activity. In root crops, foraging by *M. aluco* was highest and lowest by *M. n.sp. C*, followed by *M. grassei*, with foraging by *M. lepidus* and *M. subhyalinus* intermediate between that of *M. aluco* and *M. grassei*. In newly cultivated plots, *M. subhyalinus* and *M. aluco* foraging was the highest with *M. lepidus* and *M. grassei* foraging intermediate to these and *M. n.sp. C*, which showed the lowest foraging activity.

Species foraging also differed within each vegetation type (Table 6.5) and corresponded to many of the results above. Foraging by *M. n.sp. C* was lower than for all other species in each vegetation type, except long-term maize where this species was not recorded. In secondary woodland, yam and short-term maize, foraging activity by *M. aluco*, *M. lepidus* and *M. subhyalinus* was similar and greater than foraging by *M. grassei* or *M. n.sp. C*. In pasture, *M. lepidus* and *M. subhyalinus* foraging was greater than that of the remaining species with *M. aluco* and *M. grassei* foraging intermediate to these two species and *M. n.sp. C*. In sweet potato and groundnuts, foraging was similar amongst all species except *M. n.sp. C*. In long-term maize (farm and ranch maize were analysed together) *M. lepidus* foraging was higher than for all other species.

6.3.4 Spatial distribution of *Microtermes* on baits

As stated earlier, Table 6.2 lists vegetation types, plots and dates where spatial data were available. Diagrams showing the spatial patterns of individual *Microtermes* species on baits for each plot are given in the Appendix, see Table 6.2. Table 6.6 presents results from goodness-of-fit testing of the co-occurrence of *Microtermes* species on baits under the null hypothesis of no species interactions i.e. co-occurrence was random. Observed and expected frequencies of the co-occurrence of 0 to 5 species on baits for each plot are given in Appendix 3 . Table 6.7 and Table 6.8, respectively, give the results from goodness-of-fit testing of the occurrence of *Microtermes* spp. and individual species on baits under the null hypothesis of random distribution. Observed and expected frequencies of the occurrence of *Microtermes* spp. and species on baits are given in Appendix 4. Table 6.9 gives results of goodness-of-fit testing from contingency tables and Cramer coefficients of association between *Microtermes* species under the null hypothesis of no association.

Table 6.6 : Goodness-of-fit testing of the co-occurrence of *Microtermes* species on individual baits under the null hypothesis of no species interactions on baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa, Nigeria.

vegetation	season	month	plot	G	d.f	P
secondary woodland	wet 1	june	12	na	-	-
	dry 1	december	12	na	-	-
	dry 1	february	1	na	-	-
	wet 2	may	1	7.596	1	*
	wet 2	june	12	na	-	-
	wet 2	august	12	na	-	-
pasture	dry 1	february	4	na	-	-
	wet 2	july	4	10.782	2	***
	wet 2	july	5	22.33	3	***
sweet potato	wet 1	july	8	na	-	-
	wet 1	october	10	3.63	1	*
	dry 1	april	10	na	-	-
	wet 2	july	8	na	-	-
	wet 2	july	10	34.778	2	***
groundnut	wet 1	august	11	na	-	-
	wet 1	september	11	na	-	-
	dry 1	february	2	na	-	-
	dry 1	january	11	na	-	-
	wet 2	june	2	na	-	-
	wet 2	june	11	7.238	1	*
yam	wet 1	october	3	na	-	-
	wet 1	august	6	na	-	-
	dry 1	april	3	23.68	1	***
	dry 1	february	6	na	-	-
	dry 1	december	6	na	-	-
	wet 2	june	3	na	-	-
	wet 2	june	6	47.55	1	***
maize	wet 1	july	7	na	-	-
	dry 1	april	7	na	-	-
	dry 1	february	9	na	-	-
	wet 2	august	7	na	-	-
	wet 2	may	7	1.082	1	ns
	wet 2	june	9	na	-	-
	wet 2	may	9	na	-	-

na = not available as df < 1.

Table 6.7 : Goodness-of-fit testing of the occurrence of *Microtermes* spp. on baits in quadrats under the null hypothesis of random distribution on baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa, Nigeria.

vegetation	season	plot	month	v	G	P
secondary woodland	wet 1974	12	june	2	1.71	ns
	dry 74-75	1	february	2	3.28	ns
	dry 74-75	12	december	1	3.23	ns
	wet 1975	1	may	4	18.25	**
	wet 1975	12	june	2	7.11	*
	wet 1975	12	august	2	5.86	ns
pasture	dry 74-75	4	february	-	na	-
	wet 1975	4	july	5	6.93	ns
	wet 1975	5	july	5	43.05	***
sweet potato	wet 1974	8	july	2	6.85	*
	wet 1974	10	october	3	4.40	ns
	dry 74-75	10	april	1	2.00	ns
	wet 1975	8	july	1	0.68	ns
	wet 1975	10	july	5	7.91	*
groundnut	wet 1974	11	august	2	8.54	*
	wet 1974	11	september	-	na	-
	dry 74-75	2	february	2	3.63	ns
	dry 74-75	11	january	2	1.33	ns
	wet 1975	2	june	3	2.70	ns
	wet 1975	11	june	4	3.52	ns
yam	wet 1974	3	october	2	2.86	ns
	wet 1974	6	august	2	2.20	ns
	dry 74-75	3	april	3	6.97	ns
	dry 74-75	6	february	3	7.21	ns
	dry 74-75	6	december	2	9.63	**
	wet 1975	3	june	2	7.39	*
	wet 1975	6	june	2	2.87	ns
maize	wet 1974	7	july	1	5.73	*
	dry 74-75	7	april	1	0.89	ns
	dry 74-75	9	february	1	3.39	ns
	wet 1975	7	august	2	2.43	ns
	wet 1975	7	may	3	4.47	ns
	wet 1975	9	june	2	12.99	***

Table 6.8 : Goodness-of-fit testing of the occurrence of *Microtermes* species on baits in quadrats under the null hypothesis of random distribution on baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa, Nigeria.

vegetation	season	plot	month	species	v	G	P
secondary woodland	dry 74-75	1	february	*M. subhyalinus*	1	4.22	*
	wet 1975	1	may	*M. subhyalinus*	2	16.31	***
	wet 1975	1	may	*M. aluco*	1	0.72	ns
	wet 1975	12	june	*M. aluco*	1	2.84	ns
pasture	wet 1975	4	july	*M. subhyalinus*	3	24.78	***
	wet 1975	4	july	*M. aluco*	1	2.20	ns
	wet 1975	4	july	*M. grassei*	1	1.81	ns
	wet 1975	4	july	*M. lepidus*	2	2.98	ns
	wet 1975	5	july	*M. subhyalinus*	3	1.19	ns
	wet 1975	5	july	*M. aluco*	2	6.04	*
sweet potato	wet 1974	8	july	*M. aluco*	2	2.83	ns
	wet 1974	10	october	*M. grassei*	1	8.09	**
	wet 1974	10	october	*M. subhyalinus*	1	2.80	ns
	wet 1974	10	october	*M. aluco*	1	2.59	ns
	wet 1975	10	july	*M. subhyalinus*	2	2.99	ns
	wet 1975	10	july	*M. lepidus*	1	0.86	ns
groundnuts	wet 1975	11	june	*M. aluco*	1	0.08	ns
	wet 1975	11	june	*M. subhyalinus*	2	4.18	*
yam	wet 1974	3	october	*M. aluco*	1	1.47	ns
	wet 1974	6	august	*M. aluco*	1	9.58	**
	dry 74-75	3	april	*M. subhyalinus*	1	1.37	ns
	dry 74-75	3	april	*M. grassei*	1	0.49	ns
	wet 1975	6	june	*M. lepidus*	1	3.38	ns
	wet 1975	6	june	*M. aluco*	1	5.82	*
	wet 1975	6	june	*M. subhyalinus*	1	5.63	*
maize	wet 1975	7	may	*M. subhyalinus*	1	2.84	ns
	wet 1975	9	june	*M. subhyalinus*	2	1.74	ns
	wet 1975	9	may	*M. subhyalinus*	2	1.59	ns

Table 6.9 : Goodness-of-fit testing and Cramer coefficients of association between *Microtermes* species on individual baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa, Nigeria; under the null hypothesis of no association on baits.

			species	*M. lepidus/M. grassei*			*M. lepidus/M. sp. C*			*M. lepidus/M. aluco*			*M. lepidus/M. subhyalinus*			*M. grassei/M. sp. C*		
vegetation	plot	month	year	G	P	Cramer	G	P	Cramer	G	P	Cramer	G	P	Cramer	G	P	Cramer
secondary	12	june	wet 1974	1.6	ns	-0.01	2.9	ns	-0.01	0.41	ns	-0.03	0.9	ns	-0.02	1.6	ns	-0.01
woodland	12	december	dry74-75	5.19	*	0.2	0.49	ns	0	8.04	***	0.23	16.3	***	0.33	1.18	ns	0
	1	february	dry74-75	0.31	ns	0.002	-	-	-	9.86	***	0.26	5.98	*	0.19	-	-	-
	1	may	wet 1975	0.01	ns	-0.03	-	-	-	0.04	ns	0.03	1.3	ns	0.08	-	-	-
	12	june	wet 1975	0.01	ns	0.05	-	-	-	2.72	ns	0.15	0.35	ns	0.06	-	-	-
	12	august	wet 1975	0.44	ns	-0.02	-	-	-	0	ns	-0.03	0.4	ns	-0.06	-	-	-
pasture	4	february	dry74-75	0.01	ns	0.05	-	-	-	1.8	ns	-0.01	0.44	ns	0.12	-	-	-
	4	july	wet 1975	3.16	ns	-0.11	0.04	ns	-0.04	0.01	ns	0.01	8.42	***	0.18	0.23	ns	-0.03
	5	july	wet 1975	3.36	ns	-0.11	5.57	*	-0.14	0.11	ns	0.03	3.25	ns	-0.11	0.13	ns	-0.04
sweet	8	july	wet 1974	0.04	ns	0.03	-	-	-	0.55	ns	-0.07	0.82	ns	0.1	-	-	-
potato	10	october	wet 1974	0.43	ns	-0.06	1.97	ns	-0.01	0	ns	-0.03	3.41	ns	0.15	1.05	ns	-0.02
	10	april	dry74-75	0.34	ns	-0.03	2.76	ns	-0.01	0.86	ns	-0.02	0.34	ns	-0.03	1.88	ns	0.28
	8	july	wet 1975	1.98	ns	0.15	0.49	ns	-0.02	22.2	***	0.38	11.8	***	0.27	1.93	ns	-0.02
	10	july	wet 1975	0.16	ns	0	0.05	ns	-0.04	2.67	ns	0.11	2.63	ns	0.11	0.5	ns	0.13
groundnut	11	august	wet 1974	1.02	ns	0.19	-	-	-	0.46	ns	0.12	0.34	ns	0.11	-	-	-
	11	september	wet 1974	0.04	ns	0.03	-	-	-	0	ns	-0.02	0.12	ns	0.02	-	-	-
	2	february	dry74-75	1.09	ns	-0.08	-	-	-	0.61	ns	0.09	0.01	ns	0.04	-	-	-
	11	january	dry74-75	0.15	ns	-0.03	1.6	ns	-0.01	0	ns	0.05	3.45	ns	0.22	1.1	ns	-0.02
	2	june	wet 1975	0.77	ns	0.09	1.67	ns	-0.01	0.04	ns	-0.05	2.05	ns	0.12	1.73	ns	-0.01
	11	june	wet 1975	0.19	ns	0.01	1.55	ns	-0.01	3.38	ns	-0.11	0	ns	-0.02	1.67	ns	-0.01
yam	3	october	wet 1974	0	ns	-0.04	-	-	-	4.22	*	0.11	4.31	*	0.12	-	-	-
	6	august	wet 1974	0.04	ns	-0.04	1.73	ns	-0.01	1.66	ns	0.1	0.09	ns	0.05	2.28	ns	-0.01
	3	april	dry74-75	6.39	*	0.15	-	-	-	6.13	***	0.15	1.44	ns	0.05	-	-	-
	6	february	dry74-75	0.11	ns	-0.05	1.18	ns	-0.02	0	ns	0.02	10	***	0.23	2.17	ns	0.33
	6	december	dry74-75	2.71	ns	0.08	0.02	ns	-0.04	6.2	*	0.15	3.72	ns	0.11	0.39	ns	-0.03
	3	june	wet 1975	3.74	ns	0.11	1.26	ns	-0.02	0.81	ns	0.02	9.75	***	0.2	1.67	ns	-0.01
	6	june	wet 1975	0.72	ns	0.09	0.83	ns	-0.02	5.35	*	0.16	23.3	***	0.34	2.58	ns	-0.01
maize	7	july	wet 1974	0.19	ns	-0.03	-	-	-	0.04	ns	-0.04	1.11	ns	0.11	-	-	-
	7	april	dry74-75	0.13	ns	0.05	0.52	ns	-0.02	2.73	ns	0.15	12.4	***	0.29	0.96	ns	-0.02
	9	february	dry74-75	0.19	ns	-0.03	0.39	ns	-0.03	0.08	ns	0.07	0.01	ns	0.05	0.73	ns	-0.02
	7	may	wet 1975	1.33	ns	0.12	1.26	ns	-0.02	3.37	ns	0.17	11	***	0.28	2.42	ns	-0.01
	7	august	wet 1975	0.19	ns	-0.03	0.93	ns	-0.02	0.3	ns	0.1	0.06	ns	-0.04	0.56	ns	-0.02
	9	may	wet 1975	0	ns	0.05	0.01	ns	-0.04	0.08	ns	-0.01	0.44	ns	0.06	0.38	ns	-0.03
	9	june	wet 1975	6.02	*	0.22	0.96	ns	-0.02	0.89	ns	0.1	0.02	ns	-0.03	0.8	ns	0.16

Table 6.9 cont. : Goodness-of-fit testing and Cramer coefficients of association between *Microtermes* species on individual baits in uncultivated and cultivated sites for two wet seasons and one dry season from 1974 to 1975 at Mokwa, Nigeria; under the null hypothesis of no association on baits.

			species	*M. grassei/M. aluco*			*M. grassei/M. subhyalinus*			*M. sp. C/M. aluco*			*M. sp. C/M. subhyalinus*			*M. aluco/M. subhyalinus*		
vegetation	plot	month	year	G	P	Cramer	G	P	Cramer	G	P	Cramer	G	P	Cramer	G	P	Cramer
secondary woodland	12	june	wet 1974	0.93	ns	0.1	0.06	ns	0.07	0.41	ns	-0.03	0.9	ns	0.17	8.87	***	0.24
	12	december	dry74-75	3.5	ns	0.17	3.5	ns	0.17	0.75	ns	0.15	0.75	ns	0.15	4.09	*	0.17
	1	february	dry74-75	1.46	ns	0.11	0.43	ns	0.06	-	-	-	-	-	-	4.56	*	0.16
	1	may	wet 1975	0.53	ns	-0.06	3.85	*	0.13	-	-	-	-	-	-	3.65	ns	0.12
	12	june	wet 1975	0	ns	-0.04	0.49	ns	-0.07	-	-	-	-	-	-	0.24	ns	-0.05
	12	august	wet 1975	0	ns	0.05	7.76	**	0.29	-	-	-	-	-	-	0.19	ns	0.04
pasture	4	february	dry74-75	2.06	ns	-0.01	0.63	ns	0.14	-	-	-	-	-	-	3	ns	0.5
	4	july	wet 1975	0	ns	0.01	1.77	ns	0.09	0.13	ns	-0.03	0.02	ns	0.04	0.17	ns	0.03
	5	july	wet 1975	0.2	ns	-0.04	0.8	ns	-0.06	0.23	ns	-0.04	0.02	ns	-0.01	0.05	ns	0.02
sweet potato	8	july	wet 1974	1.11	ns	-0.08	0.25	ns	0.01	-	-	-	-	-	-	0.02	ns	0.02
	10	october	wet 1974	0.06	ns	-0.03	0.01	ns	-0.01	0.77	ns	0.15	0.91	ns	-0.02	10.8	***	0.23
	10	april	dry74-75	0.23	ns	0.09	0	ns	0.05	2.58	ns	-0.01	1.88	ns	-0.01	0.28	ns	-0.03
	8	july	wet 1975	2.3	ns	0.16	0.02	ns	0.06	0.59	ns	-0.02	0.52	ns	0.13	6.43	*	0.2
	10	july	wet 1975	0.08	ns	0.004	0.55	ns	0.06	0	ns	0.04	0.03	ns	0.03	21.6	***	0.3
groundnut	11	august	wet 1974	0.46	ns	0.12	0.34	ns	-0.03	-	-	-	-	-	-	5.84	*	0.25
	11	september	wet 1974	0.12	ns	-0.05	0.02	ns	0.06	-	-	-	-	-	-	0.26	ns	0.01
	2	february	dry74-75	0.16	ns	-0.05	0.02	ns	0.03	-	-	-	-	-	-	0.13	ns	-0.03
	11	january	dry74-75	0.47	ns	0.08	0.05	ns	0.06	0.38	ns	0.11	5.96	*	0.34	3.27	ns	0.17
	2	june	wet 1975	0.02	ns	-0.05	0	ns	0.03	1.8	ns	-0.01	0.96	ns	-0.02	0.01	ns	-0.02
	11	june	wet 1975	0.55	ns	-0.06	4.65	*	0.16	0.6	ns	0.13	0.69	ns	-0.02	4.71	*	0.15
yam	3	october	wet 1974	2.98	ns	-0.06	2.48	ns	0.17	-	-	-	-	-	-	0.07	ns	0.04
	6	august	wet 1974	0	ns	-0.02	3.56	ns	0.17	0.52	ns	-0.02	1.18	ns	-0.03	0.26	ns	0.05
	3	april	dry74-75	0.1	ns	0.01	8.29	***	0.2	-	-	-	-	-	-	7.66	**	0.2
	6	february	dry74-75	0.22	ns	0.01	0.22	ns	0.06	1.05	ns	-0.02	0.91	ns	-0.02	1.56	ns	0.1
	6	december	dry74-75	0.13	ns	0.05	1.47	ns	0.11	0.09	ns	-0.03	0.09	ns	-0.03	0.18	ns	0.05
	3	june	wet 1975	0.11	ns	-0.04	0.1	ns	0.05	2.17	ns	-0.01	1.1	ns	-0.02	0.81	ns	0.1
	6	june	wet 1975	3.91	*	0.18	0.06	ns	0.02	0.96	ns	-0.02	0.91	ns	-0.02	6.43	*	0.18
maize	7	july	wet 1974	3.45	ns	0.22	2.19	ns	0.16	-	-	-	-	-	-	1.32	ns	0.12
	7	april	dry74-75	0	ns	-0.04	2.49	ns	0.14	1.26	ns	-0.02	0.75	ns	0.15	3.94	*	-0.02
	9	february	dry74-75	0.3	ns	-0.03	0.15	ns	0.08	0.31	ns	-0.02	0.54	ns	-0.03	0.05	ns	-0.04
	7	may	wet 1975	0.3	ns	-0.03	6.62	*	0.27	2.17	ns	-0.01	1.67	ns	-0.01	1.71	ns	0.14
	7	august	wet 1975	0.08	ns	0.07	0.01	ns	-0.05	0.71	ns	-0.02	0.34	ns	-0.03	0	ns	-0.04
	9	may	wet 1975	0.29	ns	-0.06	0.73	ns	0.8	0.17	ns	0.01	0.03	ns	0.04	0	ns	0.01
	9	june	wet 1975	0.14	ns	-0.05	0.14	ns	0.05	0.96	ns	-0.02	0.27	ns	0.1	0.02	ns	-0.03

6.3.4.1 Co-occurrence of species on baits

As shown in Table 6.6, it was only possible to complete the analysis for nine plots from a total of 34. In all other cases, there were too few degrees of freedom to test the significance of the G statistic due to the low occurrence of species on baits. From the nine analyses, eight of these indicated significant species interactions and therefore non-random distribution of species on baits.

There were significant results for each vegetation type excepting short-term maize. Co-occurrence of species was significant on sweet potato plot 10 in the first wet season, on yam plot 3 in the dry season and on secondary woodland, pasture, sweet potato, groundnuts and yam in the second wet season. Comparisons of the observed and expected frequencies of species on baits where significant results were obtained show that the total number of baits where species occurred was less than expected. Comparisons also show that observed frequencies on baits were higher for two species, and occasionally three and four, than expected and less for single species, suggesting a degree of clustering among species.

6.3.4.2 Spatial distribution on baits

Goodness-of-fit testing shows that, in all but 9 occasions, results were non-significant i.e. foraging by *Microtermes* spp. on baits was random (Table 6.7).

Occasions of non-random foraging were identified in each vegetation type; wet season one for sweet potato plot 8, short-term maize plot 7 and groundnut plot 11; dry season for yam plot 6 and wet season two for secondary woodland plot 1 & 2, pasture plot 5, yam plot 3 and short-term maize plot 9.

Comparisons of observed and expected frequencies for significant results show that the occurrence of *Microtermes* foraging on two to five baits per quadrat in secondary woodland was higher than the expected values (plots 1 + 12 wet season 2). Similar trends were also observed for the remaining significant results; yam (plot 3, dry season and plot 6 wet season 2), pasture (plot 5, wet season 2), groundnuts (plot 11, wet season one) and in sweet potato (plot 8, wet season one) and short-term maize (plot 9, wet season 2). In maize plot 7 (wet season one) *Microtermes* foraging on one baits per quadrat was higher than expected.

Goodness-of-fit results examining the distribution of individual species on baits show that in all but 9 occasions foraging by species were randomly distributed (Table 6.8). Non-random foraging was identified for *M. subhyalinus* (5 plots) and *M. aluco* (3 plots) and on one plot for *M. grassei*. *M. subhyalinus* foraging was non-random in secondary woodland (plot 1, dry season and wet season two), pasture (plot 4, wet season two), groundnuts (plot 11, wet season two) and yam (plot 6, wet season two). *M. aluco* foraging was non-random in pasture (plot 5, wet season two) and yam (plot 6, wet season one and two). *M. grassei* foraging was non-random in sweet potato (plot 10, wet season one).

Comparisons of observed and expected frequencies for significant results show that there were similar trends for non-random foraging of *Microtermes* species as for *Microtermes* spp. In all these cases, higher occurrence on more than two baits than expected were recorded. Only two significant results coincided with significant results for *Microtermes* spp.; *M. subhyalinus* in secondary woodland plot 1 and *M. aluco* in pasture plot 5, both in wet season two.

6.3.4.3 Species associations on baits

Results (Table 6.9) show that, from 34 plots, there were significant species associations on 22 plots, covering all vegetation types, seasons and years. All but two species associations were shown to be positive from Cramer coefficients.

The greatest number of associations were shown between *M. lepidus/M. subhyalinus* and *M. subhyalinus/M. aluco* (10 plots each) followed by *M. lepidus/M. aluco* (7 plots). There were no associations between *M. n. sp. C* and *M. aluco* or *M. n. sp. C* and *M. grassei*. The highest number of associations were recorded on yam (13) followed by secondary woodland (10), short-term maize (5), groundnuts and sweet potato (4) and pasture (2).

In secondary woodland, *M. lepidus* was significantly associated with *M. aluco*, *M. grassei* and *M. subhyalinus* in the dry season and *M. aluco* associated with *M. subhyalinus* in the first wet and dry season. *M. grassei* was associated with *M. subhyalinus* in the second wet season. In pasture, *M. lepidus* was associated with *M. subhyalinus* in the second wet season. *M. n.sp. C* showed a negative association with *M. lepidus* in the second wet season. In sweet potato, *M. lepidus* was associated with both *M. subhyalinus* and *M. aluco* in the second wet season while *M. subhyalinus* and *M. aluco* were associated in both wet seasons. In groundnuts, *M. subhyalinus* was associated with *M. grassei* in the second wet season, *M. aluco* in both wet seasons and *M. n.sp. C* in the dry season. *M. n.sp. C* was associated with *M. subhyalinus* in the dry season. In yam, *M. lepidus* was associated with *M. aluco* and *M. subhyalinus* in all seasons and with *M. grassei* in the dry season. *M. aluco* was associated with *M. subhyalinus* in the dry season and with *M. grassei* and *M. subhyalinus* in the second wet season. *M. grassei* was associated with *M. subhyalinus* in the dry season. In short-term maize, *M. lepidus* was associated with *M. subhyalinus* in the dry season and with *M. subhyalinus* and *M. grassei* in the second wet season. *M. grassei* was associated with *M. subhyalinus* in the second wet season. *M. subhyalinus* was negatively associated with *M. aluco* in dry season.

6.4 DISCUSSION

Microtermes spp. occurrence on baits was typically less than 30% while individual species foraged on less than 20%. This is not an unusual phenomenon as shown by El Bakri (1986) and Ferrar (1982). Low occurrence on baits may be a consequence of the attractiveness of the bait substrate (c.f Abensperg-Traun, 1993). It would be advisable to use a high density of baits (n/m^2) when examining *Microtermes*, especially species foraging activity.

Percentage bait attack by species calculated as a proportion of the total number of baits attacked ($B\%_a$) proved to be the most discriminating indicator of the differences in the foraging activity of total and individual *Microtermes* species with season, vegetation and abundance.

When it was not possible to examine differences within individual vegetation types, due to a lack of samples, the analysis of foraging within vegetation groups was a useful in the study of differences due to time, species and vegetation.

6.4.1 Community structure of *Microtermes* foraging on baits

These analyses were useful as they highlighted seasonal and vegetation differences in community structure which were not apparent from analysis of foraging activity.

The trend for higher species richness in the wet seasons compared to the dry would be expected with increased foraging activity and soil abundance. Seasonal and vegetation differences in species richness in woodland and newly cleared and cultivated vegetation types can be related, in greater part, to the presence or absence of *M. n. sp. C*. In long-term ranch and farm maize, the predominance of *M. lepidus* was the most important factor.

Higher Shannon-Wiener and evenness indices in the dry season compared to the wet season reflected changes in the relative occurrence of the predominant species, *M. subhyalinus*, *M. lepidus* and *M. aluco*. The relative abundance of these species was lower in the dry season and therefore bait occurrence was more equitable amongst the species. The different seasonal trend in Shannon-Wiener and evenness indices in pasture compared to other vegetation types can be related to the relatively low foraging activity.

Interpretation of results for community structure from Shannon-Wiener and evenness indices are limited due to the qualitative nature of the data. Further comparisons of species baiting where counts of species on baits would be useful to confirm the trends identified in this study.

6.4.2 Seasonal effects on *Microtermes* foraging on baits

Seasonal differences in foraging would be expected from previous published results, with foraging higher in the wet season than dry (Buxton, 1981; La Fage et al., 1973; Haverty et al., 1974 & b; Jones et al., 1987; Ferrar, 1982b; El Bakri, 1986). However, only foraging by *M. aluco* in woodland + pasture showed obvious seasonal differences. The lack of further seasonal differences was mainly due to similar levels of foraging between the first wet season and the following dry season. There are several possible explanations for this phenomenon, although it is impossible to state from this study which would have had the most influence. Climatic differences between the years may have influenced foraging activity while site disturbance in the first year is likely to have reduced foraging. The importance of the sampling procedure must also be considered as termite foraging activity is known to fluctuate diurnally and within a season. Seasonal differences may not have been noted if sampling was not carried out at similar times within each sampling and season, especially with such a low occurrence of species on baits. Also, there may have been seasonal differences in numbers of individuals on baits which could not be determined from this study.

Changes in *Microtermes* spp. foraging with season and year can mainly be attributed to the foraging of two species; *M. lepidus* and *M. subhyalinus* in newly cultivated crops and *M. subhyalinus* in root crops and woodland + pasture. These results are to be expected as these species showed the highest population increases from 1974 to 1976 in these crops, respectively, as shown from quantitative sampling (Chapter Four). The opposite foraging pattern by *M. aluco* could be as a result of changing competition as other species increased in abundance.

6.4.3 Vegetation cover effects on *Microtermes* foraging on baits

To discuss these results adequately, it is necessary to refer to abundance data from Chapter Four.

Foraging activity by the *Microtermes* spp. population can be accounted for both by absolute abundance and relative abundance compared to other termite genera. The highest level of foraging was recorded on long-term maize where *Microtermes* spp. abundance was high and there were few other termites present to compete for food (see Chapter Four). The opposite can be applied to foraging in primary woodland where low *Microtermes* spp. abundance and low relative abundance compared with other termite genera would increase competition for resources. It must also be considered that *Microtermes* would be able to forage on more varied food source in primary woodland than in other vegetation types. This point is discussed later.

More active foraging by *Microtermes* in the second season in secondary woodland and pasture, compared to newly cultivated plots, occurred without an increase in abundance. Surface litter, density of roots in the upper soil layers and less disturbance of the soil in these sites (pasture was cleared but not cultivated) may have provided a more hospitable surface foraging environment than in the newly cultivated sites.

Similar foraging activity between wet seasons in sweet potato and groundnuts can be related to low *Microtermes* spp. abundance throughout the study. The similarity in foraging activity between years in yam can be related to presence of a food source (wooden stakes) which maintained populations throughout wet and dry seasons. The gradual increase in foraging in short-term maize mirrored an increase in *Microtermes* spp. abundance, irrespective of season. Maize is susceptible to *Microtermes* damage and maize as an alternative/preferred food source may account for the lower foraging activity on short-term maize compared to other newly cultivated plots.

Microtermes spp. foraging was generally reflected by foraging of the most abundant species, in particular *M. subhyalinus* and *M. lepidus*. Species foraging activity in each vegetation type also matched species abundance, except primary woodland. There was only one sample from this vegetation type and it would require further examination to determine if this was a representative result.

Foraging by individual species was similar on all newly cultivated and cleared plots and only differed on the least disturbed sites (woodland) and long-term cultivated sites (maize). These results again, generally, reflected species abundance levels in the individual vegetation types. *M. n.sp. C* and *M. grassei* were the least recorded species from baits while *M. subhyalinus* and *M. aluco* were the most frequently recorded species on all except long-term maize, where *M. lepidus* was the most common species on baits; *M. lepidus* was the most abundant species in long-term maize, *M. subhyalinus* was the most abundant species on all other vegetation types while *M. grassei* and *M. n.sp. C* were low in abundance. The increase in foraging by *M. subhyalinus* concurs with Usher, 1975. Foraging by *M. aluco* was higher than would be expected when compared to abundance. This may be due to competition for other food sources and/or food preferences.

M. grassei is recorded as a woodland species and this is reflected in the higher foraging activity of this species in primary woodland than in other vegetation types.

6.4.4 Spatial distribution of foraging on baits

The results suggest that foraging by *Microtermes* species may not always follow random patterns and that there may be co-occurrence related to the non-random finding of baits by species. This contradicts previous findings from Mokwa (Wood, 1981) where foraging was examined on a secondary woodland plot. Species occurrence on baits was low in this example and may have been too low to identify co-occurrence. It is also likely that there are occasions where occurrence on baits is either random or non-random as foraging activity changes both temporally and spatially.

The likelihood of non-random foraging on baits was further substantiated by significant species associations. The fewest species associations were shown in plots were foraging activity was low suggesting that there is a minimum level of foraging activity required before associations will be apparent, as also shown for co-occurrence on baits. In one plot, pasture 5 in the second wet season. foraging activity was high and it may be suggested that this may have biased results. However, species occurrence on baits was less than 50% of all baits for any species and therefore it is unlikely that "over-occurrence" affected these results. In all but two cases the significant associations between species were shown to be positive which may be related to the similar feeding preference of these associated species, attractiveness of baits due to micro-climate and/or substrate. The greatest number of associations were shown between *M. subhyalinus* and *M. aluco, M. lepidus* and *M. subhyalinus* followed by *M. aluco* and *M. lepidus. M. subhyalinus* and *M. aluco* were the dominant species on baits for each vegetation type. No associations with *M. n. sp. C* maybe related to the very low occurrence of this rare species.

Foraging activity by *Microtermes* spp. and individual species was shown to generally follow random distributions on baits. In cases where non-random foraging was recorded, two of these were plots exhibited high *Microtermes* spp. occurrence on baits and therefore there would be a bias to high bait records per quadrat. In the remaining cases, there was low occurrence on baits and an indication of clustering. This may be related to the heterogeneity of the plots and environmental factors which may make baits more palatable; soil conditions, shading etc.

Again there were few results obtained from the analysis of species distribution on baits due to limited numbers. Most non-random foraging by *Microtermes* species was shown by *M. subhyalinus* and to a lesser extent *M. aluco.* These two species were showed the highest foraging activity. Non-random foraging did not relate to over-occurrence on baits due to high foraging activity as occurrence on baits ranged from low to high for significant cases.

Non-random foraging distribution of *Microtermes* on baits maybe due to several factors e.g. spatial variability in the environment effecting the palatability of baits, foraging ranges of colonies and competition among species. Species associations may indicate that certain species (*M. subhyalinus*, *M. lepidus* and *M. aluco*) may have similar feeding preference.

Foraging behaviour may also be similar amongst these species as timing of sampling, both within the day and season, is biased towards collecting these species. Further study should examine diurnal foraging to determine if diurnal foraging differs amongst the species.

Further study is required on species associations and distribution patterns as this study can not draw conclusive assumptions on species associations or distribution patterns.

There was a loss of results due to the low numbers of species on baits, often resulting in too few degrees of freedom. This factor should be taken into consideration in future studies. It may be possible to reduce this problem by increasing the number of sampling occasions within each season and/or by carrying out diurnal studies on foraging.

6.5 CONCLUSION

The hypotheses presented in this study are re-examined:

(1) The community structure and foraging activity of *Microtermes* will be influenced by vegetation type and seasonal climate, notably reduced foraging in the dry season compared to the wet season, with successional changes identified as woodland is cleared and different crops cultivated.

(a) The identification of *Microtermes* species from foraging on baits can give an accurate indication of species composition of a *Microtermes* population and may identify differences amongst vegetation types; species richness did not vary greatly amongst woodland, newly cleared and cultivated vegetation types but was less in long-term maize.

(b) Differences in species richness in cleared and cultivated sites were linked to the presence or absence of the rare species, *M. n. sp. C.*

(c) Changes in community structure were identified by species richness, Shannon-Wiener diversity and evenness indices which highlighted seasonal and vegetation trends in species occurrence on baits which were not indicated by analyses of variance of species occurrence on baits.

(d) The usefulness of Shannon-Wiener diversity and evenness indices would be greatly enhanced by counts of species on baits.

(e) Seasonal differences in foraging activity were recorded from baits but the most significant differences were shown over time.

(f) Foraging activity on baits was significantly different amongst the vegetation types and amongst species.

(g) The percentage of baits attacked by individual species as a proportion of the total number of baits attacked by all individual species was the best indicator of foraging differences with season, vegetation type and abundance.

(h) More intensive sampling is required to complete comparisons of foraging activity of individual species in individual vegetation types.

(2) Spatial distribution of species can be detected from foraging activity.

(a) Non-random foraging was identified for *Microtermes* spp. and individual species.

(b) There was a positive association on baits among *M. subhyalinus*, *M. aluco* and *M. lepidus*.

The study suggests some methods by which the accuracy of the assessment of foraging activity may be improved. Although more time consuming, counts or estimates of foragers on baits could give a more quantitative estimate of foraging intensity. Several sampling occasions within each season along with both diurnal and seasonal timing of sampling, as discussed previously, would aim to reduce variations in foraging with environmental factors. Recording of diurnal and seasonal environmental factors when sampling e.g. rainfall, cloud cover, air temperature, soil temperature, soil moisture content to aid in the determination of best sampling time and the effects of these factors of foraging behaviour.

CHAPTER SEVEN

COMPARISON OF *MICROTERMES* ABUNDANCE IN SOIL WITH FORAGING ON SURFACE LAID BAITS

7.1 INTRODUCTION

As discussed in earlier Chapters of this present study, the Termite Research Project aimed to examine the relationship between the foraging activity and soil abundance of wood and litter feeding termites at Mokwa and, in particular, *Microtermes*, which was the dominant termite genus in the cultivated plots and a major soil pest in the region. This work had a practical objective to determine whether measurements of foraging at baits could be related to population density. Information on population density and dynamics of pest species is essential to determine the efficacy of pest control measures.

A baiting technique has the potential to be utilised as an index of population density and hence save the considerable time and labour required to make absolute measurements of termite abundance, especially of subterranean species. Preliminary results from Mokwa show that two parameters, percentage of occurrence on baits and weight of bait consumed, directly correlated with *Microtermes* abundance (Wood et al., 1977a).

This present study aims to expand the work of the Termite Research Project to examine the hypotheses that foraging activity by *Microtermes* spp. and individual species on baits corresponds to soil populations and therefore foraging activity can be used an a qualitative index of abundance and as a predictor of populations, especially of pest species.

These hypotheses will be examined by the following procedures:

1. Comparison of *Microtermes* community structure (species richness, Shannon-Wiener diversity and evenness indices) results from foraging activity (Chapter 4) and soil abundance (Chapter 5).

2. Comparison of foraging activity (Chapter Four) and soil abundance (Chapter Five) of *Microtermes* spp. and individual species.

7.2 METHODS

7.2.1 Comparison of *Microtermes* community structure

There were three seasons data available from foraging activity and soil abundance (Chapters Four and Five) which allowed direct comparisons of species richness, Shannon-Wiener diversity and evenness indices. These seasons were the first wet and dry seasons (1974) and the following wet season (1975). Too few seasons were available for primary woodland, so this vegetation type was excluded. The vegetation types were secondary woodland, long-term maize; ranch and farm maize, and newly cleared and cultivated sites; pasture, sweet potato, groundnuts, yam and short-term maize. Comparisons were carried out with occurrence on baits soil abundance from 0 to 1 m (in text, 1 m) and soil abundance from 0 to 25 cm (in text, 25 cm).

7.2.2 Comparison of foraging with abundance in soil

Comparisons of foraging data with abundance made use of the absolute soil sampling data reported in Chapter Four and foraging activity from Chapter Five. Simple linear regressions were fitted to compare *Microtermes* foraging activity with soil abundance from 0 to 1 m and 0 to 25 cm depth intervals. Analysis was carried out on data for combined wet and dry seasons and for wet and dry seasons individually. Abundance data were transformed using logarithms ($\log_{10} x + 1$). Relative abundance of species at both depths were derived from the quantitative data and arcsine transformed to correct for non-normality.

7.3 RESULTS

7.3.1 Comparison of *Microtermes* community structure

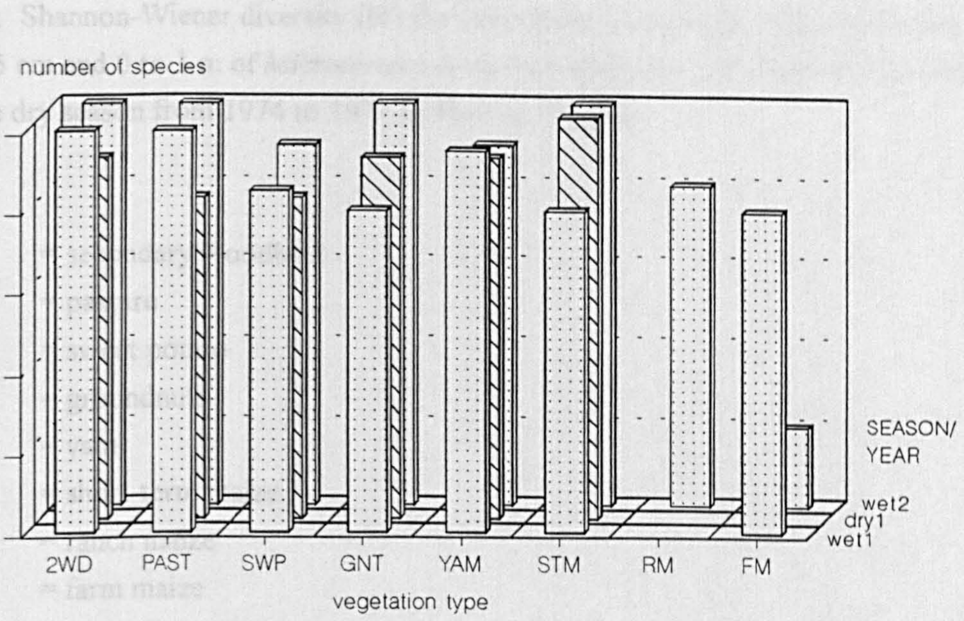
Figure 7.1 shows mean species richness for occurrence on baits, soil abundance from 0 to 25 cm and from 0 to 1 m. Figure 7.2 shows Shannon-Wiener diversity (H') for occurrence on baits, soil abundance from 0 to 25 cm and from 0 to 1 m. Figure 7.3. shows Evenness (J') for occurrence on baits, soil abundance from 0 to 25 cm and from 0 to 1 m. Throughout the results section, the term *diversity* refers to the Shannon-Wiener diversity index.

Species richness, in all vegetation types except long-term maize, was higher on baits than for soil abundance where species richness was higher for 1 m than 25 cm. In newly cleared and cultivated groundnuts, yam and short-term maize, species richness for soil abundance for 1 m increased from first to second wet season where it was only slightly less than on baits. In certain vegetation types, seasonal effects in species richness differed between baits and soil abundance; in secondary woodland, species richness on baits was higher in wet seasons than in the dry season while species richness from soil abundance for both depths indicated the reverse.

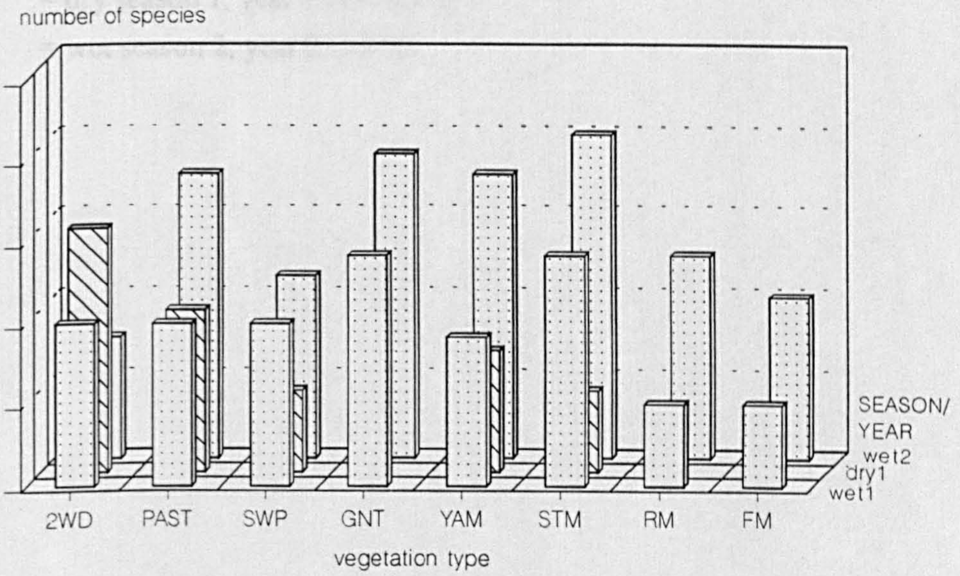
Figure 7.1 : Mean species richness for occurrence on baits and soil abundance from 0 to 25 cm and 0 to 1 m of *Microtermes* in uncultivated and cultivated sites for two wet and one dry season from 1974 to 1975 at Mokwa, Nigeria.

KEY
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

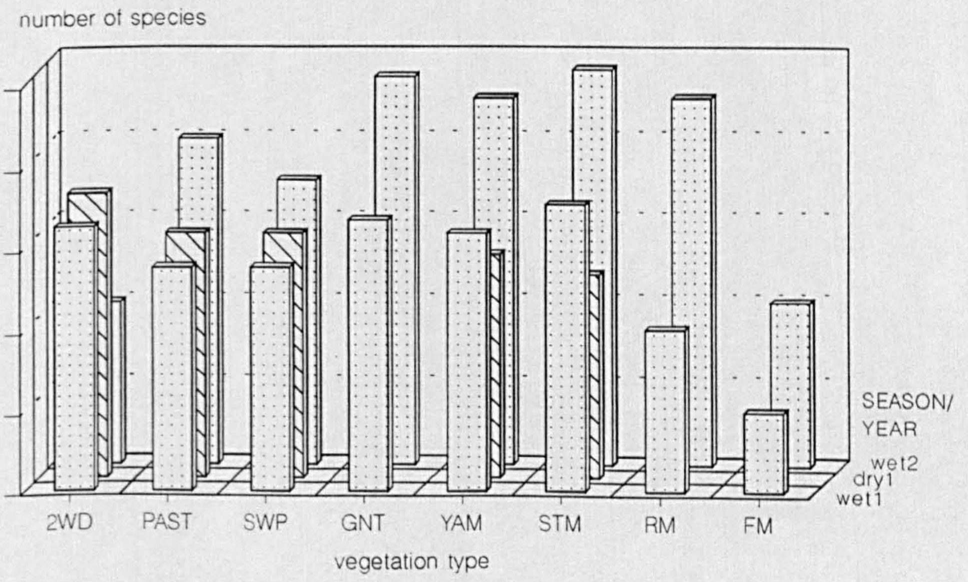
WET1 = wet season 1, year 1 (1974)
DRY1 = dry season 1, year 1 (1974/75)
WET2 = wet season 2, year 2 (1975)



species richness on baits



species richness to a soil depth of 25 cm



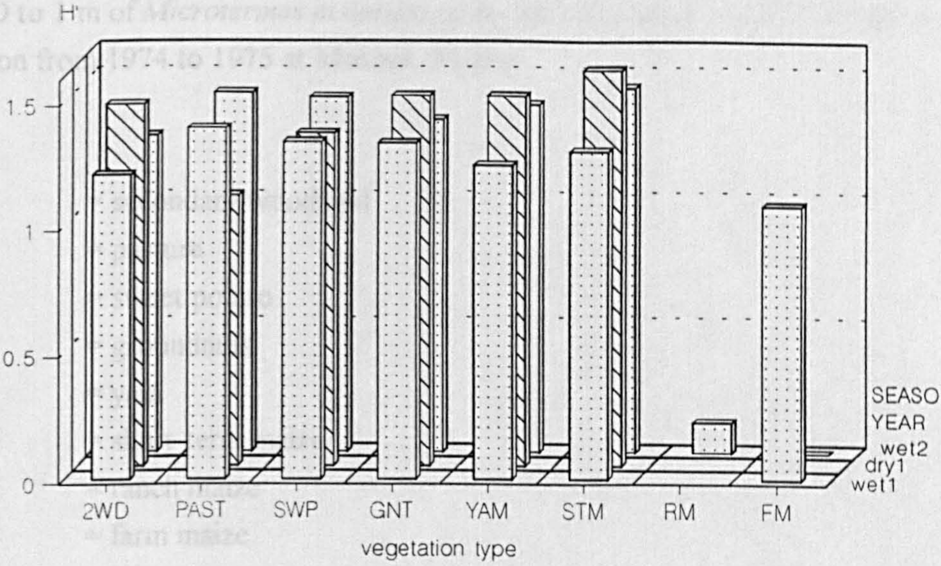
species richness to a soil depth of 1 m

Figure 7.2 : Shannon-Wiener diversity (H') for occurrence on baits and soil abundance from 0 to 25 cm and 0 to 1 m of *Microtermes* in uncultivated and cultivated sites for two wet and one dry season from 1974 to 1975 at Mokwa, Nigeria.

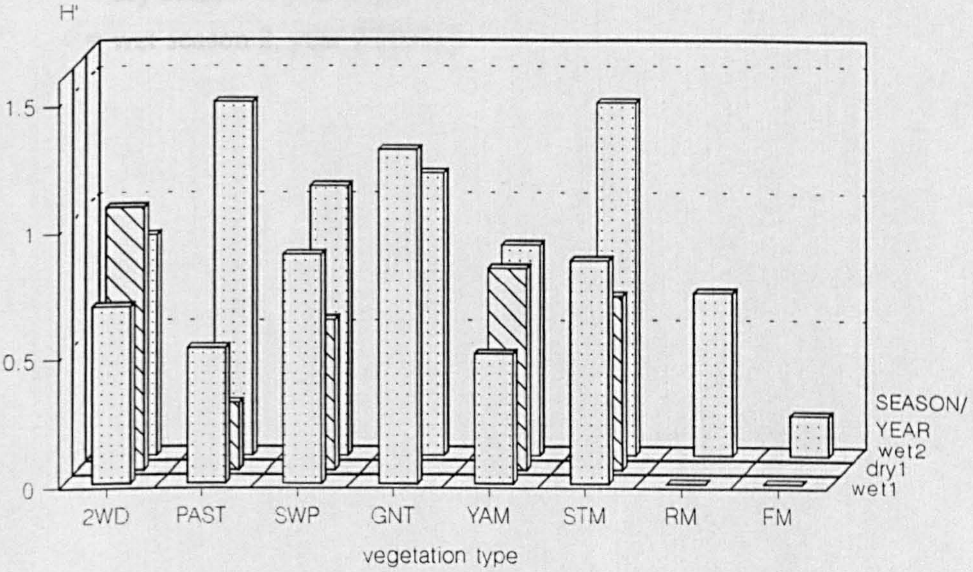
KEY
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

WET1 = wet season 1, year 1 (1974)
DRY1 = dry season 1, year 1 (1974/75)
WET2 = wet season 2, year 2 (1975)

diversity on baits



diversity to a soil depth of 25 cm



diversity to a soil depth of 1 m

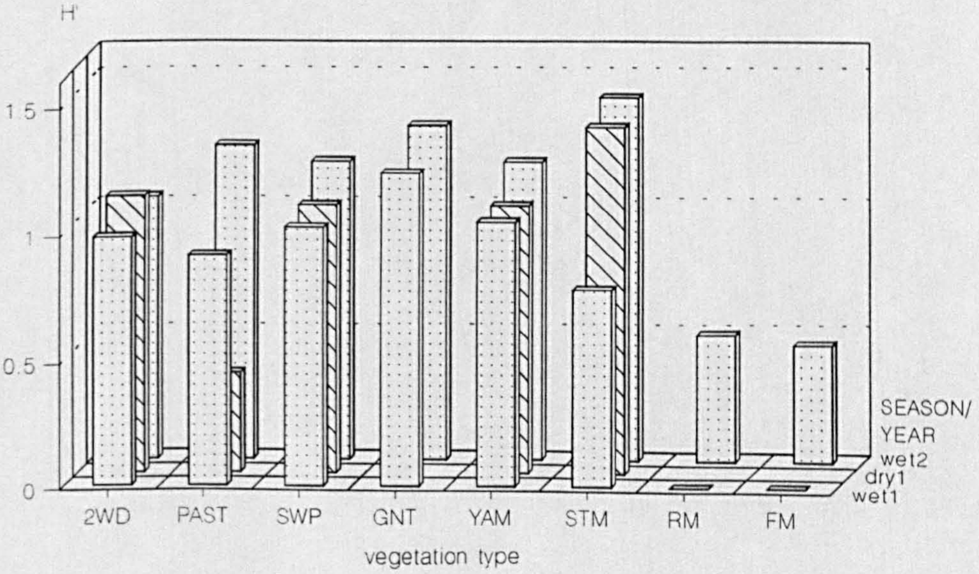
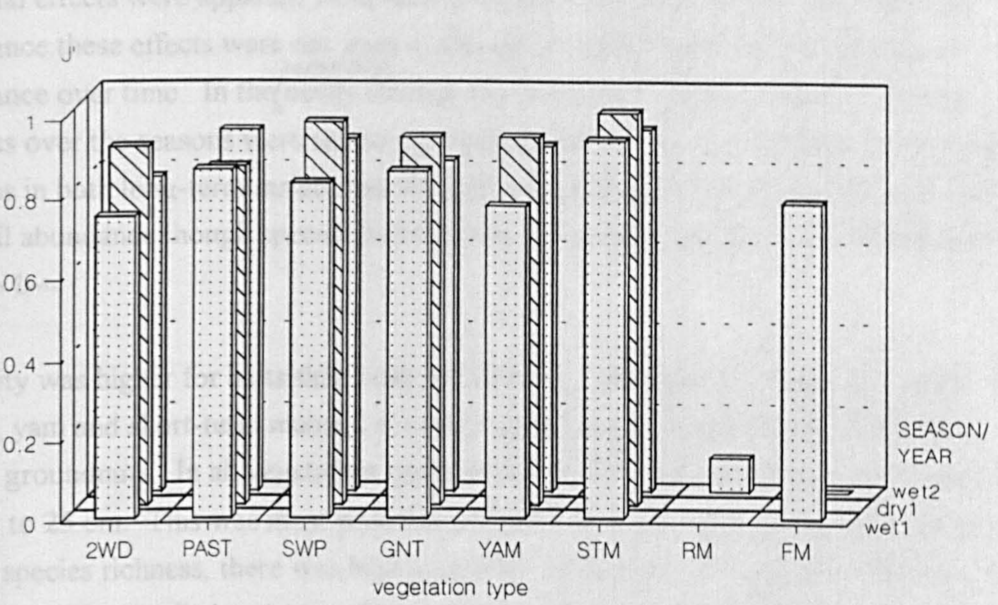


Figure 7.3. : Evenness index (J') for occurrence on baits and soil abundance from 0 to 25 cm and 0 to 1 m of *Microtermes* in uncultivated and cultivated sites for two wet and one dry season from 1974 to 1975 at Mokwa, Nigeria.

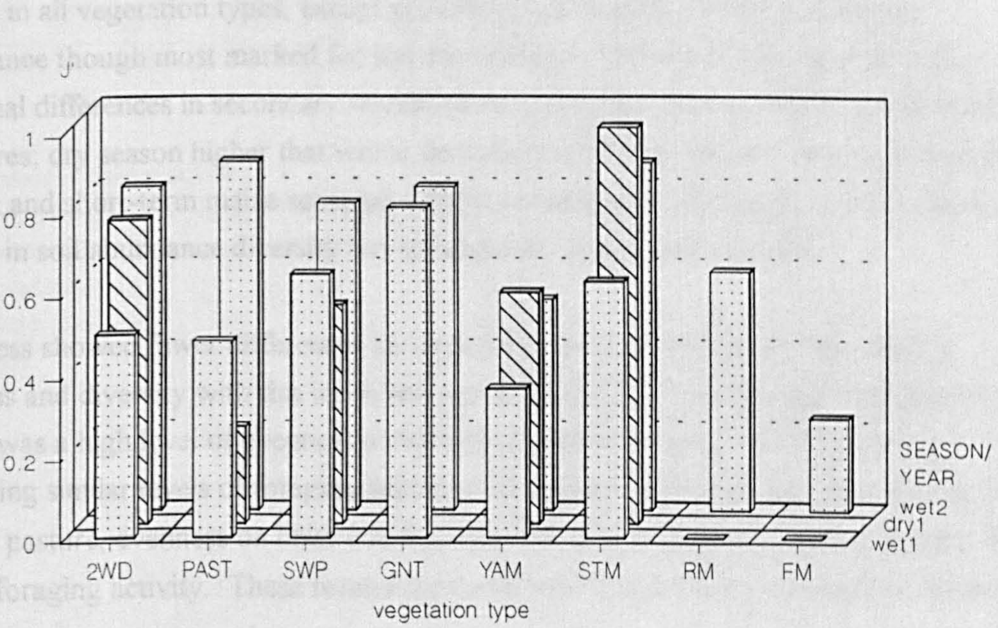
KEY
2WD = secondary woodland
PAST = pasture
SWP = sweet potato
GNT = groundnuts
YAM = yam
STM = short-term maize
RM = ranch maize
FM = farm maize

WET1 = wet season 1, year 1 (1974)
DRY1 = dry season 1, year 1 (1974/75)
WET2 = wet season 2, year 2 (1975)

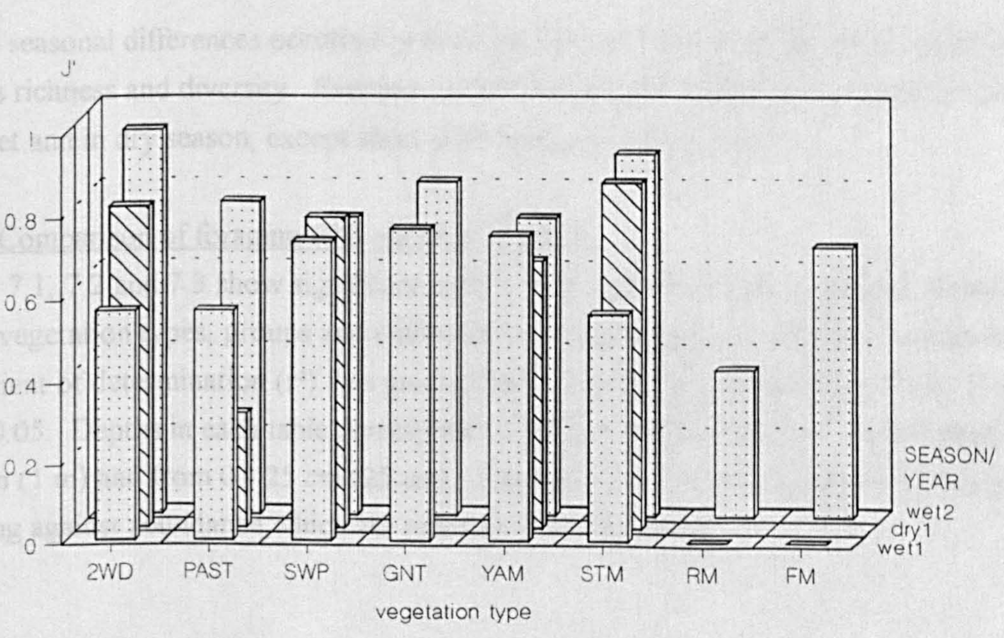
evenness on baits



evenness to a soil depth of 25 cm



evenness to a soil depth of 1 m



Seasonal effects were apparent from baits in pasture and sweet potato but from soil abundance these effects were not shown, though possibly masked by the increases in soil abundance over time. In the remaining newly cleared and cultivated sites, increases in species richness over the seasons were not so pronounced on baits as for soil abundance. Species richness in both long-term maize sites showed a high degree of variation for both baits and soil abundance though species richness was generally lower for soil abundance to 25 cm than 1m.

Diversity was higher for baits than both soil depths in secondary woodland, pasture, sweet potato, yam and short-term maize, i.e. same vegetation types as for species richness except groundnuts. In all vegetation types, diversity from soil abundance was higher for 1 m than to 25 cm. This was most pronounced in the first wet season, except in pasture. As for species richness, there was high variability in diversity in the long-term maize sites for both baits and soil abundance. The increase in diversity from first to second wet season in all vegetation types, except groundnuts, was noted from baits and soil abundance though most marked for soil abundance to 25 cm and less marked in baits. Seasonal differences in secondary woodland and pasture were recorded from all diversity measures; dry season higher that wet in secondary woodland and the reverse in pasture. In yam and short-term maize seasonal differences indicated by diversity on baits were not shown in soil abundance diversity due to increases in abundance with time.

Evenness showed fewer differences between baits and soil abundance than species richness and diversity with this index less variable with year, season and vegetation type. There was a high level of evenness on baits throughout the study (0.749 - 0.977) indicating similar levels of foraging amongst the species. In almost all vegetation types, except pasture, evenness on baits was higher in dry season than wet season on baits due to lower foraging activity. These results are partly a reflection of the overall low occurrence on baits

Where seasonal differences occurred in evenness for soil, they were similar to those for species richness and diversity. Evenness in soil was slightly higher for 1 m than 25 cm in first wet and in dry season, except short-term maize and groundnuts.

7.3.2 Comparison of foraging with abundance in soil

Tables 7.1, 7.2 and 7.3 show significant results from regression and correlation analysis for all vegetation types, groups and individual vegetation types, respectively, where the coefficient of determination (r^2) was greater than 30% and the probabilities for the F value (P) ≤ 0.05. Depths in each table correspond to species abundance in soil (n/m^2) from 0 - 100 cm (1 m) and from 0 - 25 cm (25 cm). Figures 7.4 to 7.14 are regression plots of foraging against abundance which are referred to in the results.

Table 7.1 : Significant interactions* from simple linear regression and correlation of *Microtermes* foraging on baits with abundance in soil in all vegetation types; where $r^2 \geq$ 30% and $P \leq 0.05$.

season	species	soil depth (cm)	dependent variable (foraging)	independent variable (abundance)	r2	F-value	P	n
both	all	100	B%a	m2	30.2	64.03	<0.005	150
wet	*M. lepidus*	100	B%a	%	69.55	50.25	<0.005	24
wet	*M. lepidus*	100	B%a	m2	56.27	28.31	<0.005	24
wet	*M. lepidus*	100	B%l	%	47.11	19.6	<0.005	24
wet	*M. lepidus*	100	Ba	%	47.23	19.69	<0.005	24
wet	*M. lepidus*	100	B%a	%	73.92	62.37	<0.005	24
wet	*M. lepidus*	100	B%a	m2	53.64	25.46	<0.005	24
wet	*M. lepidus*	100	B%l	%	46.44	19.08	<0.005	24
wet	*M. lepidus*	100	Ba	%	44.63	17.35	<0.005	24
wet	*M. aluco*	100	B%a	m2	31.59	10.16	<0.005	24

* significant interactions from 252 regressions and correlations

KEY

Ba = number of baits attacked

B%a = percentage of baits attacked per species from total attacked by Microtermes

B%l = percentage of baits attacked from the total laid out

m2 = abundance n/m2

% = relative abundance

Figure 7.4 : Scatter-plot of *Microtermes* spp. foraging activity, as percentage occurrence on baits (B%l), against total abundance to 1 m soil depth (n/m²) in all vegetation types.

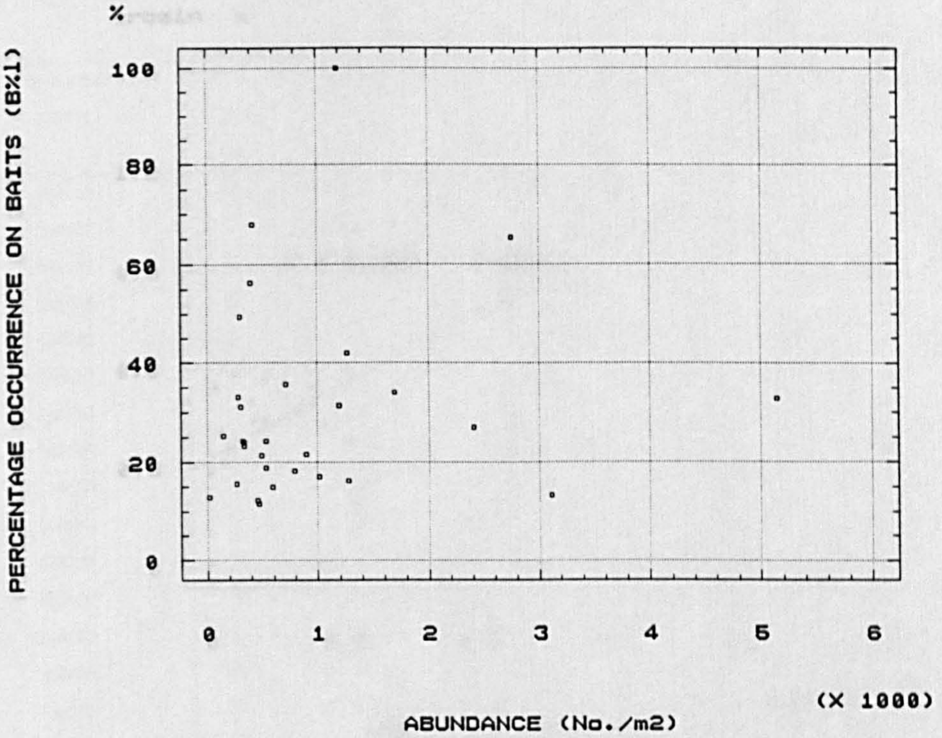


Figure 7.5 : Scatter-plot of all *Microtermes* species foraging activity, as percentage occurrence on baits (B%a), against species abundance (n/m²) to 1 m soil depth in all vegetation types.

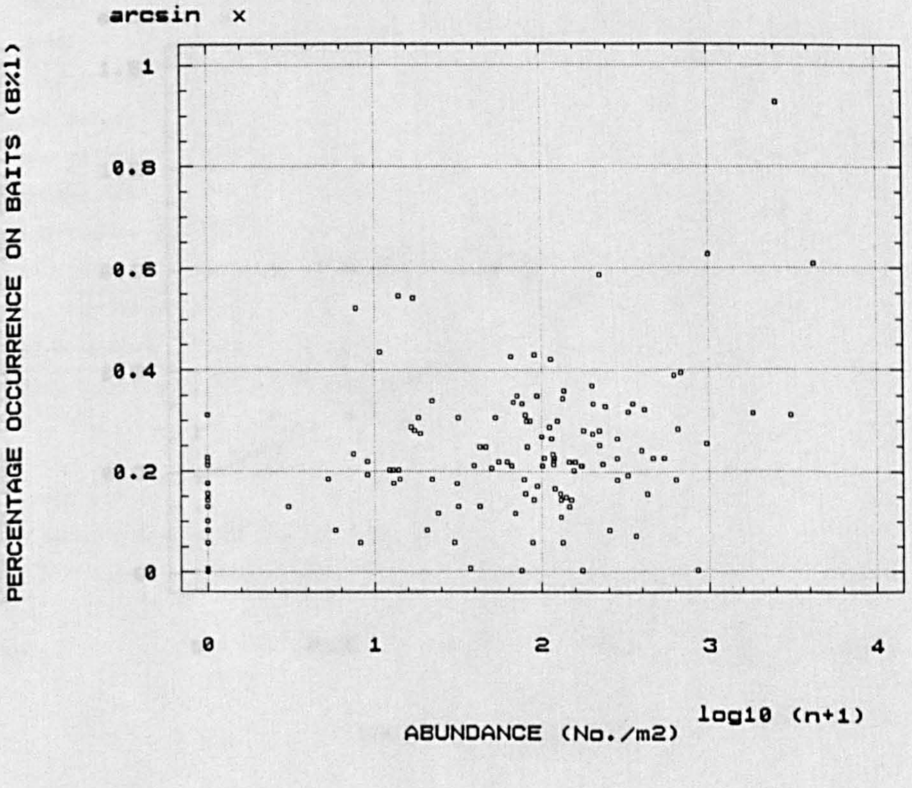


Figure 7.6 : Regression plot of *Microtermes lepidus* foraging activity, as percentage occurrence on baits (B%a), against relative abundance to 1 m soil depth (%) in all vegetation types for wet seasons only.

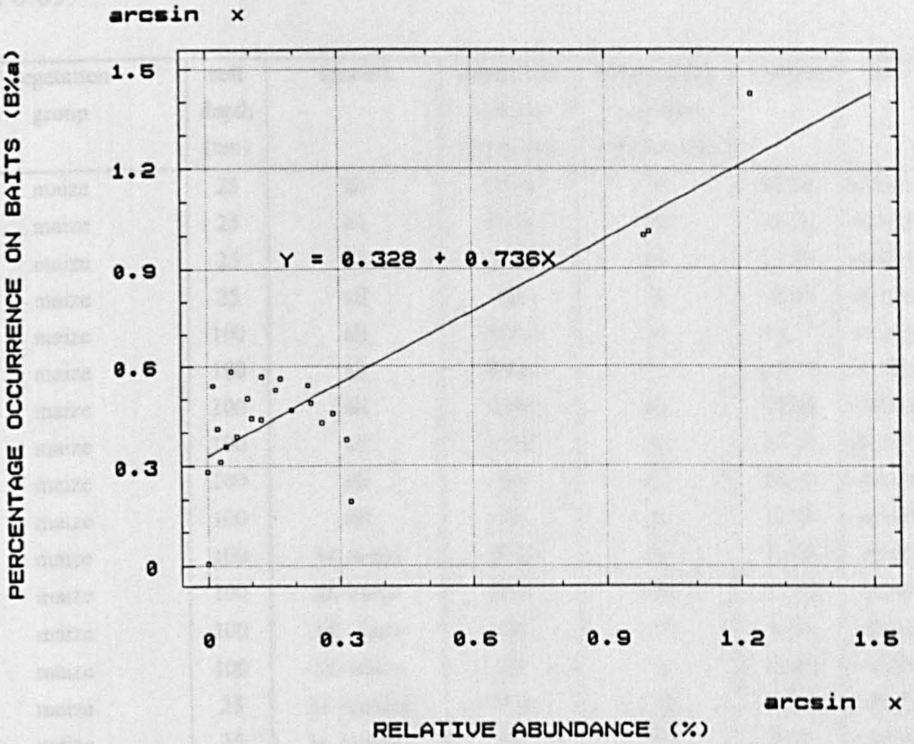


Figure 7.7 : Regression plot of *Microtermes lepidus* foraging activity, as percentage occurrence on baits (B%a), against species abundance (n/m²) to 25 cm soil depth in all vegetation types for wet seasons only.

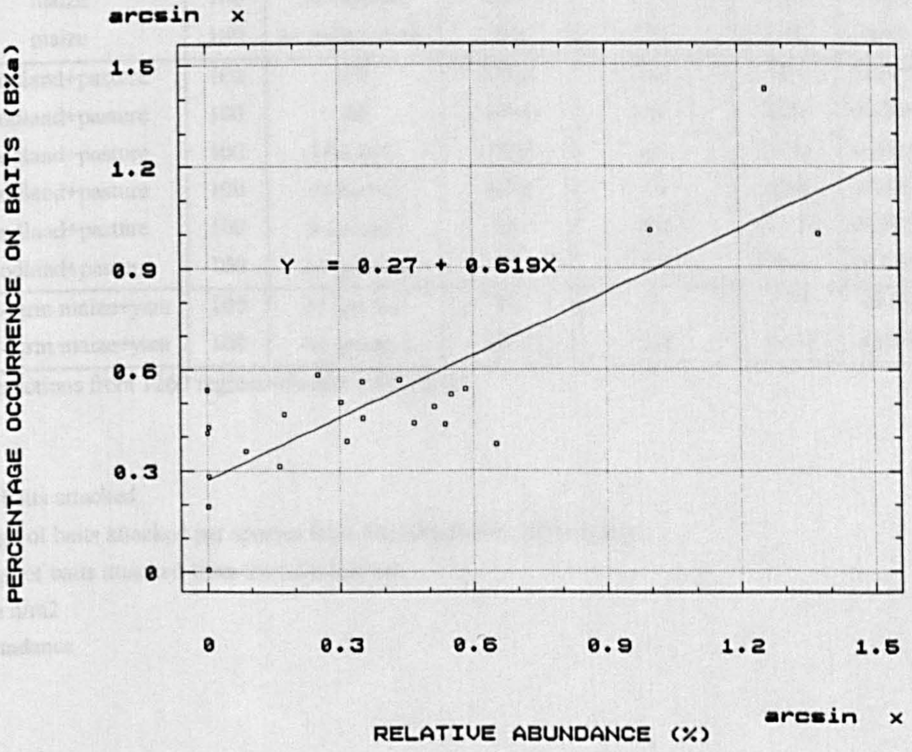


Table 7.2 : Significant interactions* from simple linear regression and correlation of *Microtermes* foraging on baits with abundance in soil in vegetation groups; where $r^2 \geq 30\%$ and $P \leq 0.05$.

season	vegetation group	soil depth (cm)	species	dependent variable (foraging)	independent variable (abundance)	F-value	P	r2	n
both	maize	25	all	B%a	%	32.24	<0.005	53.32	30
both	maize	25	all	B%a	m2	21.07	<0.005	42.94	30
both	maize	25	all	B%l	%	15.38	<0.005	35.46	30
both	maize	25	all	Ba	%	13.63	<0.005	32.74	30
both	maize	100	all	B%a	%	84.17	<0.005	72.84	35
both	maize	100	all	B%a	%	24.97	<0.005	43.07	35
both	maize	100	all	B%l	m2	78.88	<0.005	70.5	35
both	maize	100	all	B%l	%	22.94	<0.005	41.01	35
both	maize	100	all	Ba	m2	58.93	<0.005	64.1	35
wet	maize	100	all	Ba	%	17.99	<0.005	69.22	10
wet	maize	100	*M. aluco*	B%l	%	12.69	<0.05	76.32	6
wet	maize	100	*M. aluco*	B%l	m2	12.57	<0.05	75.87	6
wet	maize	100	*M. aluco*	Ba	%	8.53	<0.01	68.08	6
wet	maize	100	*M. aluco*	Ba	%	11.45	<0.05	74.12	6
both	maize	25	*M. lepidus*	B%a	m2	6.53	<0.05	56.63	7
both	maize	25	*M. lepidus*	Ba	%	7.04	<0.05	58.48	7
both	maize	25	*M. lepidus*	B%a	%	17.04	<0.01	77.31	7
wet	maize	25	*M. lepidus*	B%a	%	50.25	<0.005	69.55	7
both	maize	100	*M. lepidus*	B%a	m2	7.88	<0.05	61.18	7
both	maize	100	*M. lepidus*	B%a	%	63.09	<0.005	92.66	7
both	maize	100	*M. lepidus*	B%l	%	9.99	<0.05	66.65	7
both	maize	100	*M. lepidus*	Ba	%	8.9	<0.05	64.04	7
wet	maize	100	*M. lepidus*	B%a	%	67.85	<0.005	94.43	7
wet	maize	100	*M. lepidus*	B%a	m2	15.72	<0.05	79.61	7
wet	maize	100	*M. lepidus*	B%l	%	8.79	<0.05	66.66	7
wet	maize	100	*M. subhyalinus*	Ba	%	4.66	<0.05	53.63	7
both	woodland+pasture	100	all	B%a	m2	27.1	<0.005	38.18	50
both	woodland+pasture	100	all	B%l	%	22.04	<0.005	31.47	50
both	woodland+pasture	100	*M.n.sp.C*	B%l	m2	21.16	<0.005	30.59	50
both	woodland+pasture	100	*M.n.sp.C*	B%l	%	8.68	<0.05	52.03	10
both	woodland+pasture	100	*M.n.sp.C*	Ba	m2	175.39	<0.005	95.64	10
wet	woodland+pasture	100	*M. grassei*	Ba	m2	223.21	<0.005	97.81	7
both	short-term maize+yam	100	*M. grassei*	Ba	%	4.79	<0.05	40.62	9
both	short-term maize+yam	100	*M. grassei*	B%a	m2	10.52	<0.05	67.79	7

* significant interactions from 1260 regressions and correlations

KEY

Ba = number of baits attacked

B%a = percentage of baits attacked per species from total attacked by Microtermes

B%l = percentage of baits attacked from the total laid out

m2 = abundance n/m2

% = relative abundance

Figure 7.8 : Regression plot of *Microtermes* species foraging activity, as percentage occurrence on baits (B%a), against abundance to 1 m soil depth (n/m²) in maize for both seasons.

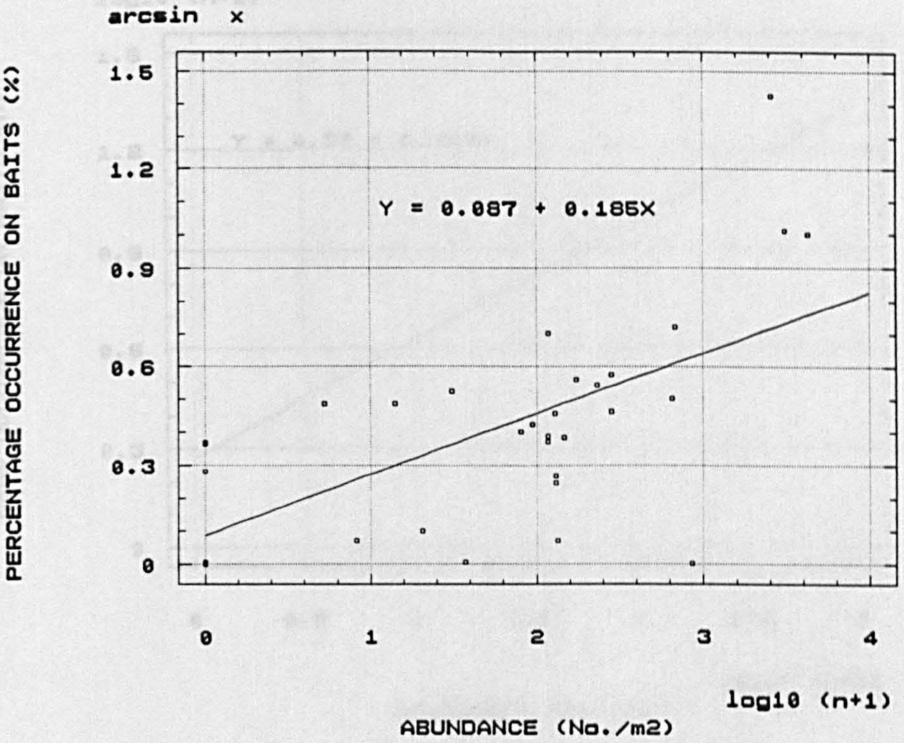


Figure 7.9 : Regression plot of *Microtermes lepidus* foraging activity, as percentage occurrence on baits (B%a), against relative abundance (%) to 1 m soil depth in maize for wet seasons only.

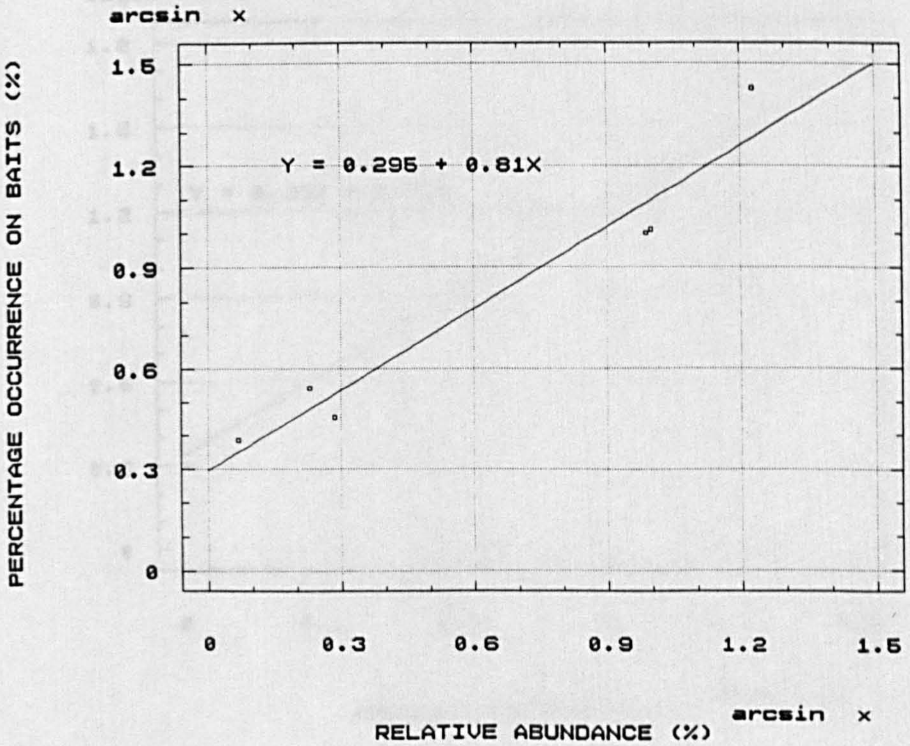


Figure 7.10 : Regression plot of *Microtermes aluco* foraging activity, as mean occurrence on baits, against abundance to 1 m soil depth (n/m²) in maize for wet seasons only.

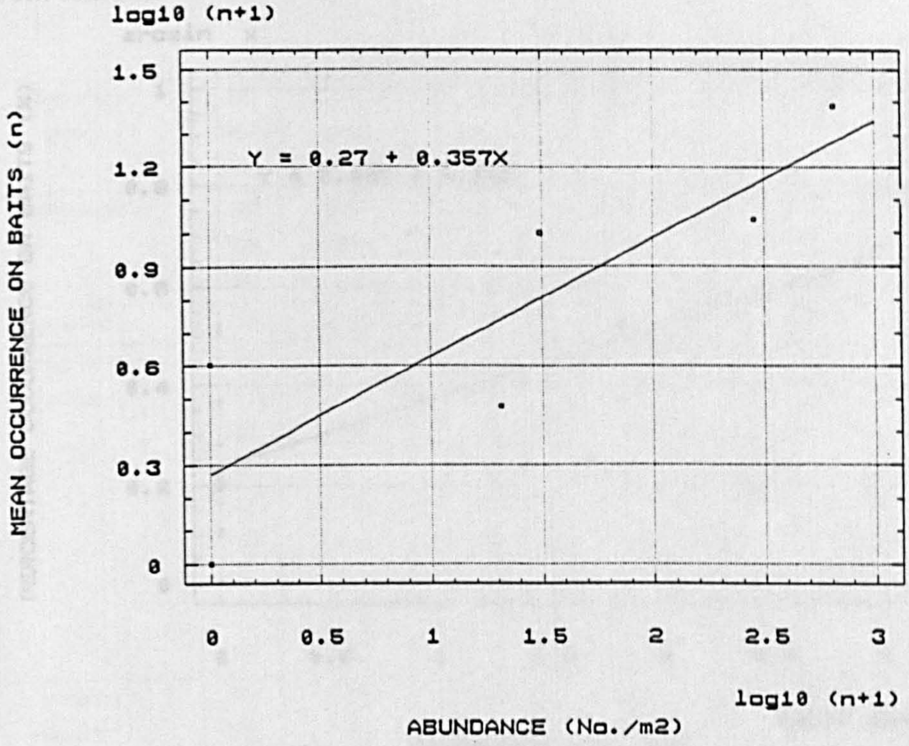


Figure 7.11 : Regression plot of *Microtermes subhyalinus* foraging activity, as mean occurrence on baits against relative abundance to 1 m soil depth (%) in maize for wet seasons only.

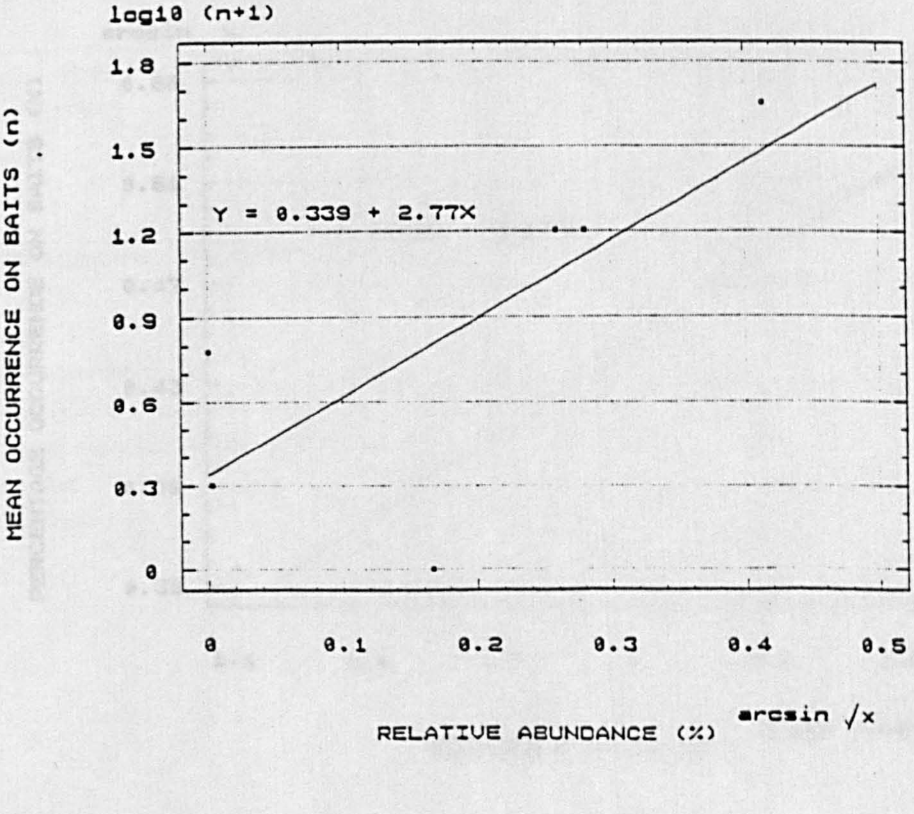


Figure 7.12 : Regression plot of *Microtermes* species foraging activity, as percentage occurrence on baits (B%a), against abundance to 1 m soil depth (n/m²) in woodland/ pasture for both seasons.

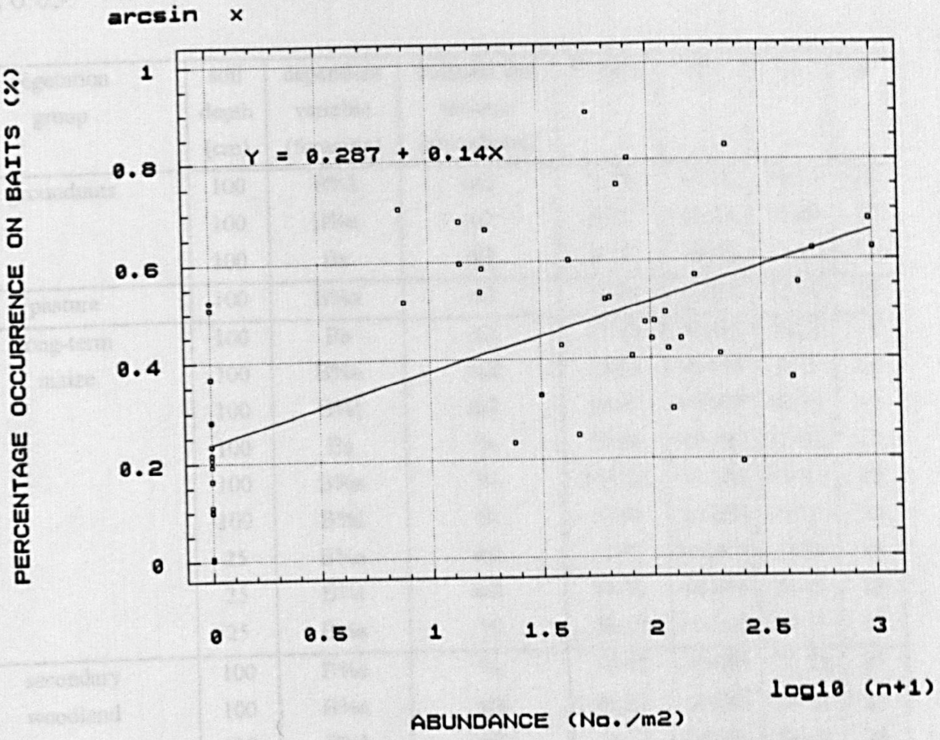


Figure 7.13 : Regression plot of *Microtermes lepidus* foraging activity, as percentage occurrence on baits (B%a), against abundance to 1 m soil depth (n/m²) in yam and short-term maize for both seasons.

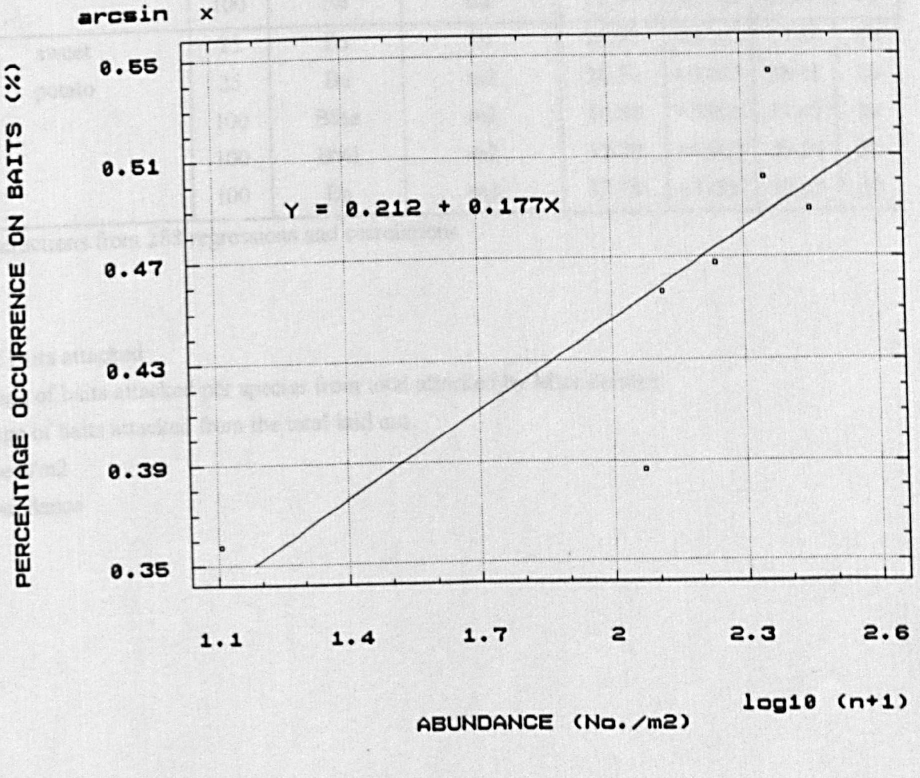


Table 7.3 : Significant interactions* from simple linear regression and correlation of *Microtermes* foraging on baits with abundance in soil in each vegetation type; where $r^2 \geq 30\%$ and $P \leq 0.05$.

season	vegetation group	soil depth (cm)	dependent variable (foraging)	independent variable (abundance)	F-value	P	r2	n
wet	groundnuts	100	B%l	m2	5.72	<0.05	30.57	15
wet		100	B%a	m2	6.91	<0.05	34.09	15
wet		100	Ba	m2	6.52	<0.05	33.41	15
both	pasture	100	B%a	m2	11.28	<0.005	32.77	25
wet	long-term maize	100	Ba	m2	13.13	<0.005	50.23	15
wet		100	B%a	m2	13.64	<0.005	51.2	15
wet		100	B%l	m2	12.35	<0.005	48.71	15
wet		100	Ba	%	79.66	<0.005	85.97	15
wet		100	B%a	%	124.52	<0.005	90.55	15
wet		100	B%l	%	13.64	<0.005	51.2	15
wet		25	B%a	m2	17.44	<0.005	57.29	15
wet		25	B%l	m2	14.36	<0.005	52.48	15
wet		25	B%a	%	58.14	<0.005	81.73	15
both	secondary woodland	100	B%a	%	10.07	<0.005	74.12	25
both		100	B%a	m2	20.11	<0.005	56.63	25
both		100	B%l	m2	16.17	<0.005	58.48	25
both		100	Ba	m2	12.77	<0.005	77.31	25
wet		100	B%a	m2	8.7	<0.05	69.55	15
wet		100	Ba	%	7.78	<0.05	61.18	15
wet		100	Ba	m2	6.83	<0.05	92.66	15
wet	short-term maize	25	Ba	m2	7.59	<0.05	66.65	15
wet		100	B%a	%	7.55	<0.05	64.04	15
wet		100	B%l	m2	16.16	<0.005	94.43	15
wet		100	Ba	%	6.67	<0.05	79.61	15
wet		100	Ba	m2	15.97	<0.005	66.66	15
wet	sweet potato	25	Ba	%	16.42	<0.005	53.63	20
wet		25	Ba	m2	26.32	<0.005	38.18	20
wet		100	B%a	m2	14.52	<0.005	31.47	20
wet		100	B%l	m2	17.79	<0.005	30.59	20
wet		100	Ba	m2	17.79	<0.005	52.03	20

* significant interactions from 288 regressions and correlations

KEY

Ba = number of baits attacked

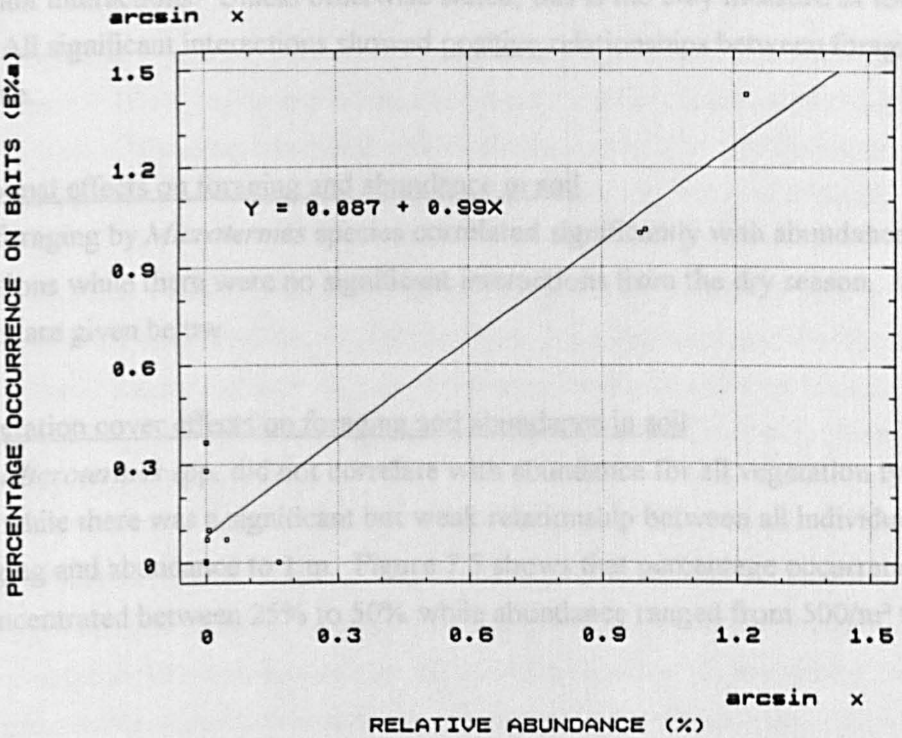
B%a = percentage of baits attacked per species from total attacked by Microtermes

B%l = percentage of baits attacked from the total laid out

m2 = abundance n/m2

% = relative abundance

Figure 7.14 : Regression plot of *Microtermes* species foraging activity, as percentage occurrence on baits (B%a), against relative abundance to 1 m soil depth (%) in long-term maize for wet seasons only.



Analysis using species foraging as a percentage of baits attacked calculated as a proportion of the total number of baits attacked ($B_{\%a}$; see Chapter Six) produced the most significant interactions. Unless otherwise stated, this is the only measure of foraging considered. All significant interactions showed positive relationships between foraging and abundance.

7.3.2.1 Seasonal effects on foraging and abundance in soil

Wet season foraging by *Microtermes* species correlated significantly with abundance on several occasions while there were no significant interactions from the dry season. Wet season results are given below.

7.3.2.2 Vegetation cover effects on foraging and abundance in soil

Foraging by *Microtermes* spp. did not correlate with abundance for all vegetation types (Figure 7.4) while there was a significant but weak relationship between all individual species foraging and abundance to 1 m. Figure 7.5 shows that percentage occurrence on baits was concentrated between 25% to 50% while abundance ranged from 500/m^2 to 1500/m^2.

Wet season foraging by *M. lepidus* correlated with abundance to 1 m and 25 cm; the best relationships were shown with relative abundance (Table 7.1). The predominance of *M. lepidus* in soil to 1 m in long-term maize is mainly responsible for the relatively high coefficient of determination with 1 m relative abundance (Figure 7.5) and the relationship with abundance to 25 cm is a more accurate representation of a relationship between foraging and abundance (Figure 7.6).

Significant correlations between foraging and abundance within vegetation groups (Table 7.2) were more numerous in maize than in woodland + pasture, as discussed below. There were no significant correlations in root crops.

In the maize group, foraging by all individual species did correlate significantly with abundance with r^2 ranging from 41.01% to 72.84%. However, there were a few occasions where foraging was zero but abundance was high (e.g. Figure 7.8.) which will have biased these results. Foraging by *M. lepidus*, *M. aluco* and *M. subhyalinus* showed significant regressions with abundance. *M. lepidus* foraging showed a strong correspondence with abundance to 1 m and 25 cm for both seasons and in the wet season; *M. lepidus* foraging correlated most significantly with relative abundance to 1 m in the wet season (Figure 7.9, $r^2 = 94.43\%$). Foraging by *M. aluco*, as occurrence on baits (B_a) was most closely related to abundance to 1 m in the wet seasons (Figure 7.10; $r^2 = 74.12\%$. The most significant correlation of *M. subhyalinus* foraging with abundance was shown with wet season occurrence on number of baits (B_a) with relative abundance to 1 m (Figure 7.11; $r^2 = 53.63\%$).

In the group woodland + pasture, *Microtermes* spp. foraging correlated poorly with abundance. Figure 7.12 shows several occasions where foraging coincided with zero abundance. *M. n.sp. C* foraging compared well to abundance to 1 m. However, this species was only recorded in two soil sampling occasions and this result is artificial.

There were no significant correlations in the newly cultivated crops group. This group was further divided into sweet potato with groundnuts and short-term maize with yam as these crops showed similar *Microtermes* spp. abundance levels. In short-term maize and yam, foraging by *M. lepidus* correlated significantly with abundance to 1 m (Figure 7.13; $r^2 = 67.8\%$); not a strong relationship.

Only foraging by all individual species was examined in individual vegetation types (Table 7.3) as there were too few sampling occasions to examine relationships between the foraging and abundance of *Microtermes* spp. or individual species. There were several significant regressions in secondary woodland, sweet potato, groundnuts and pasture. However, all results indicated weak relationships between foraging and abundance ($r^2 < 60\%$). Higher coefficients of determination were shown by all individual species in long-term maize (Figure 7.14; $r^2 = 90.55\%$). However, this reflected the dominance of *M. lepidus* both on baits and in the soil.

The problems of sampling *Microtermes* populations and analysis of data are illustrated by the fact that there were several occasions when foraging was recorded and species abundance was zero and, on a few occasions, where a species was recorded from soil sampling but not from baits.

7.4 DISCUSSION

7.4.1 Comparison of *Microtermes* community structure

Species richness was greater on baits, with few seasonal differences, than from soil sampling with rarer species being recorded in both seasons. This result is not unusual as soil sampling has less likelihood of collecting species with very low abundance than a food resource. The lack of seasonal differences in species richness on baits is also not unusual as the same species will still be foraging even if abundance and activity are reduced. Seasonal and year effects were similar between the two soil depths but more pronounced for 25 cm. It may be suggested that a combination of soil sampling to 25 cm and baiting would be sufficient to identify species composition and population dynamics.

Differences in the Shannon-Wiener diversity index with vegetation type, seasons and years were more apparent in soil abundance than on baits. It would be useful to compare further using counts of species on baits to calculate this diversity index. Shannon-Wiener diversity, as for species richness, was generally higher for 1 m soil depth than 25 cm. However, the differences exhibited were similar between the two depths and, if absolute values for this diversity index (which include the total species richness of a habitat) are not required, then soil sampling from 25 cm would suffice. Changes in the upper soil depths will be more pronounced due to disturbance, soil conditions and food availability. Further study could identify the most suitable soil depth; in long-term maize sites, sampling to 25 cm would certainly suffice. Shannon-Wiener diversity and evenness indices highlighted similar trends. Therefore, It may be worthwhile to use other diversity indices for comparison, i.e. similarity indices.

7.4.2 Comparison of foraging and abundance in soil

Foraging of all species collectively did not show a significant relationship with abundance. This was due, partly, to occasions where species occurred on baits and not in the soil and vice versa. More intensive sampling both with baits and soil cores may reduce the "loss" of species in sampling, as discussed below. However, baiting may record species which are foraging from colonies located outside sampling area and to minimise this, suitable buffer zones should be constructed around the sampling area.

Comparisons were often most significant when foraging was compared to the relative abundance of a species. This phenomenon was most marked in vegetation types where there was a high abundance of single species ie. *M. lepidus* in long-term maize.

Foraging corresponded to the abundance of the three most common species (*M. lepidus*, *M. aluco* and *M. subhyalinus*) within certain vegetation groups with foraging by these species increasing as abundance increased in maize and a similar result for *M. lepidus* in newly cultivated short-term maize and yam. Good relationships between foraging activity and abundance were more prevalent in maize crops than in other vegetation types or groups and for *M. lepidus* than for other species.

The results for *M. lepidus* are encouraging as this species, as previously stated, is a well documented pest of cereals in West Africa and the ability to use baits as an abundance indicator for this species would be useful in predicting potential crop damage.

Comparisons of foraging and abundance were most significant using abundance figures from the 1 m soil depth. This is a highly labour intensive and expensive procedure. However, results also show significant regressions for abundance in the top 25 cm and the use of a more intensive soil sampling regime in the top 25 cm could make these relationships more significant.

More intensive sampling of the top 25 cm of soil at the most active periods of foraging would collect species during foraging and reduce the errors introduced into the data when soil is sampled at greater depths. This would also hopefully reduce the number of occasions when records of foraging or abundance of individual species were very low.

The results suggest that wet season data would be sufficient to derive significant regressions and high coefficients of determination between foraging and abundance. The results also show that there is potential for the use of baits as an index of population abundance, although there is no basis, at present, for the qualitative estimation of abundance of the total *Microtermes* population from foraging on baits. This study was able to show that, for certain species, foraging on bait can be related to abundance. Further work is required to examine this further in individual vegetation types.

For both sections of this study and as discussed previously, further study of foraging activity should examine the use of counts of species on baits to determine whether these would improve the relationships between foraging activity and abundance.

7.5 CONCLUSION

The hypotheses presented in this study are re-examined:

1. Foraging activity by *Microtermes* spp. and individual species on baits corresponds to soil populations.

(a) The identification of *Microtermes* species from foraging on baits can give an more accurate indication of species richness than soil sampling.

(b) Measures of community structure, other than species richness, to examine differences in species occurrence on baits with vegetation cover, seasons and years did not compare well with diversity indices calculated from soil abundance.

(c) More accurate assessments of foraging activity could be achieved by several methods. It can be suggested that counts or estimates of foragers on baits could give a more quantitative estimate of foraging intensity, although this would be more time consuming. Several sampling occasions within each season and/or timing of sampling, as discussed previously, would reduce differences due to environmental factors and allow comparisons of species foraging between individual vegetation types.

(2) Foraging activity can be used an a qualitative index of abundance and as a predictor of populations, especially of pest species.

(a) Foraging activity assessed from baits can be correlated positively with soil abundance. However the use of baits as an accurate qualitative assessment of soil abundance requires more intensive study to eliminate, as far as possible, the inconsistencies shown by this study and, particularly, to enable comparisons of individual species foraging activity and soil abundance within individual vegetation types.

(b) Species foraging correlated most significantly with soil abundance when only wet season assessments are carried out.

(c) The assessment of foraging by *M. lepidus* on baits has potential as a useful and more economical method than soil sampling of determining this species abundance.

(d) As previously discussed in Chapter Six , further work should determine whether species counts on baits would improve comparisons between foraging activity on baits and soil abundance.

CHAPTER EIGHT

CONCLUSION

8.1 Summary

This section summarises the work as a whole and whether the hypotheses proposed at the beginning of this study are verified.

Primary and secondary woodland

Microtermes abundance ranged from 180 to 900/m^2 in primary woodland and from 238/m^2 to 1455/m^2 in secondary woodland with populations concentrated above 50 cm, particularly in the wet season. In both woodland sites, *Microtermes* species were, generally, more abundant in the wet season compared to the dry season and seasonal differences in abundance coincided with changes in abundance in the top 50 cm of the soil.

In both woodland sites, *M. subhyalinus* (39/m^2 to 895/m^2) was the most abundant species followed by *M. grassei* (42/m^2 to 262/m^2). Seasonal differences in the abundance and distribution of *Microtermes* can be related to seasonal differences in the abundance of these two species in the top 50 cm of the soil. The higher *Microtermes* populations in secondary compared to primary woodland, especially in wet seasons were due to higher abundance of *M. subhyalinus* and to a lesser extent *M. grassei* and *M. aluco*. *M. aluco* was also more abundant above 50 cm than in primary woodland.

Diversity of *Microtermes* as determined from soil sampling was lower in primary woodland than secondary woodland. A similar phenomenon was observed in species richness of *Microtermes* (and all termite species) in Southern Cameroon forest plots where. it is suggested, this may be a feature of patch colonisation (Eggleton, Bignell, Sands, Waite, Wood & Lawton, in press). At Mokwa, two to three species were typically recorded in primary woodland and three to four in secondary woodland with *M. aluco* and *M. lepidus* more common in secondary woodland than primary woodland. There were no apparent seasonal differences in diversity in primary woodland while in secondary woodland, diversity was greater in the dry season compared to the wet season. In secondary woodland, *Microtermes* diversity was greater from sampling carried out to 1 m compared to 25 cm.

Results from fungus comb abundance and distribution indicate that, although populations were concentrated above 50 cm in the soil, *Microtermes* nest at lower soil depths in both seasons; typically below 50 cm in primary woodland and below 25 cm in secondary woodland. In secondary woodland, fungus combs were fewer and lighter in the wet compared to the dry season. Fungus combs did not vary in numbers or weight between the seasons in primary woodland. In the dry season, fungus combs were concentrated in the lowest soil depths. Fungus combs were lighter and of lower total dry weight in secondary compared to primary woodland. Fungus combs of *M. grassei*, *M. subhyalinus* and *M. lepidus* were collected in primary woodland and fungus combs for all species were collected in secondary woodland. Seasonal differences in fungus comb numbers, individual and total dry weights were recorded for *M. subhyalinus* and *M. grassei*. The total dry weight of fungus combs was related to abundance and individual dry weight of combs in primary woodland and to abundance of combs only in secondary woodland.

In primary woodland, three species were recorded from baits; *M. grassei*, *M. subhyalinus* and *M. aluco*. This is a similar number to soil sampling except *M. lepidus* was recorded instead of *M. aluco*. In secondary woodland, species richness and Shannon-Wiener diversity from baits were higher than from soil sampling with all five *Microtermes* being recorded from baits in the wet season and from four to five species in the dry season. Diversity was greater in the wet season compared to the dry season as more species were more frequently recorded. In both woodland sites, *M. grassei* and *M. subhyalinus* followed by *M. aluco* were the most frequently occurring species on baits. Seasonal/yearly differences in *Microtermes* foraging activity in secondary woodland correspond to differences in the foraging activity of *M. subhyalinus* and *M. grassei*, the most frequently occurring species on baits. Signs of non-random foraging behaviour in secondary woodland were detected for all species except *M. n.sp. C*.

Therefore, *Microtermes* distribution in soil was similar between primary and secondary woodland though *Microtermes* were more abundant in secondary woodland than in primary woodland, particularly in the top 50 cm of the soil. It can be suggested that the differences in *Microtermes* community structure and abundance between primary and secondary woodland are influenced by the relative abundance of other termite genera. In secondary woodland, *Microtermes* was relatively more abundant (52.29%) than in primary woodland (20.26%) which would result in reduced competition for food resources and nest space from other termite genera, as discussed in Chapter One (Wood et al., 1977a). This would allow *Microtermes* to increase in abundance and move up in the soil, both to forage and to construct fungus combs (Wood and Johnson, 1978; Josens, 1974).

Microtermes populations in primary and secondary woodland were higher than would be expected from other studies, in particular earlier results from the Termite Research Project, although results in this study do agree with previous studies that *Microtermes* populations are concentrated in top 50 cm of the soil (Josens, 1974; Lepage, 1974; Black and Wood, 1989; Wood and Johnson, 1978; Wood et al., 1977a). The differences in population estimates may be due in part to sampling depth differences i.e. lower soil populations would be expected when sampling from above 50 cm (c.f. Lepage, 1974; Josens, 1972).

Sampling to a greater soil depth may have reduced calculated total abundance. For example, Black and Wood (1989) examined *Microtermes* abundance in secondary woodland (and maize) to a soil depth of 2 m while this study examined the *Microtermes* populations to a depth of 1 m. Also, estimates may differ due to different sampling periods; the earlier results of the TRP utilised data from the first and second years only at Mokwa (Wood et al., 1979; Wood and Johnson, 1978; Black and Wood, 1989). In other studies, sampling periods are often not comparable (or stated) and/or sampling was done on a single occasion where populations may have been low i.e. at start of the wet season/end of dry season (Lavelle and Pashanasi 1989; Dangerfield, 1990; Lepage, 1974; Josens, 1972).

Differences in *Microtermes* populations dynamics between the two woodland sites corresponded to differences in fungus comb dynamics. In primary woodland, *Microtermes* fungus combs (all species) were concentrated below 50 cm in both seasons while in secondary woodland fungus combs were more abundant higher up in the soil. This may be due to reduced competition for nesting space due to the lower abundance of other termite genera in secondary woodland.

In primary woodland, there were no seasonal differences in fungus comb abundance but there was a reduction in fungus comb individual weights in the dry season compared to the wet season which may correspond to seasonal differences in food availability with changes in soil distribution. Two possible explanations for this are that *Microtermes* were unable to build combs in the upper soil horizons in the wet season, due to the relatively high abundance of other termite genera or that the soil micro-climate did not change sufficiently in the dry season to warrant movement of combs. This can be compared to secondary woodland where fungus combs were both more abundant, especially in above 50 cm in the soil, and heavier in the wet season compared to the dry season. The same factors may apply; *Microtermes* combs might be constructed in the upper soil horizons in the wet season (with increased foraging activity) due to the lower relative abundance of other termite genera and/or to changes in the soil micro-climate changes resulting in movement of combs.

Another indication that there was a difference in the population dynamics of *Microtermes* between primary and secondary woodland was that *M. grassei* combs were considerably lighter and lower in the soil in primary woodland while *M. aluco* combs became more abundant in secondary woodland compared to primary woodland. *M. grassei* is recognised as a woodland species (Wood, 1981) and this is further substantiated by this species pre-dominance and high fungus comb weights and abundance in both woodland sites compared to cleared and cultivated sites.

Results from the present study agree with previously published results from the Termite Research Project (Wood and Johnson, 1978) for secondary woodland with similar total dry weights (g/m^2) of *Microtermes* fungus combs which were more abundant above 50 cm in the wet season and below 50 cm in the dry season. However, in the present study, fungus combs in primary woodland were more abundant lower in the soil although individual dry weights follow the previously described trend in distribution. The individual dry weights of fungus combs lie within the range recorded by El Bakri (1986) but were higher than the mean of 1 g recorded by Wood and Johnson (1978). This result may be low as the mean dry weight was derived from fungus combs from several vegetation types. The abundance of *M. subhyalinus* fungus combs recorded in Southern Guinea savanna woodland by Josens (1972) ranged between 0.1 to 4.8/m^2 with a maximum of 16.5/m^2. The abundance of *Microtermes* combs in this study lies within this range but never goes above 4/m^2.

Newly cleared and cultivated sites

Pasture : *Microtermes* abundance ranged from 248/m^2 to 1204/m^2 with abundance higher in the wet season than in the dry season. Populations were concentrated above 50 cm in the wet season and with the decrease in abundance from wet to dry season, there was a decrease in populations in the top 50 cm. In the second year, *Microtermes* were more abundant above 25 cm in wet season and below 50 cm in the dry season compared to the first year. This study suggests that there was no initial change in the abundance of *Microtermes* with the introduction of pasture after clearing woodland but there was a change in soil distribution, with increased *Microtermes* abundance in the top 25 cm. The change in soil distribution may be related to the reduction in the abundance of other termite genera with clearing since *Microtermes* was relatively more abundant in pasture (68.9%) than in secondary woodland (52.3%) (Wood et al., 1977a). The reduction in competition for resources would allow increased foraging activity in the upper soil layers and therefore increased population densities. *Microtermes* abundance in pasture did not increase with this increased foraging activity. It may be that the sampling period was not long enough to detect increases in *Microtermes* abundance (pasture was only sampled for the first two years). Alternatively, food supply may have been insufficient to support any increase in total abundance while food quality changes resulted in a change in community structure, as discussed below. The changing role of predators must also be considered, especially ants (Longhurst, 1977)

M. subhyalinus was the most abundant species in cultivated sites and was more abundant in the wet season (863/m^2) compared to the dry (5/m^2). This seasonal difference in abundance was marked by a change in depth distribution, with *M. subhyalinus* concentrated above 25 cm in the wet season and below 50 cm in the dry season.

Abundance of all the remaining species was less than 247/m². Differences in the soil distribution of species were recorded. *M. lepidus* were most abundant in the top 50 cm of the soil in each season. *M. n.sp. C* was only found above 25 cm in the soil while *M. grassei* was most abundant below 25 cm, though populations were lower than in secondary woodland. *M. aluco* was most abundant below 50 cm in the first year and above 50 cm in the second year.

Species richness from soil sampling was similar to that in secondary woodland; two to three species in the top 25 cm and three to four species to a depth of 1 m. Species richness described from baits was higher than that determined from soil sampling (as in woodland sites) and was similar to secondary woodland in both seasons; four species present in the dry season and five in the wet season. In the first year after clearing, diversity from soil sampling was slightly less than in secondary woodland and lower in the top 25 cm of the soil than for 1 m. By the second year, diversity was higher than in secondary woodland at both depths Diversity determined from baits was higher than that for secondary woodland.

M. subhyalinus was the most frequently occurring species on baits as well as the most abundant species in the soil. Foraging activity of the remaining species was relatively higher than expected from their low soil abundance, while there were indications of non-random foraging on baits by *M. subhyalinus* and *M. aluco* and association of foraging between *M. subhyalinus* and *M. lepidus*.

There was thus some indication that the clearing of woodland for pasture leads to an increase in *Microtermes* diversity in the wet seasons, especially in the top 25 cm of the soil, with species abundance higher in the top 25 cm of the soil than in secondary woodland. Increases in the top 25 cm can be explained by *M. lepidus*, *M. aluco* and *M. n.sp. C* populations being located higher in the soil profile than in woodland. *M. grassei* populations become concentrated further down in the soil and may be unable to compete as effectively for space with other *Microtermes* species when other termite genera are relatively less abundant. This competition may be for food or nesting space but further study would be required to determine which was the limiting factor.

Sweet potato : *Microtermes* abundance ranged from 223/m² to 526/m² with no seasonal differences in abundance, though soil distribution differed between the seasons; populations were lower in the top 50 cm in the dry season compared to the wet season. In the first year, *Microtermes* were most abundant above 50 cm in both seasons and, by the third, year, from 25 to 50 cm in the wet season and 25 to 75 cm in the dry season. Population densities were low throughout the study with *M. subhyalinus* (70/m² to

243/m^2) and *M. aluco* (76/m^2 to 263/m^2) the co-dominant species. There were changes in the soil distribution of *M. subhyalinus*, *M. aluco* and *M. lepidus*.

Species richness was similar to pasture at both depths with more species recorded in the top 1 m than the top 25 cm (two to four species for 1 m compared with one to two species for 25 cm). Diversity, as measured by Shannon-Wiener and evenness indices, was similar to pasture for 1 m sampling but higher in the top 25 cm in the first year than for pasture and woodland. Diversity increased progressively from the first to the third year, especially in the top 25 cm of the soil where wet season diversity was considerably higher than dry season diversity.

Species richness and diversity indices from baits were greater than from soil sampling with four to five species recorded with one species not recorded in the dry season; *M. n.sp. C*. *Microtermes* foraging activity was greater in the wet seasons compared to the dry season. Foraging activity was similar for *M. subhyalinus, M. aluco, M. grassei* and *M. lepidus* while *M. n.sp. C* foraging was much less than for these species. There were indications of non-random foraging by *M. grassei* and association on baits between *M. lepidus, M. subhyalinus, M. aluco* and *M. grassei*.

Microtermes were relatively more abundant in this crop (77.73%) than in secondary woodland (52.29%) or pasture (68.89%) (Wood et al., 1977a) and it may be expected that *Microtermes* populations would increase with reduced competition/interference. However, after the clearing of woodland and cultivation of sweet potato, *Microtermes* abundance declined to levels equivalent to dry season populations in secondary woodland. Seasonal differences in abundance were not apparent as there was no increase in abundance or foraging activity in the wet season . Diversity did increase because species low in abundance in woodland were more abundant in sweet potato plots.

These successional changes can be related to food type/quality. Sweet potato is poor low food quality for *Microtermes* with few records of sweet potato being attacked by this genus of termites (Harris, 1969). It probable that initial soil disturbance caused by ploughing (after clearing) reduces nesting populations of all termites in the upper soil horizons. In the following years, *Microtermes* populations were unable to recover due to the lack of food; as illustrated by *M. subhyalinus*, the most abundant species, which declined in abundance and moved down in the soil. Increases in abundance in the top 25 cm could be due to increased foraging activity on what food resources were available e.g. residual roots from woodland. Increases of species rare in woodland (*M. lepidus*, *M. n.sp. C* and *M. aluco*) may be due to reduced competition from other termite genera which are not able to survive the effects of clearing and cultivation. *M. lepidus* was the only species which increased substantially in abundance and clearly moved up in the soil.

This species may have different feeding preferences to other *Microtermes* species as discussed further below.

Groundnuts : *Microtermes* abundance, sampled only in the wet seasons, ranged from 507/m^2 to 902/m^2 with populations concentrated above 50 cm and often highest in the top 25 cm of the soil. *M. subhyalinus* was the most abundant species (290/m^2 to 430/m^2) with the remaining species similar in abundance (below 250/m^2). All species were most abundant in the top 50 cm although by the third wet season, *M. aluco, M. grassei* and *M. n.sp. C* were less abundant in the top 25 cm than in the first wet season.

In the first wet season, species richness from soil sampling was similar to secondary woodland in the top 1 m (three species) and higher than secondary woodland in the top 25 cm (three species). Species richness increased throughout the study and by the third wet season four to five species were recorded for 1 m and three to four species for 25 cm. The differences in species numbers coincide with the presence/absence of *M. grassei* and *M. n.sp. C*. Shannon-Wiener diversity was constant throughout the study and slightly higher for 1 m than 25 cm.

Species richness and diversity from baits were similar to those recorded for soil sampling to 1 m and greater than those recorded for 25 cm. Foraging activity by all *Microtermes* and individual species was similar amongst the seasons/years. *M. subhyalinus* and *M. aluco* were the most frequently occurring species on baits. There were indications of non-random *Microtermes* foraging and associations in foraging by *M. subhyalinus* and all other species except *M. lepidus*.

As in all other newly cleared plots, *Microtermes* were relatively more abundant in groundnuts (84.9%) than in secondary woodland (Wood et al., 1977a). However there was little change in *Microtermes* abundance and distribution with the introduction of groundnuts after secondary woodland. Food type/availability was sufficient to maintain *Microtermes* populations at similar levels to those in secondary woodland but were insufficient either in quantity or quality to allow population increases. Populations may be sustained on residual below ground organic matter from secondary woodland, or populations may take longer to increase than the three years of this study. Environmental factors, especially local rainfall, may also limit *Microtermes* abundance (Johnson and Gumel, 1981; Johnson et al, 1981a).

Diversity did increase, as in pasture and sweet potato, due to the presence of species absent or rare in secondary woodland. *M. subhyalinus* was still the most abundant species but *M. aluco* replaced *M. grassei* as the second most abundant species. As in pasture, *M. grassei* may not be able to maintain populations in competition for food and space with other *Microtermes* species. It is also possible that *M. grassei* populations fall due to different soil micro-climate conditions and/or food type compared to those in secondary woodland.

Yam : *Microtermes* abundance ranged from 411/m² to 1801/m² and was greater in the wet season than in the dry season . Abundance increased from the first to third wet season from 589/m² to 1801/m². *Microtermes* were concentrated above 25 cm in the wet season and above 50 cm in the dry season. Increases in abundance and diversity indices were most marked in the top 50 cm throughout the study.

In the first wet season, *M. subhyalinus* was the most abundant species (374/m²) while the remaining three species populations were less than 100/m²; *M. n.sp. C* was not recorded. *M. subhyalinus* (1098/m²), *M. lepidus* (251/m²), *M. grassei* (162/m²) and *M. n.sp. C* (105/m²) increased in abundance by the second wet season. *M. lepidus* (486/m²) and *M. grassei* (252/m²) further increased in abundance to the third wet season, when *M. lepidus* became co-dominant with *M. subhyalinus*. *M. subhyalinus* and *M. grassei* were most abundant in the top 25 cm in the first wet season and between 25 and 50 cm in the third wet season while *M. lepidus* showed the reverse soil distribution changes. *M. aluco* and *M. n.sp. C* were initially most abundant between 50 and 75 cm and by the third wet season both were concentrated above 25 cm. *M. lepidus* and *M. subhyalinus* populations were higher in the wet seasons than in the dry seasons.

Species richness from baits was four to five species throughout the study with Shannon-Wiener diversity less in the dry season than in the wet seasons. *M. aluco* and *M. subhyalinus* were the most frequently occurring species on baits. Foraging activity by *M. lepidus* and *M. subhyalinus* was higher in the dry season than in the wet seasons. Foraging by *Microtermes* was occasionally non-random and associations in foraging were shown between all species except *M. n.sp. C*.

The cropping of yams after clearing woodland results in a rapid increase in *Microtermes* populations and diversity, especially in wet seasons, after the first year of cropping. These increases were most marked in the top 50 cm of the soil where there was an increase in abundance of all species. Changes in soil distribution were observed relative to secondary woodland; *M. n.sp. C*, *M. grassei* *M. aluco* and *M. lepidus* moved up in the soil, the latter two species into the top 25 cm, while *M. subhyalinus* moved down to 25 - 50 cm. In contrast to pasture, sweet potato and groundnuts, there was a further change in species composition as *M. lepidus* becomes co-dominant with *M. subhyalinus*. These changes may be associated with the availability of a good quality food supply (from the stakes used to support yams) and with a reduction in competition or interference from other termite species. *Microtermes* spp. in yams accounted for 90.9% of all termites compared to 52.3% in secondary woodland (Wood et al., 1977a). A large food supply would promote increases in the foraging and abundance of all species above 50 cm in the soil.

The movement of *M. subhyalinus* down in the soil may be as a result of competition from other *Microtermes* species in the top 25 cm of the soil and/or to the feeding strategy of this species changes, as discussed below.

Short-term maize : *Microtermes* abundance ranged from 306/m² to 1544/m² and increased from the first to third wet season. Populations were concentrated in the top 25 cm in the first wet season with an increase in abundance in all soil horizons in each following wet season, particularly above 50 cm. By the third wet season *Microtermes* were most abundant in the top 50 cm. Abundance was lower in the top 50 cm in the dry season compared to the wet seasons.

M. subhyalinus was the most abundant species in the first year (199/m²). By the third year both *M. subhyalinus* and *M. lepidus* increased in abundance to become co-dominant (655/m² and 602/m², respectively); all other species had densities below 200/m². Amongst the vegetation types, *M. n.sp. C* was most abundant in short-term maize. *M. lepidus* increased in abundance in all soil depths but mainly in the top 50 cm while *M. subhyalinus* increased in abundance between 50 and 75 cm.

The diversity of *Microtermes* from soil sampling changed with time. Species richness increased in both depths and, by the third wet season, four species were recorded from the top 1 m and three to four from the top 25 cm. Shannon-Wiener diversity, initially greater for 1 m than 25 cm, increased to similar levels in both depths by the third wet season (a similar result to yam and groundnuts). Comparable changes were recorded in diversity at baits. *M. subhyalinus* and *M. aluco* showed the highest foraging activity on baits with an increase in activity by all species from the first to second wet season.

Microtermes fungus combs in short-term maize were more abundant than in woodland and more abundant in the wet season than in the dry season, especially in the top 75 cm. In the wet season, fungus combs were concentrated between 50 and 75 cm. In the dry season fungus combs were concentrated below 25 cm and less abundant in the top 25 cm than in the wet season. *Microtermes* fungus combs were a similar weight to those in primary woodland with no seasonal differences. Fungus combs of all species were collected in the wet season and all species except *M. n.sp. C* in the dry season. *M. subhyalinus* combs were the most abundant and combs of this species and those of *M. grassei* were most abundant in the wet season compared to the dry season. In the wet season, combs of *M. n.sp C* were the heaviest amongst the species and those of *M. lepidus* were the heaviest in the dry season.

The cropping of maize, after clearing woodland, resulted in a rapid increase in *Microtermes* populations and diversity in wet seasons, after the first year of cropping. These occurred at all depths but were greatest in the top 50 cm of the soil. The increases at each depth correspond to changes in soil distribution relative to secondary woodland. As with other newly established plots, the relative abundance of *Microtermes* also increased in maize (83.4%) as other termite species became less abundant (Wood et al., 1977a).

M. lepidus move up in the soil and concentrated populations in the top 50 cm of the soil, *M. grassei* abundance (lower than woodland) evened out in all depth intervals. As in yam, *M. subhyalinus* moved down in the soil (to 25 - 50 cm), further supporting the hypothesis that this move was as a result of the build up of other species populations in the top 25 cm of the soil, especially *M. lepidus*. *M. lepidus* may increase in abundance with preferred food type or more aggressive foraging behaviour in the absence of other termite genera. *M. subhyalinus* may have the ability to change feeding sites with no adverse effects on abundance i.e. feeding on maize roots at lower depths. A flexibility in both feeding strategy and food types may account for the predominance of this species in all vegetation types, except long-term maize. This flexibility is illustrated by the change in cropping from maize to sweet potato, as discussed below. It is also possible that *M. lepidus* has different nesting behaviour than other *Microtermes* species as shown by this species having fungus combs concentrated above 50 cm and combs which were heavier in the dry season compared to the wet season.

Seasonal climate influenced *Microtermes* abundance and fungus combs numbers and dry weights with the expected re-distribution at lower soil depths in the dry season in response to reduced soil moisture and increased soil temperature plus reduction in food availability. This movement was to greater depths than in secondary woodland probably as a result of lower food availability and more extreme changes in soil micro-climate; less shade therefore greater effect of insolation on soil (c.f. Josens, 1977; Lepage, 1974)

In comparison to secondary woodland, community structure and soil distribution of fungus combs changed with the introduction of maize; *M. lepidus* combs were more abundant in top 50 cm, *M. grassei* combs concentrated above 25 cm in both seasons and *M. aluco* combs were concentrated between 25 - 50 cm in wet season and below 25 cm in dry season (mainly 75 - 100). This may be a result of reduced competition for nest space due to the reduction of other termite genera (relative abundance of *Microtermes* = 83.36%). The total dry weight of *Microtermes* fungus combs (4.25 g/m^2) was less than recorded by Wood and Johnson, 1978, (7.4 g/m^2). However, the present study incorporates data from a larger number of sample dates and some re-identified combs.

Change in crops

This present study has shown that changes in crops alter *Microtermes* community structure and species abundance. The ability to predict such changes has a potential use in pest management (Southwood, 1977; Conway, 1976; Stenseth, 1987). However further study is required to substantiate the trends shown in the present study as crop rotations may increase as well as decrease pest populations (Wright, 1984; Lashomb and Ng, 1984).

(1) Sweet potato to maize. There was no significant change in the abundance of *Microtermes* although there was a reduction in numbers in the top 25 cm. *M. lepidus* numbers declined significantly, mainly in the top 50 cm. There was a decrease in all measures of diversity, especially for 25 cm, to lower levels than in the first wet season of sweet potato. Species richness declined from close to 4 to 2 species for 1 m and from 2 to 1 species for 25 cm.

The reduction in *Microtermes*, especially *M. lepidus*, in the top 25 cm may be due to soil disturbance destroying fungus combs and the lack of food until maize has been cropped for sufficient years to sustain populations. This crop change has a potential use to reduce the risk or amount of yield loss from *M. lepidus* in maize.

(2) Maize to sweet potato. There was no significant changes in *Microtermes* abundance however *M. subhyalinus* numbers increased significantly above 50 cm coinciding with a decrease in the abundance of *M. lepidus* at the same depth. Species richness did not change but Shannon-Wiener and evenness indices declined corresponding to the changes in species abundance.

This decline in *Microtermes* abundance may have been expected as sweet potato is a poor food however the reduction of *M. lepidus* supports the hypothesis that this species has a food preference for maize while *M. subhyalinus* has a more diverse feeding range, possibly sustaining populations on maize root residues.

(3) Groundnut to yam. *Microtermes* increased, at all depth intervals and mainly above 25 cm, to the highest abundance for any crop in the study. *M. lepidus* and *M. aluco* increased in abundance, mainly above 25 cm. The depth distribution of *M. subhyalinus* altered with numbers concentrated in the top 25 cm and below 75 cm. These changes did not alter community structure. These trends coincide with those recorded when yam was

initially cultivated from cleared woodland; species increase in abundance and changes in soil distribution with the availability of food from stakes. *Microtermes* spp. competition for space or food results in the change in soil distribution of *M. subhyalinus*.

(4) Yam to groundnut. Species richness and Shannon-Wiener diversity declined to the levels shown in the first year of yam cultivation. *Microtermes* decreased, most noticeably in the top 50 cm, although numbers were still concentrated above 25 cm. *M. lepidus* and *M. subhyalinus* also declined in the top 50 cm, especially above 25 cm. *M. aluco* numbers increased above 25 cm, where it replaced *M. subhyalinus* and *M. lepidus* as the most abundant species. *M. grassei* numbers decreased between 25 and 50 cm and *M. n.sp. C* numbers decreased in the top 25 cm. The resulting abundance of each species was similar, except for *M. subhyalinus* which was less abundant, to densities similar to those recorded in the first year groundnuts in the newly established randomised block.

This decline in *Microtermes* abundance may have been expected when comparing this to the initial introduction of groundnuts after clearing where the lack of increase in *Microtermes* populations coincided with the lack of food/poor food quality. As in the earlier cultivation of groundnuts, *Microtermes* were concentrated in the top 25 cm of the soil as foraging continued on crop residues and/or remnants of stakes.

The changes in food type/availability was sufficient to maintain *Microtermes* populations at similar levels to those in secondary woodland but were insufficient either in quantity or quality to allow population increases. Populations may be sustained on residual below ground organic matter from secondary woodland, or populations may take longer to increase than the three years of this study allowed.

Long-term maize sites

Microtermes were more abundant in long-term maize than all other vegetation types; abundance ranged from 802/m^2 to 3131/m^2. In both sites, populations were concentrated in the top 25 cm of the soil. Species richness from both soil sampling and baits ranged from one to four species, with *M. lepidus* the most common species recorded. Shannon-Wiener diversity for soil sampling and baits also varied with year; from 0 to 1. *M. lepidus* was the most abundant species in both long-term maize sites (640/m^2 to 3109/m^2) with populations of the remaining three species less than 500/m^2; *M. n.sp. C* was not recorded in these sites. *M. lepidus* was most abundant in the top 25 cm while the remaining species were most abundant in the top 50 cm.

Microtermes fungus combs in ranch maize (dry season only) were more numerous and higher in total dry weight than in short-term maize and woodland sites, though fungus combs were of similar individual weights. Fungus combs were most numerous between 25 cm and 50 cm though heaviest in the top 25 cm with total dry weight concentrated above 50 cm. Fungus combs from all *Microtermes* species except *M. n.sp. C* were collected from ranch maize.

The total dry weight of fungus combs (> 7 g/m^2) concurs with previously published results from the Termite Research Project (Wood and Johnson, 1978). However, seasonal distribution differed in this study with dry season combs concentrated above 50 cm as opposed to below 50 cm. This can be attributed to *M. lepidus* combs, which as described above may have a different nesting behaviour to other *Microtermes* species.

Therefore, the long-term cultivation of maize leads to a large reduction in the diversity of *Microtermes*, with *M. lepidus* the dominant species ,although the relative abundance of *Microtermes* was lower (77.2%) than in newly cultivated maize (83.4%) due to the increased abundance of *Amitermes* which is also a termite pest of maize (Wood et al., 1980a). Species richness of the whole termite community was much reduced in long-term maize (5 spp.) compared to newly cultivated maize (13 spp.) (Wood et al., 1977a). This reduction in abundance of most termites species allows *M. lepidus* to increase in abundance in response to a combination of reduced competition or interference with food availability. The remaining *Microtermes* species were still present though at low populations which were probably maintained either by nest sites below 1 m or by new colonies re-establishing as alates settle in maize from surrounding vegetation types. These other species can increase in abundance when *M. lepidus* abundance is lowered possibly in response to climate and/or food availability.

To conclude this section the hypotheses proposed at the beginning of this study are reiterated and assessed in light of the results.

(1) SOIL POPULATIONS

"The community structure and abundance of *Microtermes* will be influenced by vegetation type and seasonal climate. Changes in abundance will correspond to changes in distribution in the soil, notably lower populations in the dry season compared to the wet season with corresponding movements down in the soil. Successional changes in community structure and abundance of species will be identified as woodland was cleared and different crops cultivated. These changes may have predictive value in assessing populations of pest species and therefore potential yield losses".

a. Community structure of *Microtermes* differs with vegetation cover with the highest diversity in newly cleared and cultivated crops after the first year of disturbance and lowest in long term cultivated maize followed by primary woodland. Successional changes were identified in community structure after clearing and cultivation. In primary and secondary woodland, *M. subhyalinus* was the most abundant species, followed by *M. grassei*. After the establishment of pasture, sweet potato and groundnuts, *M. subhyalinus* remains the most abundant species while either *M. aluco* or *M. lepidus* become the next most abundant species. With the establishment of crops either susceptible to *Microtermes* attack, i.e. maize, or where alternative food sources are available, i.e. wooden stakes used for yams, then *M. subhyalinus* still remains a predominant species but in association with *M. lepidus*. Finally, the long-term cultivation of maize results in the dominance of *M. lepidus*.

b. Vegetation cover did influence *Microtermes* total abundance with an increase in abundance in yams and maize while populations decreased in sweet potato, in relation to food availability and quality. Results show that, irrespective of vegetation cover, *Microtermes* were most abundant in the top 50 cm of the soil with a marked concentration of *Microtermes* above 25 cm in long-term maize sites, due to the predominance of *M. lepidus*. There was a more marked influence of vegetation cover on the abundance and distribution of individual species with changes in *Microtermes* abundance and distribution related to the abundance and distribution of the most abundant species; *M. subhyalinus* was the most abundant species in woodland, *M. subhyalinus* and *M. lepidus* were the most abundant species in newly cleared and cultivated sites and *M. lepidus* was the most abundant species in long-term cultivated maize.

c. Seasonal climate influences on abundance and distribution have been detected but these were often masked by temporal changes in abundance either due climate or cultivation. Seasonal changes in *Microtermes* abundance were most marked in crops where wet season abundance was greater than 500/m². Amongst the species, *M. subhyalinus* exhibited the greatest seasonal changes in abundance.

d. The results from this study indicate that changes in *Microtermes* community structure, abundance and distribution following clearing and cultivation are sufficiently consistent to be considered an ecological succession and hence may have predictive value for the assessment of potential crop losses. However, further research would be required to define the model by which pest species populations could be assessed. The requirements for this as discussed below in recommendations for future research.

(2) FUNGUS COMBS

"The abundance of fungus combs of *Microtermes* spp. and individual species will be influenced by vegetation type and seasonal climate and will correspond to changes in the community structure and abundance of *Microtermes* species. Differences in the abundance of fungus combs will correspond to changes in soil distribution, notably a movement down in the soil with a decline in weight in the dry season compared to the wet season".

Species trends require to be substantiated as the majority of *Microtermes* fungus combs were not identified to species due to the loss of specimens.

a. Vegetation cover influenced *Microtermes* fungus comb dynamics; fungus combs were most abundant in ranch maize, followed by secondary woodland and maize and least abundant in primary woodland. The abundance of fungus combs reflected the soil abundance of species in particular vegetation types. *M. subhyalinus* populations were highest and fungus combs most abundant amongst the species in short-term maize and secondary woodland while *M. n.sp. C.* populations were lowest and fungus combs fewest amongst the species in secondary woodland and short-term maize. In long-term (ranch) maize, *M. lepidus* was the dominant species and its fungus combs were the most abundant.

Fungus combs were lightest in long-term maize but heaviest in primary woodland where populations were amongst the lowest and foraging activity, fungus comb abundance and total dry weight were lowest. There was also differences between the two in the soil distribution of populations and fungus combs. These factors, as stated previously, may have been due to differing environmental conditions, especially soil conditions, between the two vegetation types and/or different behaviour of the most abundant species, especially with respect to competition from other termites. Primary woodland, an undisturbed site, would provide a more stable environment for nest construction with the soil being less affected by climatic fluctuations and holding a greater store and variety of residual plant matter. But this would be balanced against competition with other termites for food and, probably more importantly, space. It can be suggested that, in primary woodland, a low population of *Microtermes* was maintained in a few concentrated nest sites which best suited the environment. The previous record of *M. grassei* as a forest species (Wood, 1981) is supported by the observation that this species constructed the heaviest fungus combs in woodland. In long-term maize sites, a large *Microtermes* (*M. lepidus*) population was maintained from many light fungus combs which one assumes can be rapidly constructed and reallocated in response to changing environmental conditions.

b. There were no seasonal changes in the abundance of combs but combs were constructed at different depths between the seasons. The dry weights of individual combs did change with season; generally individual dry weights were lower in the dry season, except M. lepidus, as discussed earlier.

(3) FORAGING ACTIVITY

"The community structure and foraging activity of *Microtermes* will be influenced by vegetation type and seasonal climate, notably reduced foraging in the dry season compared to the wet season, with successional changes identified as woodland is cleared and different crops cultivated. Spatial distribution of species can be detected from foraging activity".

a. An influence of vegetation type on the foraging activity of *Microtermes* was only demonstrated in long-term maize and primary woodland with highest foraging in the former and lowest foraging activity in the latter. Foraging activity did not differ amongst the newly cleared and cultivated sites and secondary woodland, although foraging in short-term maize did increase progressively throughout the study irrespective of season. The lack of differences in *Microtermes* foraging results may be due to the sampling procedure and/or the length of the study, which may have been too short to highlight differences which may occur after clearing and cultivation.

b. Differences were not detected in the community structure of foraging *Microtermes* but there were species differences in activity amongst the vegetation types. In primary woodland, *M. grassei* was the most actively foraging species followed by *M. subhyalinus*. In secondary woodland, *M. aluco* replaced *M. grassei* to become the most actively foraging termite along with *M. subhyalinus*. In all newly cleared and cultivated sites (in the second year), *M. subhyalinus* was the most actively foraging termite with either *M. lepidus* and/or *M. aluco* while in long-term maize *M. lepidus* was the most actively foraging termite. The results do not clearly identify successional changes with clearing and cultivation, as discussed in future recommendations below.

Baiting was a useful indicator of species richness and has shown potential as a quantitative index of abundance. In all vegetation types, baiting recorded more species than soil coring except in the last year of cropping in the newly cleared and cultivated sites and in ranch maize. In all cases where species richness was greater from baits, this was due to collection of species with known low abundance (*M. n.sp. C*) or with low abundance in a particular vegetation type (i.e. *M. grassei* in sweet potato). It is possible that records of species from foraging and not from soil sampling is due to the extension of a species foraging range from adjacent sites/habitats. It is also probable that these species maintained very low populations with low nest (fungus comb) densities, possibly in lower soil depth intervals.

c. Seasonal climate influences on foraging activity were only detected in only sweet potato. This is most likely as a result of methodology rather than a true reflection of foraging activity. As discussed in Chapter Six, only occurrence of species on baits was recorded. Seasonal differences would have probably been detected if individuals on baits had been counted or if consumption rates of baits had been measured.

d. The results from the examination of the spatial distribution of *Microtermes* on baits was inconclusive and further research is required to determine whether associations detected are as a result of sampling methods (i.e. occurrence on baits as opposed to relative abundance).

(4) FORAGING ACTIVITY AND SOILS ABUNDANCE RELATIONSHIPS

Foraging activity by *Microtermes* spp. and individual species on baits correspond to soil population density and therefore foraging activity can be used an a qualitative index of abundance and as a predictor of populations, especially of pest species.

a. Species richness of *Microtermes* can be sampled more conveniently from foraging on baits than soil sampling but other measures of community structure from baits did not correspond with those calculated from soil abundance.

b. Foraging activity assessed from baits can be correlated positively with soil abundance. However the use of baits as an accurate qualitative assessment of soil abundance requires more intensive study which would enable comparisons of the foraging activity and soil abundance of individual species, especially of *M. lepidus*, within individual vegetation types.

8.2 Discussion

This study has highlighted differences in *Microtermes* abundance in soil, foraging activity and fungus comb numbers, dry weight and total dry weight for the total population and for individual species between uncultivated and cultivated sites at Mokwa in the Southern Guinea savanna vegetation zone of Nigeria. The present study supports the view put forward by Danks (1988) that species identification is a prerequisite for systematic studies with reliable taxonomy the basis for all meaningful research and, specifically, pest management. The capability to identify *Microtermes* species and relate with ecological knowledge is essential in the determination of potential pest problems within agroecosystems is required in the understanding of pest outbreaks (c.f. Stenseth, 1987).

Previous authors have recorded that *Microtermes* are more abundant in agricultural systems than natural or semi-natural habitats (Kooyman and Onck, 1981; Wood et al., 1977; Lepage, 1972) with Kooyman and Onck (1981) recording a higher abundance of *Microtermes* in annual rather than perennial crops. The present study suggests that *Microtermes* are most abundant in maize and yams but it is not possible to make conclusive statements on *Microtermes* abundance in other crop types and natural/semi-natural vegetation. In all crops, population densities are linked to seasonal weather conditions, methods and length of cultivation and type of crop.

It is probable, as proposed by Sands (1961), that *Microtermes* are better adapted to habitat disturbance than many other termite genera due partly to an ability to move nest and populations in the soil and partly to their wide range of food preferences. However, the present study has shown that the ability to adapt to habitat disturbance and change differs amongst the five sympatric species of *Microtermes*. The sympatry of the five species is maintained by niche differentiation which is in itself controlled by vegetation cover in conjunction with seasonality (c.f. Pontin, 1963). The practical implications for the development of pest management are discussed below.

Yield losses in maize due to *Microtermes* increase as the duration of monocropping maize increases (Wood et al. 1980a) with a decline in termite diversity and an increase in the abundance of *M. lepidus*, as shown in the present study. Pest problems in agroecosystems often increase as diversity decreases but a good understanding of the ecological mechanisms which are responsible for differences in abundance of species are required in the development of sound pest management options (c.f. Risch, Andow and Altieri, 1983; Redfearn and Pimm, 1987; Van Emden and Williams, 1974). Insect herbivores, especially monophagous species, are more likely to reach high densities in monocultures of crops as a result of reduced predator diversity and/or resource concentration and not as a result of a change in the trophic structure of the insect community (Risch et al., 1983).

Agricultural diversification often leads to reduced pest populations (Risch et al., 1983; Andow, 1985; Perrin and Phillips, 1978) but the mechanisms involved are poorly understood. Previous studies of pest problems have often focused on rapid outbreaks but with termites there is usually a progressive increase in pest species as termite community structure changes. Further study is required to determine methods to reduce pest species increases through the judicious use of cultivation practises, i.e. crop rotation and tillage (Southwood, 1977b; Conway, 1976; Stenseth, 1987; Wright, 1984; Lashomb and Ng, 1984, Logan, Cowie and Wood, 1990).

Previous studies on the co-existence of sympatric termite species have identified possible mechanisms of niche differentiation; nest site and structure (Wood and Lee, 1971; Nobble, Diggle and Whitford, 1989; Sands, 1961; Bodot, 1969; Josens, 1972, 1977), feeding preferences and strategy differences (Jones and Trosset, 1991; Haverty et al. 1975; Wood, 1981) and intraspecific aggression (Pearce, Cowie, Pack and Reavey, 1990; Jones and Trosset, 1991). Abe (1977) postulated that resource allocation at species level relative to competition was a determinant of termite community structure. Further research is required to determine the importance of these mechanisms in niche differentiation in *Microtermes* species, in addition to the reproductive isolating mechanisms described by Wood (1981). Different feeding preferences or strategies amongst the species are possible as shown by different abundance in woodland sites and crops.

The community of sympatric *Microtermes* species show a range of ecological reproductive strategies at the population level (c.f. MacArthur and Wilson, 1967; Stenseth, 1987). *M. grassei* and *M. n.sp. C* can be considered as K-strategists, being slow to increase in abundance with larger nest sites than other species and being most prevalent in habitats where environmental variability is low (i.e. woodland). *M. lepidus* and *M. subhyalinus* can be considered r-strategists by displaying high intrinsic rates of increase in habitats where environmental variability is high and termite diversity is low . It is generally agreed that r-strategist are mostly likely to become pest species (Southwood, 1977).

Lavelle and Meyer (1980) examined the structure of the soil faunal community in West African Guinea savanna (Côté d'Ivoire) as influenced by edaphic, biotic, climatic and anthropogenic environmental factors. The authors identified eight factors (from 13) which were responsible for 63.7% of the total variance in soil faunal structure. Most of these variables were environmental i.e. grass fires, soil moisture and temperature, microclimate due to vegetation cover and soil physical factors. Anderson and Swift (1983) described the influence of environmental factors in a declining scale;

macroclimate>microclimate>resource quality>organism. In both circumstances, ecological processes which influence population dynamics and community structure are influenced to a high degree by quantity and quality of plant cover in conjunction with seasonal climate, especially in tropical savannas (Lamotte and Bourliére, 1978).

Dynamics of *Microtermes* populations in the different habitats at Mokwa can be examined in terms of ecological processes (c.f. Lavelle and Meyer, 1980; Usher, 1988; Whitford et al., 1983). Woodland sites in Guinea savanna would contain a more diverse vegetation cover than cleared and cultivated sites (c.f. Menaut, 1983). The nature of the plant cover would tend to restrict the influence of seasonal climate on the soil. Soil water losses and soil temperature fluctuations would be reduced due to shade from plant cover as well as high levels of soil surface litter and below ground organic matter. A large proportion of plant biomass in savannas is found below ground level, concentrated in the top 30 cm of the soil (Lamotte, 1978; Menaut, 1983) while plant production is often in excess of turnover with a build up of organic matter towards the dry season (Bourliére and Hadley, 1983). The availability of plant matter both in the soil and on the soil surface would support termite populations in the dry season. The result is a distinct vertical stratification of populations in response to soil characteristics, i.e. organic matter levels and microclimate (Lavelle, 1983). This can be seen in the concentration of *Microtermes* above 50 cm in the soil with little seasonal movement.

Surface litter, fallen dead woody material, humic organic matter in soil and roots provide a diverse range of food types which have a heterogeneous spatial distribution. The wide range in food types is reflected in the wide range of termite feeding types and species numbers in woodland and forest areas (Wood et al., 1997a; Lepage 1974; Eggleton et al., in press). This suggests a high degree of niche partitioning as postulated for ants in West African Guinea savanna at Lamto (Lévieux, 1983). This author suggests that, in partitioning food resources, soil volume is the limiting factor and ants exploit this through different strategies such as species exploiting a limited soil volume, colony densities remaining low to reduce competition and through specialised diets.

Similar mechanisms may be important in the niche differentiation of *Microtermes* species. It is possible that competition for nesting space favour species which tend to build larger more or less mobile nests (*M. grassei* and *M. n.sp. C*) or have ability to colonise patches (*M. subhyalinus*). Differences in *Microtermes* populations between the two woodland sites can be considered on the basis of disturbance levels. Although more than fifteen years old, secondary woodland would be likely to have a different plant species composition to the undisturbed primary woodland site with corresponding effects on soil microclimate and organic matter type and availability (c.f. Keay, 1953; Smyth and Montgomery, 1962).

The clearing of woodland results in an immediate change in food type and availability for termites as litter input is of lower quality and a fraction that of woodland (Anderson and Swift, 1983; Collins, 1979). There are changes in the soil microclimate with change in organic matter input and increased influence of insolation and rainfall (Menaut, 1983). Higher soil temperatures and soil moisture levels in conjunction with reduced soil organic matter levels would tend reduce populations in the upper soil horizons. Nest sites concentrated in the upper soil horizons and species which feed on soil organic matter (i.e. humiverous species) would be at increased risk from desiccation (Wood et al., 1977a; Josens, 1972). Termite species would, thus, require an ability to move nest sites in soil in response to seasonal influences on soil microclimate. In the dry season, a movement of nests down in the soil would reduce the risk of desiccation when the upper soil horizons become hotter and dry out. Foraging activity and soil populations would also be reduced in dry season since the upper soil horizons would be less hospitable to foragers, while food would be limited with no above ground plants and reduced decomposition of surface organic matter. Termites require various degrees of decomposition of matter to make food palatable (Krishna and Weesner, 1969).

Ploughing intensifies the effects on the soil microclimate by reducing soil organic matter further, altering soil structure and favouring aeration (Lal, 1987) as well as destroying termite nest sites (Wood et al., 1977a). Cropping also further reduces soil organic matter; in maize and cassava fields, soil organic matter was approximately 46% less than in adjacent fallows and woodland (Lal, 1987). Thus, clearing and cultivation would tend to maintain species with a degree of resilience but which also have flexibility to adapt.

Other soil organisms have a role in soil processes, interspecific interactions, such as competition or interference for food and nest sites, and also predation, especially ant species. These soil organisms will also be effected, to a greater or lesser degree, by changes in habitat and will, in turn, influence the community organisation and abundance of termites (Wood et al., 1977b; Whitford et al., 1983; Brian 1979; Lavelle, 1983).

8.3 Recommendations for future research

The following briefly summarises some of the points from the individual sections on abundance, foraging and fungus combs which deal with sampling techniques and possible future studies on *Microtermes*.

1. Soil abundance and distribution

This study has provided some of the most extensive data on termite populations by using an intensive soil coring over a period of years which is an extremely time-consuming (and costly) task. It is unlikely that a similar study could be repeated and further comparison of sampling methods should be undertaken to develop standard sampling methods which will give accurate data and allow comparative analyses between studies. These methods must also consider how to reduce errors brought into the data from sampling nest sites.

This study has shown that population dynamics, particularly of the most abundant species can be determined from sampling the top 50 cm of the soil. However a full representation of species richness, diversity and abundance can only be achieved from sampling to depth, unless other methods are used to collect less common species i.e. baiting. Recommended future requirements are :

i. A time series analysis of population dynamics

Progressive sampling of *Microtermes* abundance throughout seasons and years within different crops and similar crops of different ages, in association with environmental monitoring, to enable accurate assessment of population dynamics.

ii. Sampling to determine differences in feeding sites of *Microtermes* species

Sampling with further sub-division of top 25 cm of soil.

iii. Identification of foraging ranges of colonies from soil sampling

Non-random sampling procedure to identify locations of species activities and possible foraging ranges of colonies (also see foraging below).

2. Foraging activity

The use of baits both as a determinant of foraging activity and as a qualitative index of soil abundance has yielded encouraging results but requires closer examination. Baits have also been shown to be useful in determining species composition. However, this study lacked counts or estimates of individual foragers on baits which would provide a relative estimate of foraging activity over a habitat and amongst species. Further studies should incorporate this procedure.

Further work should also determine whether there are differences in diurnal foraging activity of species which were not examined in this study. An initial study of foraging on a diurnal basis should compare foraging activity with measurements of the soil microclimate i.e. temperature and soil moisture. Recommended future requirements are :

i. The production of a suitable qualitative sampling procedure to determine population abundance

This requires further work on comparing species abundance with foraging activity, determining the best substrate for "baiting" and the optimum sampling strategy which would be both efficient and economical. This study used only one bait substrate, softwood. There are no published data on the feeding preferences of *Microtermes* species for different baiting materials. It may be a more effective strategy to assess foraging activity by using several different baits to include the range of food type available the habitats being sampled (or a composite including all material).

ii. To examine foraging behaviour of *Microtermes* spp. and individual species

Non-random foraging and species associations have been identified in this study. Further research is required to determine whether these results are an artefact of the sampling technique and, if not, then what the regulators of this behaviour are i.e. food preferences, palatability of baits, spatial variation in habitat, i.e. shading from vegetation cover, soil microclimate.

iii. To examine foraging ranges of *Microtermes* species

It is known that *Macrotermes* can forage up to 50 m from its central nest, however, there is no published information on the foraging ranges of single colonies of *Microtermes* species (or other subterranean termites). The baiting procedures followed in this study could be used, along with a "marker", to determine foraging ranges. This is of particular use in crop loss studies; within-plot crop losses may be due to termites invading from outside the experimental area and therefore crop loss will not directly relate to species/termite abundance.

iv. Field determination on the usefulness of dyes to study *Microtermes* activity

The use of dyes, incorporated into baits, has been used successfully in previous studies in the USA to examine various aspects of subterranean termite foraging activity (Jones and Trosset, 1991). Termites consume baits, the dye is ingested and retained, for a time, in the gut from where it is visible with the naked eye. The laboratory usefulness of several dyes has been determined but field use of the above procedure has not, to date, been used in Africa or with Macrotermitinae.

3. Fungus comb dynamics

The present study could only provide limited data on the dynamics of *Microtermes* fungus combs. The digging of soil pits is even more labour intensive and time consuming than soil coring but will provide useful results. The use of large diameter cores should be compared to pits to determine whether this would be a suitable alternative. The accuracy of future studies can be improved by increasing the number of samples taken in each season. Recommended future requirements are :

i. Time series analysis of fungus comb dynamics

Progressive sampling of *Microtermes* fungus combs throughout seasons and years within different crops and similar crops of different ages, in association with environmental monitoring, to enable accurate assessment of dynamics.

ii. Examination of the effect of soil tillage on *Microtermes* population abundance, species composition and nesting behaviour

Preliminary results from this study suggest tillage may influence *Microtermes* nesting behaviour which, in turn, effects abundance and foraging.

4. In areas with pronounced wet and dry seasons, wet season sampling is adequate to examine *Microtermes* abundance, foraging activity or nesting behaviour.

5. To aid in comparative work and to reduce within and between habitat variation for all sampling methods, sampling at similar times within each day (especially when examining foraging activity) and dates within a season.

6. The use of cultural methods to prevent/control or reduce *Microtermes* populations increases

Non-chemical control of termites was recently reviewed by Logan, Cowie and Wood (1990) and this highlighted several possible methods of control in crops. However, few if any of these have been evaluated, although in this study *Microtermes* abundance, especially that of *M. lepidus*, was shown to alter when crops were changed. Suggested areas of study must be inter-cropping and crop rotation but other areas of interest where there is little information available are - 1. the use of resistant crop varieties, 2. the use of mulches either to repel termites or encourage them to feed on an alternative food source.

7. Field assessment of yield losses due to *Microtermes* and the relative importance of individual species in crop damage

i. The comparison of yield losses and crop damage with *Microtermes* populations studies to examine economic thresholds with regards to termite damage and control and qualitative estimates of *Microtermes* abundance (i.e. baiting) in crop loss prediction.

ii. The use of qualitative abundance estimates (i.e. baits) in crop loss prediction.

8. Long-term monitoring experiments

The long-term monitoring of field studies is essential to obtain accurate information on population dynamics of, not only, *Microtermes* but also other termite genera.

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APPENDICES

APPENDIX ONE

WEST AFRICAN AND SUDANESE *MICROTERMES* (ISOPTERA; MACROTERMITINAE)

1. *M. aluco* (Sj.) Sjöstedt (1904).
   Syn. *M. feae* Silv. (Silvestri 1912)

2. *M. congoensis* (Sj.) Sjöstedt (1911).
   Syn. *M. kasaiensis* (Sj.) Sjöstedt (1913)

3. *M. depauperata* Silv. Silvestri (1914).
   Syn. *M. subhyalinus* var. *depauperata* Silv. (1914)

4. *M. lepidus* Sj. Sjöstedt (1924).
   Syn *M. hollandi* Grassé. Grassé (1937)

5. *M. najdensis* Harris. Harris (1964).

6. *M. subhyalinus* Silv. Silvestri (1914).
   Syn. *M. sudanensis* (Sj.) Sjöstedt (1926), *M. toumodiensis* Grassé. Grassé (1937)

7. *M. tragardhi* (Sj.) Sjöstedt (1904).
   Syn. *M. thoracalis* Sj. Sjöstedt (1926)

8. *M. grassei* Ghidini. Ghidini (1955)
   Syn. *M. vadschaggae* var. *dubius* Grassé. Grassé (1937) but *M. dubius* name preoccupied by *M. dubius* Fuller (1922)

9. *M. sp.K n.sp.*

10. *M. sp.Y n.sp.*

11. *M. sp.C n.sp.*

12. *M. sp.J ?n.sp.*
    (close to *M. albopartitus* (Sj.) Sjöstedt 1926, *M. bouvieri* (Sj). Sjöstedt 1926).

13. *M. sp.O ?n.sp.*
    (alates only, c.f. *M. magnocellus* (Sj.) Sjöstedt 1914).

14. *M. comprehensa* Silv. Silvestri (1914).

Syn. *M. congoensis* var. *comprehensa* (Sj.) Silverstri 1914, *M. feae* var. *pusillus* Silv. Silvestri (1914).

Requiring further examination -

15. *M. somaliensis* (Sj.) Sjöstedt (1912) - Alates.

16. *M. somaliensis* Sj. Sjöstedt (1927).

but name preoccupied by 14, *Eutermes somaliensis*.

Not available for examination

17. *M. subhyalinus* var. *neghelliensis* Ghidini. Ghidini (1973).

18. *M. problematicus* Grassé. Grassé (1937).

KEY TO SOLDIERS

l = length; w = width.

1. Antennae with 15 segments *M. najdensis*
- Antennae with 12 - 14 segments 2

2. Antennae with 14 segments 3
- Antennae with 12 - 13 segments 5

3. Fore-tibia noticeably inflated (l ÷ w = 3.0 - 3.6) 4
- Fore-tibia only slightly inflated (l ÷ w = 3.7 - 3.9) ....*M. sp.Y*

4. Head l x w _ (fore-tibia l x hind-tibia l) = 1.45 - 1.81; long setae on head less than twice the length of antennal segment II; long pronotal setae less than twice the length of antennal segment V .....*M. lepidus*
.........*M. sp.K*

- Head l x w _ (fore-tibia l x hind-tibia l) = 1.72 - 2.04; long setae on head more than twice the length of antennal segment II; long pronotal setae more than twice the length of antennal segment V .*M. sp.C n.sp*

5. Head subrectangular; pronotum distinctly narrower than head at mandible base; fore-tibia not inflated (l ÷ w = 3.8 - 4.4) 6

- Head with lateral margins curved; pronotum equal to/slightly wider than head at mandible base; fore-tibia inflated (l ÷ w = 3.1 - 3.9) 10

6. Anterior half of labrum with one terminal pair of long setae and posterior to these two very short pairs located medially; head setae short; mandibles slender; margins of head slightly curved; fore-tibia l x hind-tibia l = 0.144 - 0.18; head l x w = 1.26 - 1.33
........*M. depauperata*

- Anterior half of labrum with one terminal pair of long setae and posterior to these two or more moderately long pairs; fore-tibia l x hind-tibia l = 0.166 - 0.28, when less than 0.19 then head l x w greater than 1.34 7

7. Head l ÷ w = 1.21 - 1.38; fore-tibia l x hind-tibia l = 0.197 - 0.30; mandible l _ postmentum l = 0.97 - 1.14, greater than 1.01 if head l ÷ w is greater than 1.35; labrum with two pairs of moderately long setae in row medially behind terminal pair 8

- Head l ÷ w = 1.35 - 1.56, but when less than 1.39 then fore-tibia l x hind-tibia l less than 0.19 (one exception) and/or mandible l ÷ postmentum l less than 1.01; labrum with setae variable, either long or short setae behind and lateral to terminal pair, but not in row 9

8. Fore-tibia l x hind-tibia l = 0.197 - 0.23; fore-tibia l x hind-tibia l _ head w at mandibles = 0.38 - 0.469; head w x hind-tibia l = 0.29 - 0.35 .... *M. aluco*

- Fore-tibia l x hind-tibia l = 0.254 - 0.30; (fore-tibia l x hind-tibia l) ÷ head w at mandibles = 0.478 - 0.528; head w x hind-tibia l greater than 0.37 .... *M. sp.J*

9. Head l = 0.81 - 1.05; fore-tibia l x hind-tibia l = 0.166 - 0.25 .... *M. comprehensa*

- Head l = 1.09 - 1.23; fore-tibia l x hind-tibia l = 0.23 - 0.28 .... *M. congoensis*

10. Labrum with terminal pair of long setae and several pairs of moderately long setae scattered over distal two-thirds .... *M. tragardhi*

- Labrum with terminal pair of long setae and only two or three moderately long setae distally 11

11. Lateral margins of head distinctly and evenly curved so that maximum head width is approximately mid-way between antennal sockets and posterior margin; postmentum short (l ÷ w = 1.06 - 1.27) .... *M. subhyalinus*

- Lateral margins of head slightly and unevenly curved so that maximum head width is nearer to posterior margin than antennal sockets; postmentum long (l ÷ w = 1.33 - 1.66) .. .. *M. grassei*

APPENDIX TWO

STATISTICAL METHODS

For a sample of readings, x_1, x_2, x_3 . . . x_N; assuming random sampling from a normal population.

1. SAMPLE MEAN.

$$\bar{x} = [(x_1 + x_2 + x_3 \ldots + x_N)]/N$$
$$= \Sigma x/N$$

2. SAMPLE VARIANCE.

$$s^2 = [(x^2) - (x)^2/N]/N-1$$

3. SAMPLE STANDARD DEVIATION.

$$SD = \sqrt{(s^2)}$$

4. SAMPLE STANDARD ERROR.

$$SE = \frac{SD}{\sqrt{n}}$$

5. SHANNON-WIENER DIVERSITY INDEX (H')

$$H' = -\Sigma p_i . \ln(p_i)$$

where p_i = proportion of individuals belonging to the ith species (Pielou, 1974; Zar, 1981).

6. EVENNESS INDEX (J')

$$J' = H'/H'_{max}$$

where H'_{max} = ln k and is the maximum possible diversity for a set of data consisting of k catagories (Pielou, 1974; Zar, 1981).

7. ONE WAY ANALYSIS OF VARIANCE.

(a) Results:

			Results			
	1	2	3	4	... k	
Replicates	x_{11}	x_{21}	x_{31}	x_{41}	... x_{k1}	
	x_{12}	x_{22}	x_{32}	x_{42}	... x_{k2}	
	x_{13}	x_{23}	x_{33}	x_{43}	... x_{k3}	
	...	...	...	..	...	
	x_{1n}	x_{2n}	x_{3n}	x_{4n}	... x_{kn}	
Treatment totals	T_1	T_2	T_3	T_4	... T_n	GT = grand total
Treatment means	X_1	X_2	X_3	X_4	... X_n	X = grand mean

(b) Compute *correction term* (C)

C = square of the sum of all values of X divided by the total number of values (equivalent to variance calculation for sample mean)

= $[(GT)^2]/kn$

(c) Compute *total sum-of-squares* (SS)

SS = X^2 - C, where X^2 is SS in a variance calculation.

(d) Compute *sum-of-squares for between treatments* (SST)

SST = ZT^2/n - C

(e) Compute *sum-of-squares for error* (SSE)

SSE = SS - SST

(f) Prepare table:

Sources of variation	Sums-of-squares	Degrees of freedom	Mean-squares	F value
Treatments	SST	k-1	MST = SST/k-1	MST/MSE
Error	SSE	k(n-1)	MS = SSE/k(n-1)	-
Total	SS	(kn-1)	-	-

(g) If computed value of F is equal to or exceeds the tabulated value for F at k-1 and k(n-1) degrees of freedom where $P \leq 0.05$ then reject Null hypothesis that treatment means are equal and accept that there are significant differences between treatment means.

8. TWO WAY ANALYSIS OF VARIANCE (with replication).

(a) Results:

	Treatments						
Blocks	1	2	3	4	...	k	Block totals
1	x_{111} to Q_{11} x_{11n}	x_{211} to Q_{21} x_{21n}	x_{311} to Q_{31} x_{31n}	x_{411} to Q_{41} x_{41n}	...	x_{k11} to Q_{k1} x_{k1n}	B_1
2	x_{121} to Q_{12} x_{12n}	x_{221} to Q_{22} x_{221n}	x_{321} to Q_{32} x_{32n}	x_{421} to Q_{42} x_{42n}	...	x_{k21} to Q_{k2} x_{k2n}	B_2
			......to....				
b	x_{1b1} to Q_{1b} x_{1bn}	x_{2b1} to Q_{2b} x_{2bn}	x_{3b1} to Q_{3b} x_{3bn}	x_{4b1} to Q_{4b} x_{4bn}	...	x_{kb1} to Q_{kb} x_{kbn}	B_b
Treatment total	T_1	T_2	T_3	T_4	...	T_k	Grand total GT
Treatment means	X_1	X_2	X_3	X_4	...	X_k	Grand mean X

(b) Compute $C = GT^2/kbn$ (there are *kbn* values of X)

(c) Compute $SS = ZX^2 - C$ (as before)

(d) Compute $SSQ = ZQ^2/n - C$
(there are now *n* replicates in each sub-class)

(e) Compute $SSE = SS - SSQ$
(error is now estimated from variation within sub-classes)

(f) Compute $SST = ZT^2/bn - C$
(there are now *bn* values for each treatment)

(g) Compute $SSB = ZB^2/kn - C$
(there are now *kn* values in each block)

(h) Compute $SSTB = SSQ - (SST + SSB)$

(i) Prepare table:

Sources of variation	Sum-of-squares	Degrees of freedom	Mean squares	F value
Treatments	SST	k-1	MST = SST/(k-1)	MST/MSI
Blocks	SSB	b-1	MSB = SSB/(b-1)	MSB/MSE
Interaction	SSTB	(k-1)(b-1)	MSI= SSTB(k-1)(b-1)	MSI/MSE
Error	SSE	kb(n-1)	MSE = SSE	-
Total	SS	kbn-1	-	-

(j) If computed value of F is equal to or exceeds the tabulated value for F at (k-1)(b-1)/kb(n-1) degrees of freedom where $P \leq 0.05$ then reject Null hypothesis that treatment means are equal and accept that treatments vary significantly from block to block.

9. POISSON DISTRIBUTION.

$P(X) = [e^{-\mu}\mu^{x}]/X!$

where P(X) is the probability of X occurring and μ is the population mean number of occurrences.

10. BINOMIAL DISTRIBUTION.

$P(X) = [n!/X!(n-X)!]p^{X}q^{n-X}$

where P(X) is the probability of X individuals occurring in a category from a random sample of size n.

$p^{x}q^{n-x}$ = the probability of a sample containing of X items of probability p and q as the probability of with n-X items occurring.

11. LOG-LIKELIHOOD STATISTIC (G).

$G = 2\Sigma O.\ln(O/E) = 4.60517\Sigma O.\log_{10}(O/E)$

where O is the observed frequency and E the expected frequency.

12. YATES CORRECTION FOR CONTINUITY IN LOG-LIKELIHOOD ANALYSES OF 2 X 2 CONTINGENCY TABLES.

For;

	A	B	
C	f_1	f_2	R_1
D	f_3	f_4	R_2
	C_1	C_2	

Where $f_1f_4-f_2f_3$ is negative, add 0.5 to f_1 and f_4 and subtract 0.5 from f_2 and f_3.

Where $f_1f_4-f_2f_3$ is positive, subtract 0.5 to f_1 and f_4 and add 0.5 from f_2 and f_3.

13. CRAMER CONTINGENCY COEFFICIENT.

$\text{ø} = [f_1 f_4 - f_2 f_3]/\sqrt{C_1 C_2 R_1 R_2}$; ranging from 0 to 1.

14. REGRESSION AND CORRELATION ANALYSIS.

(a) Results:

Data set of independant (x) and dependant variables (y) plotted on scatter plot.

independant variable	dependant variable
x_1	y_2
x_2	y_2
x_3	y_3
...	...
x_n	y_n

(b) Compute using equations above:

x y
x^2 y^2
x y
n xy

(c) Compute slope regression coefficient (b); the slope of the best fit line through y & x.

$$b = \frac{xy - (\ x)(\ y)/n}{x^2 - (\ x)^2/n}$$

(d) Compute the intercept (a) from the ; equation of the straight line Y = bX + a.

Substitute y for Y
x for X

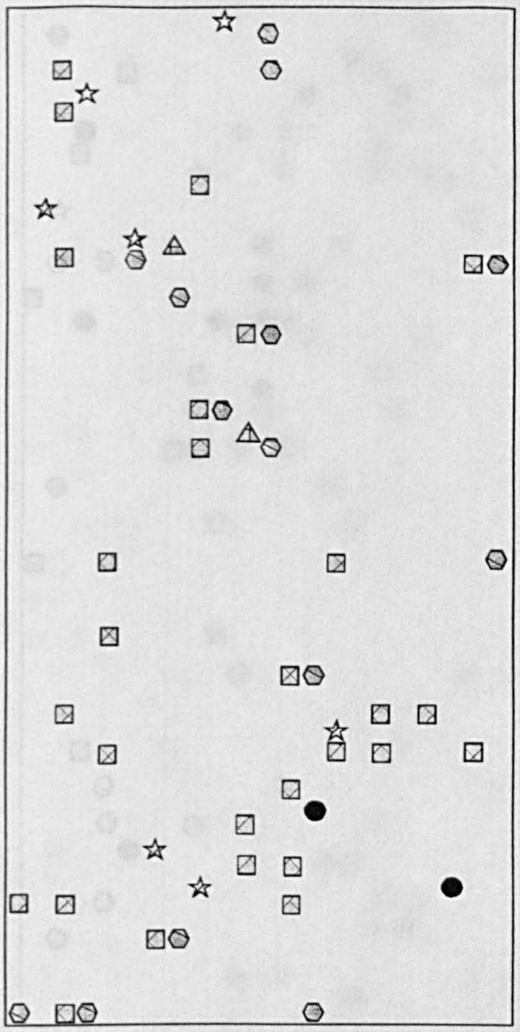
(e) Compute correlation coefficient (r).

$$r = \frac{xy}{\sqrt{(x^2 - y^2)}}$$

15. TAYLOR'S POWER LAW: the variance of a population is proportional to a fractional power of the arithmetic mean, expressed as $s^2 = ax^b$, where a and b are constants; a is dependent on the size of the sampling unit and b is an index of dispersion.

APPENDIX THREE

MICROTERMES SPECIES FORAGING ON BAIT IN UNCULTIVATED AND CULTIVATED SITES AT MOKWA, NIGERIA



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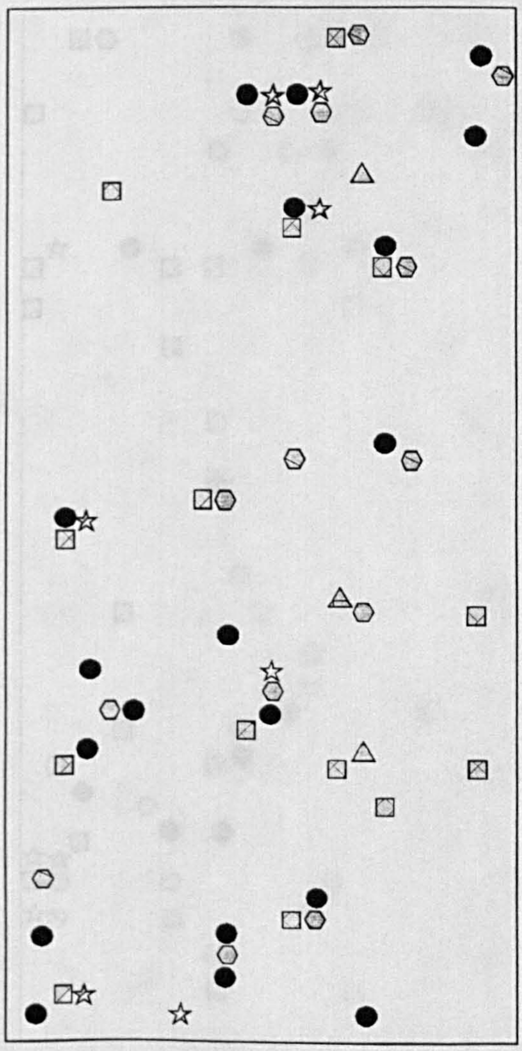
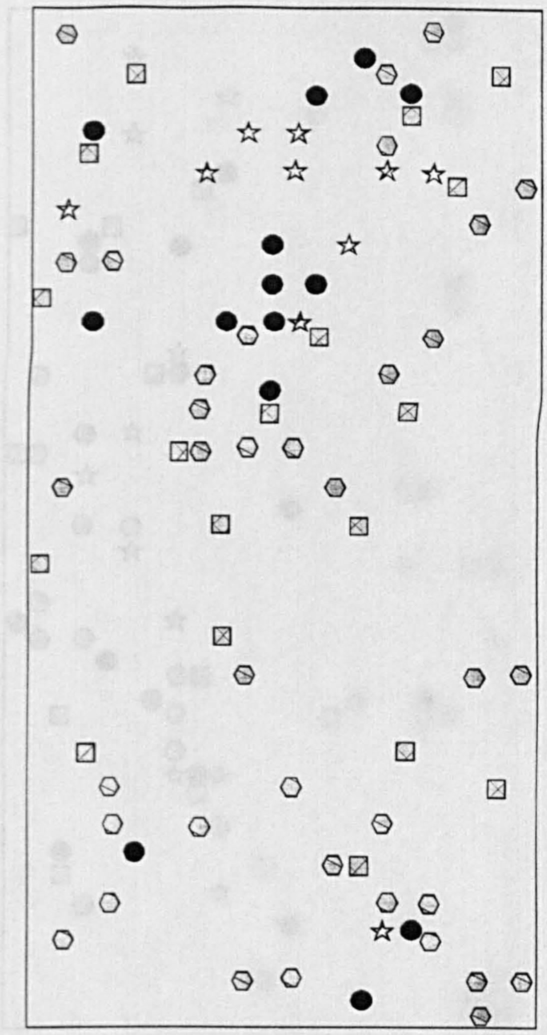
june 74



secondary
woodland 12
december 74

Spatial distribution of Microtermes species foraging on baits.

symbol	SPECIES
●	*M. lepidus*
☆	*M. grassei*
⬡	*M. subhyalinus*
⊠	*M. aluco*
△	*M. n. sp. C*



secondary
woodland 12
june 75

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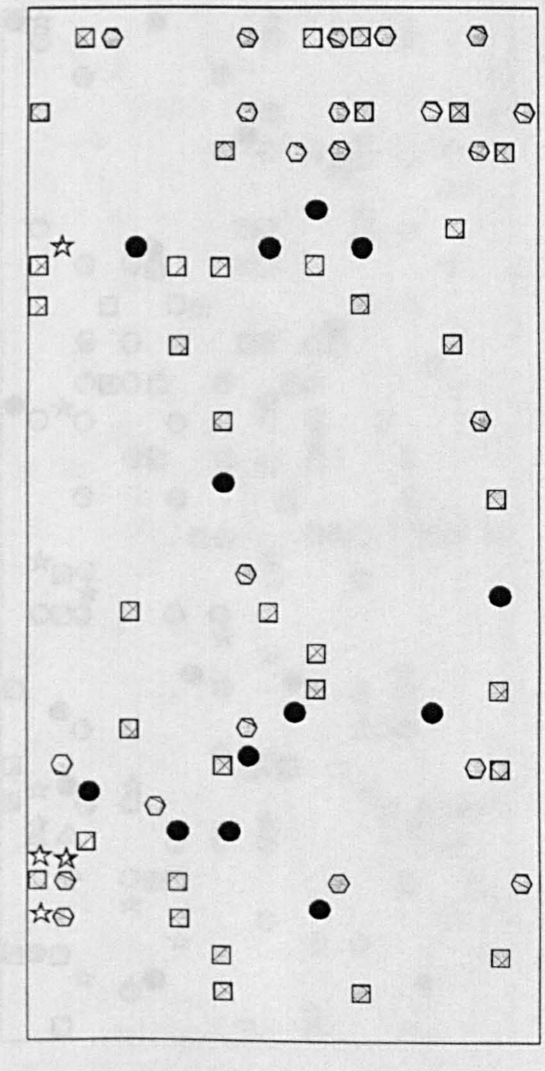

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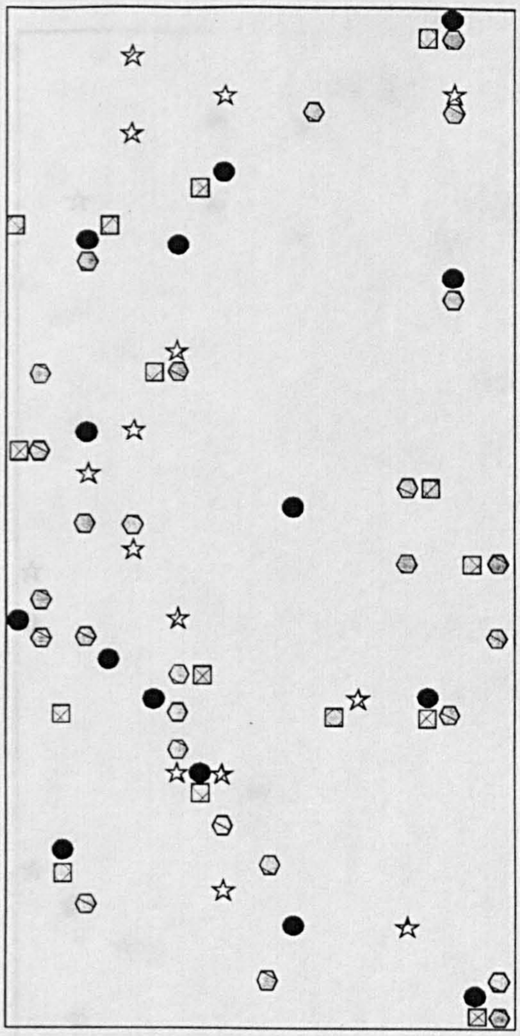
wood 12
august 75



secondary
woodland 1
february 75

Spatial distribution of Microtermes species foraging on baits.

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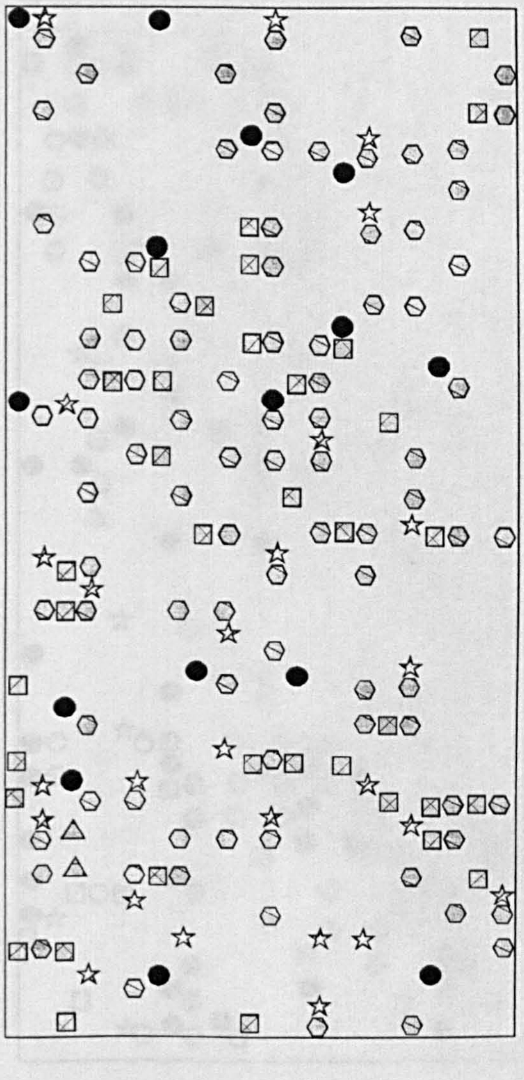
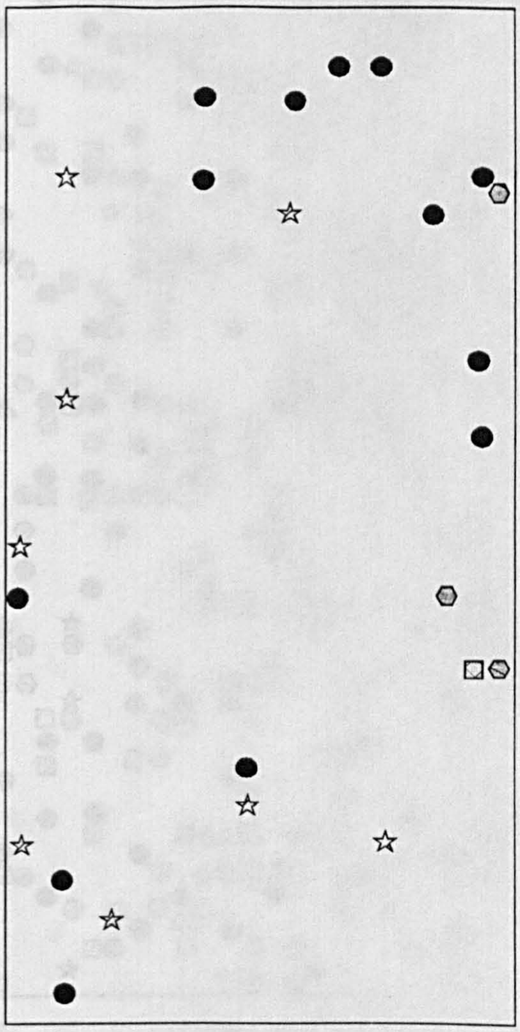
☒	*M. aluco*
△	*M. n. sp. C*



secondary
woodland 1
may 75



pasture 4
february
75

Spatial distribution of Microtermes species foraging on baits.

symbol	SPECIES
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⬢	*M. subhyalinus*
⊠	*M. aluco*
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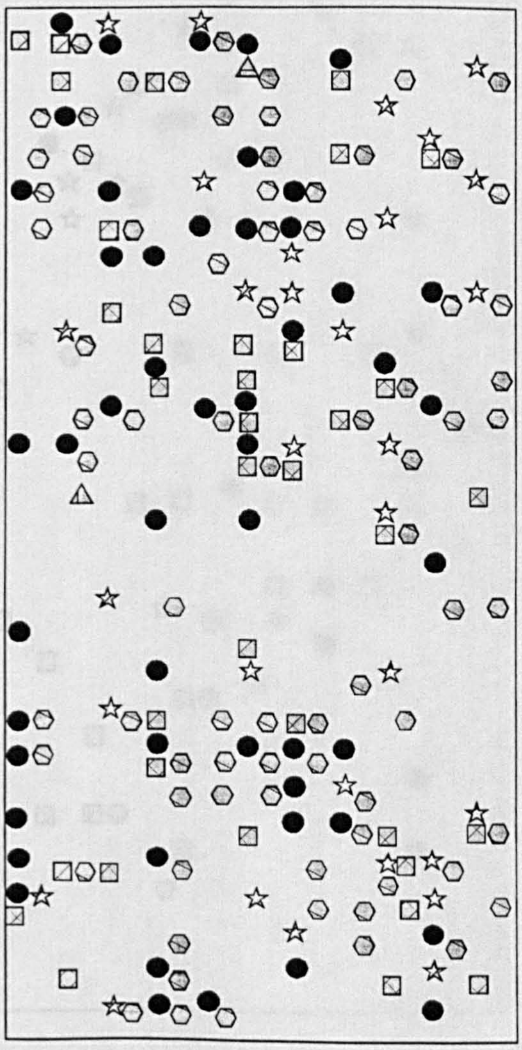
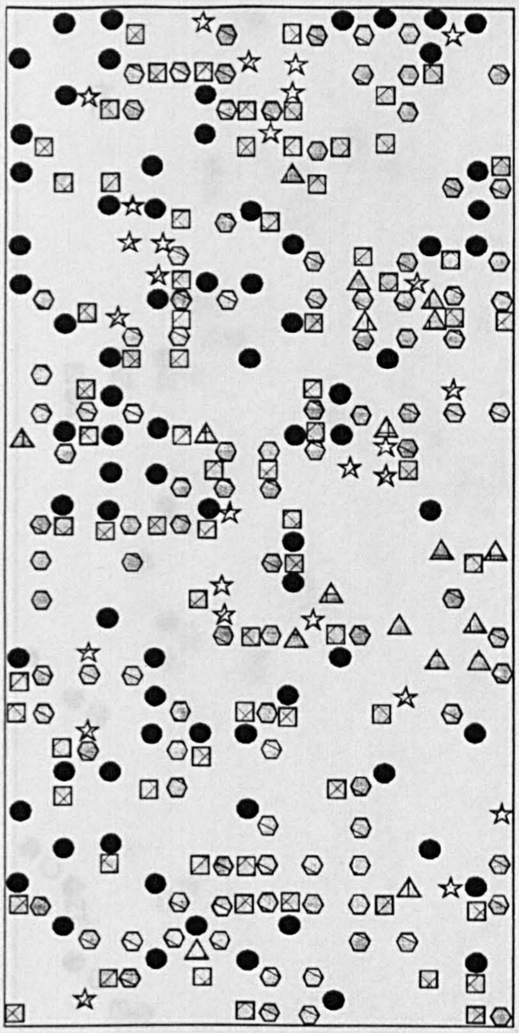


pasture 4
july 75



pasture 5
july 75

Spatial distribution of Microtermes species foraging on baits.

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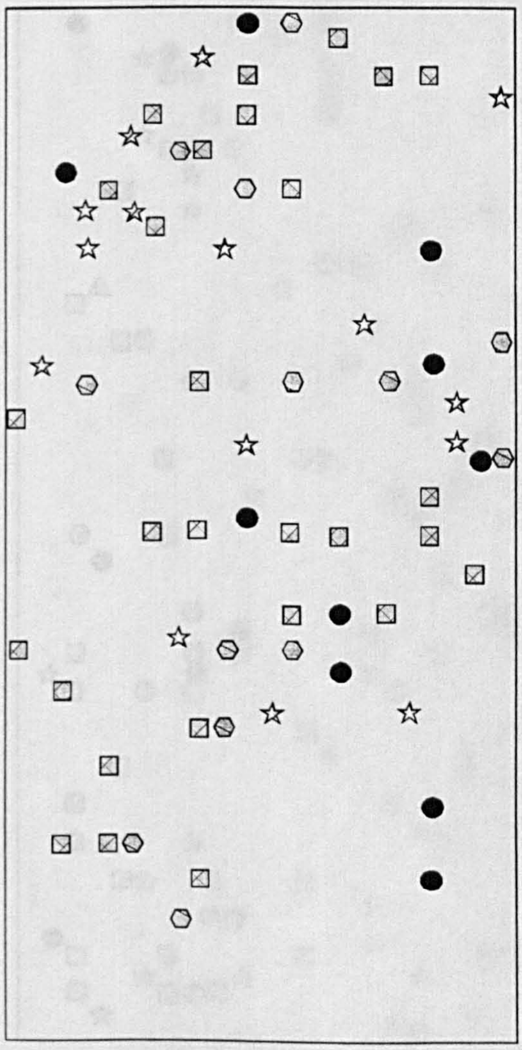
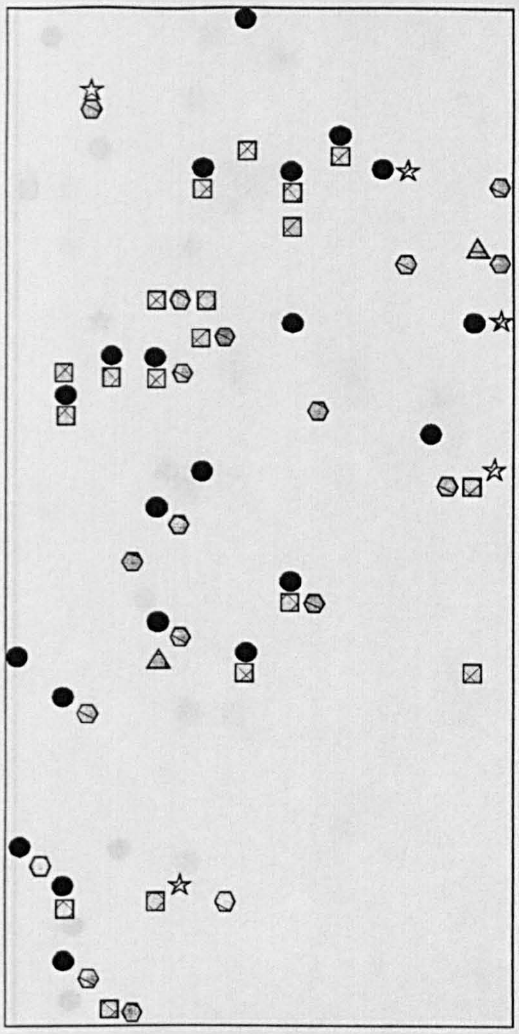


sweet
potato 8
july 74



sweet
potato 8
july 75

Spatial distribution of Microtermes species foraging on baits.

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⊠	*M. aluco*
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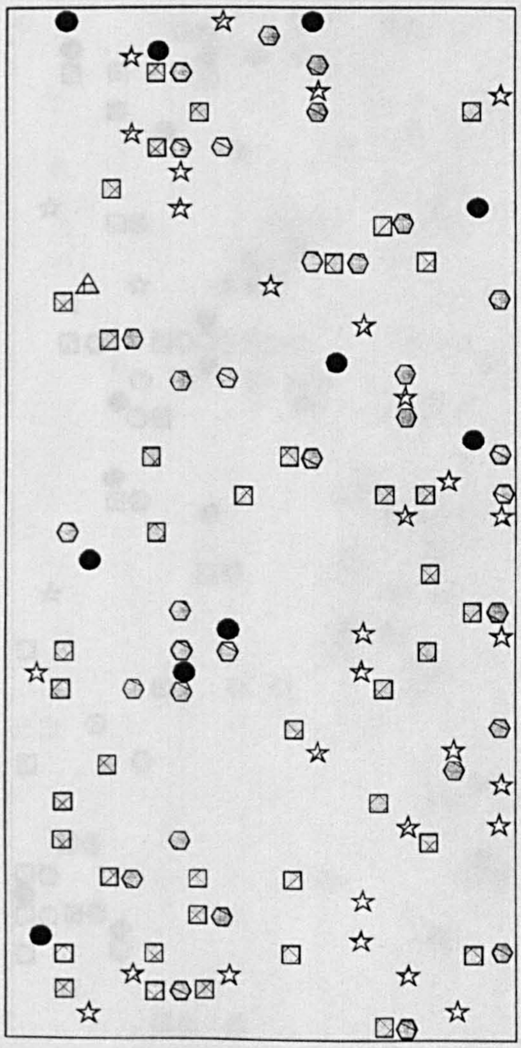
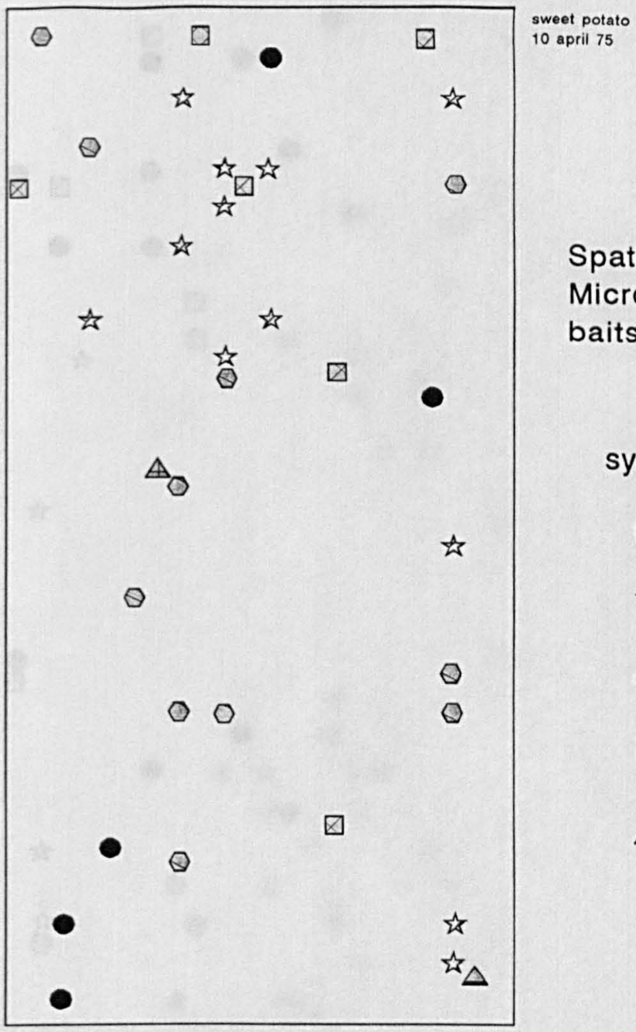
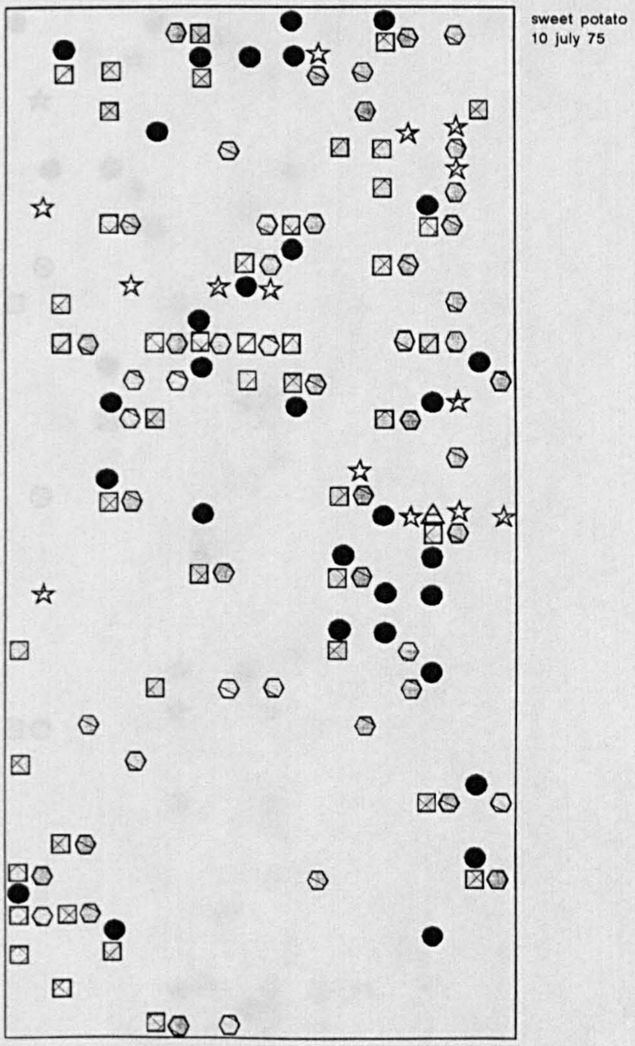


sweet
potato 10
october 74





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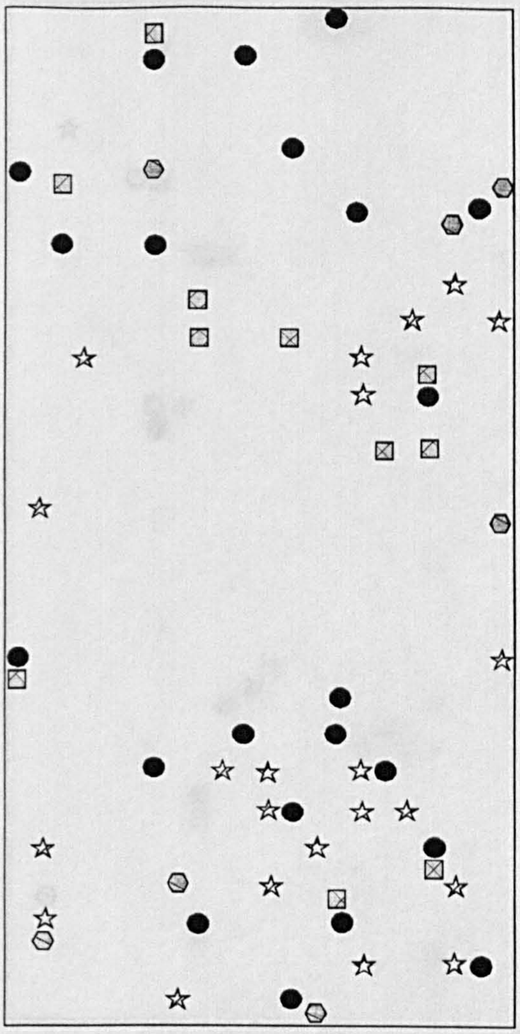

groundnuts 2
february 75

Spatial distribution of Microtermes species foraging on baits.

symbol	SPECIES
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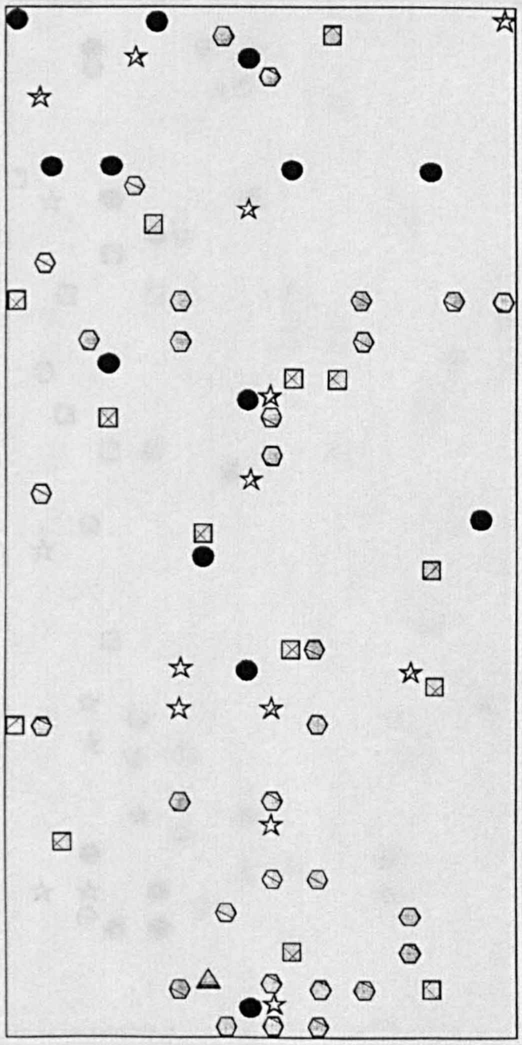
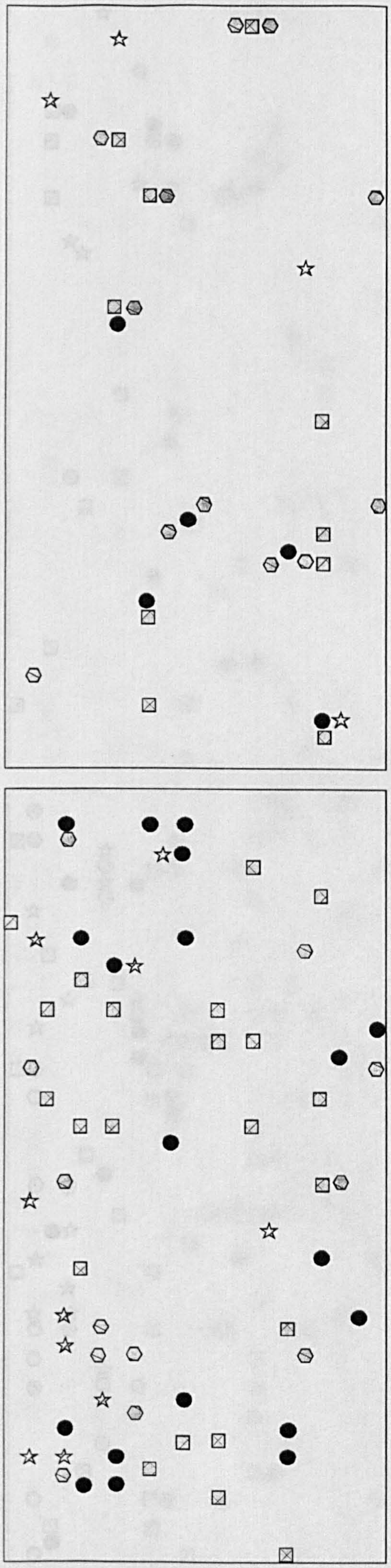
☆	*M. grassei*
⬣	*M. subhyalinus*
⊠	*M. aluco*
△	*M. n. sp. C*



groundnuts 2
june 75



Spatial distribution of Microtermes species foraging on baits.

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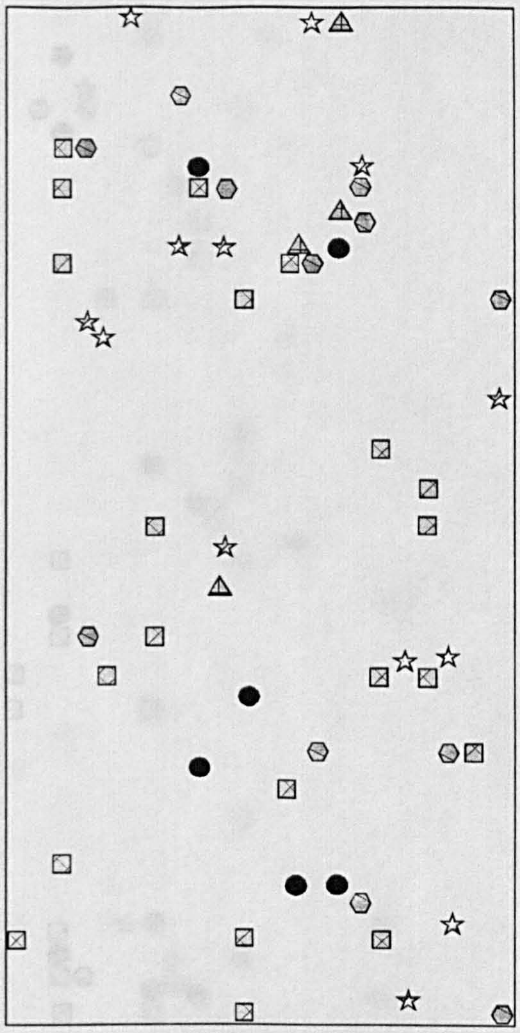

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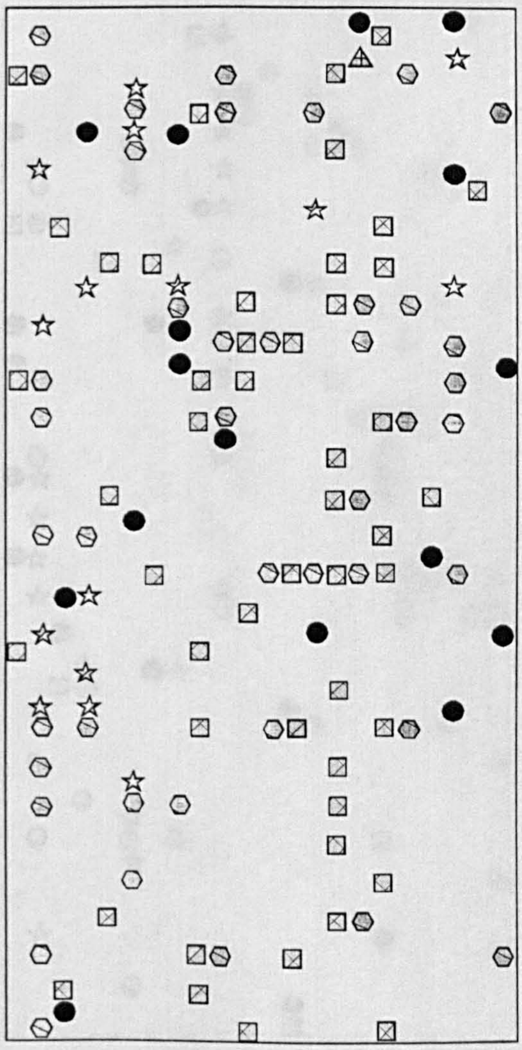
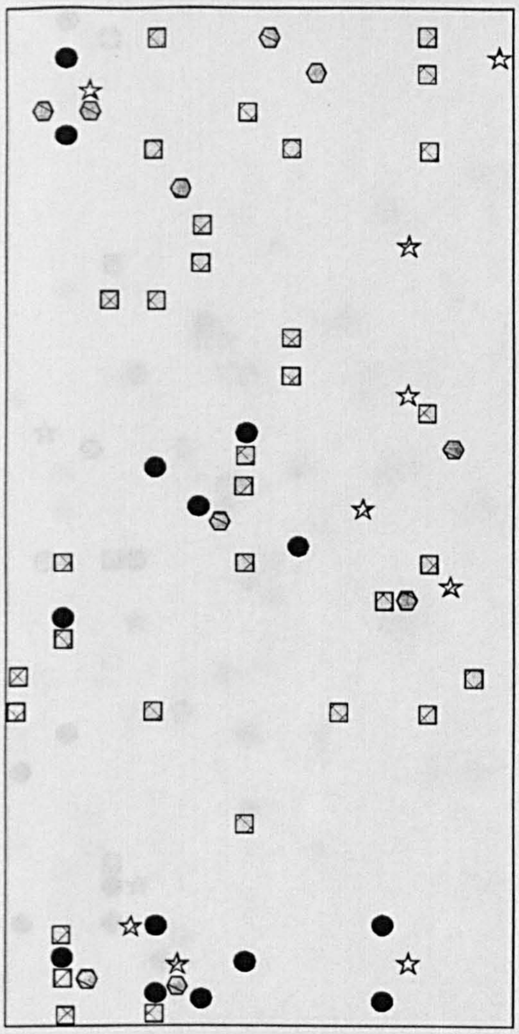
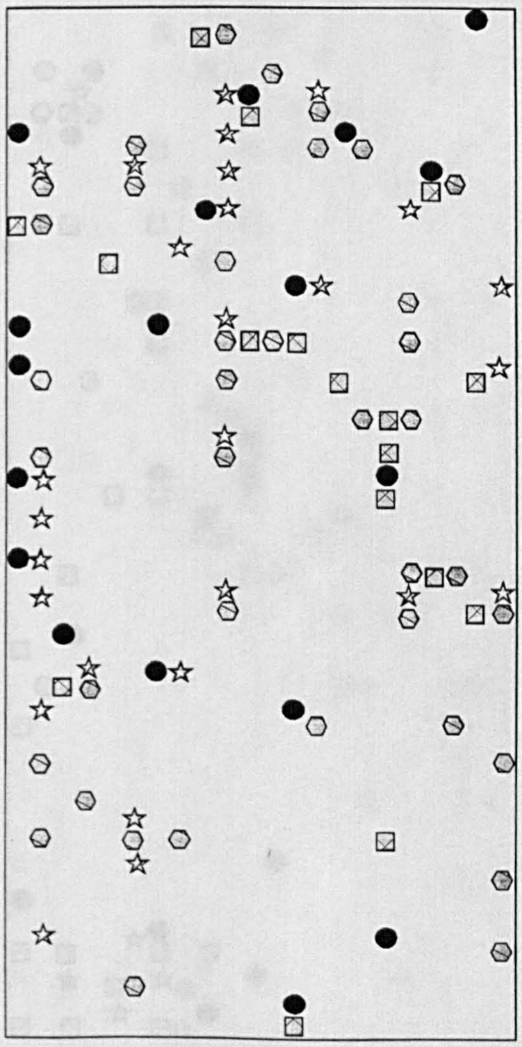




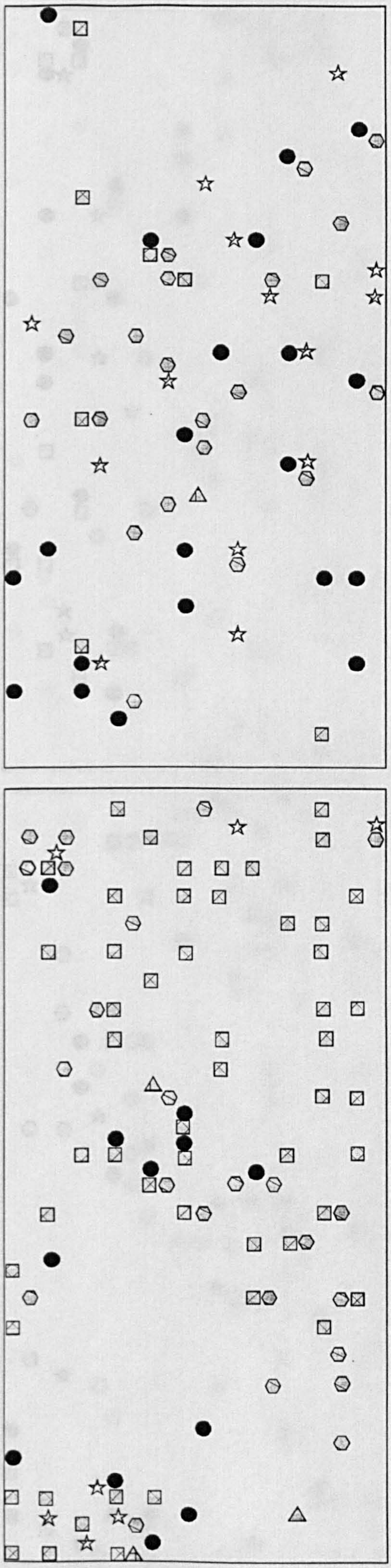
yam 3
october 74

Spatial distribution of Microtermes species foraging on baits.

symbol	SPECIES
●	*M. lepidus*
☆	*M. grassei*
⬢	*M. subhyalinus*
☒	*M. aluco*
▲	*M. n. sp. C*



yam 3 april 75



yam 3 june 75

yam 6 august 74

Spatial distribution of Microtermes species foraging on baits.

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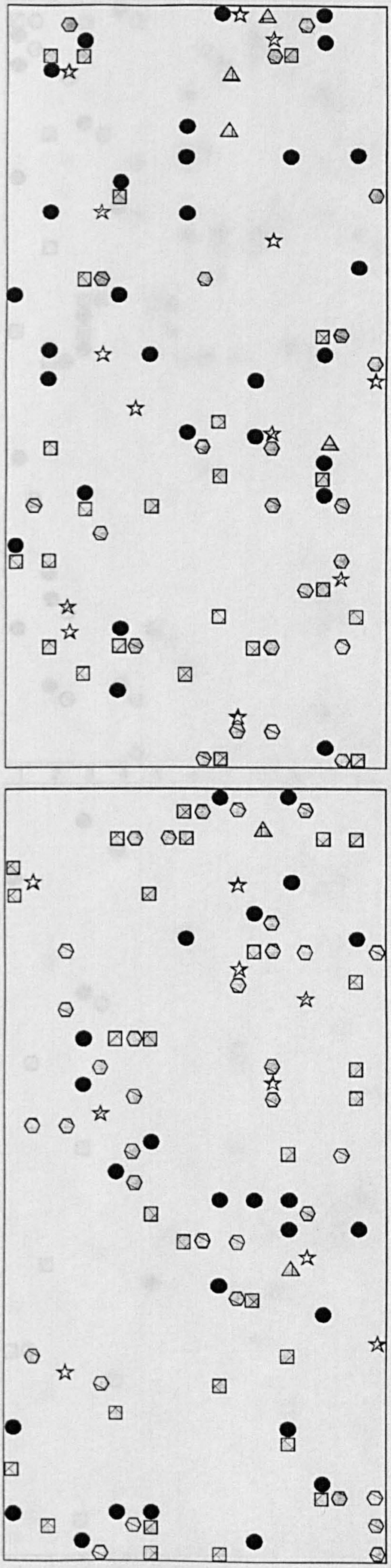

Spatial distribution of Microtermes species foraging on baits.

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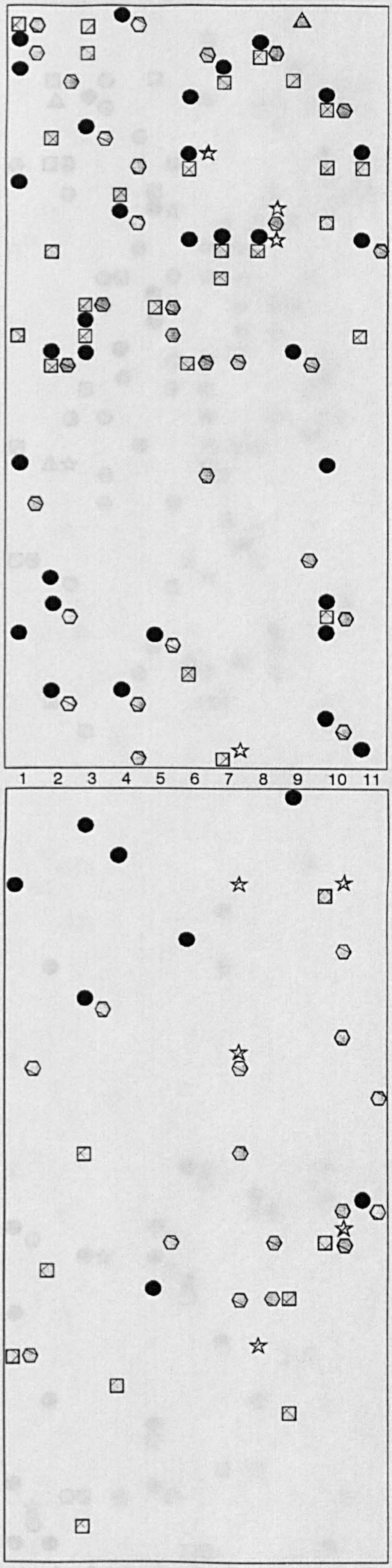

Spatial distribution of Microtermes species foraging on baits.

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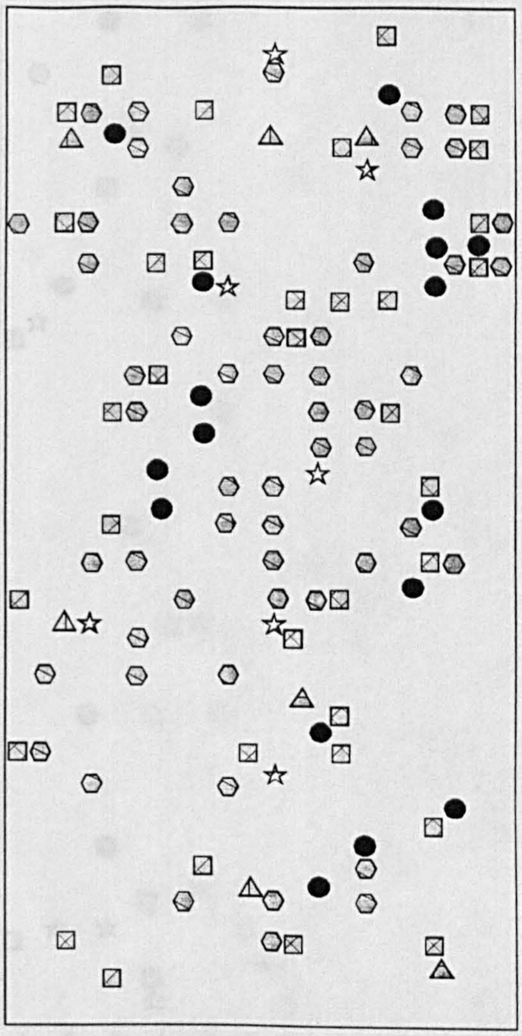

maize 7
april 75

Spatial distribution of Microtermes species foraging on baits.

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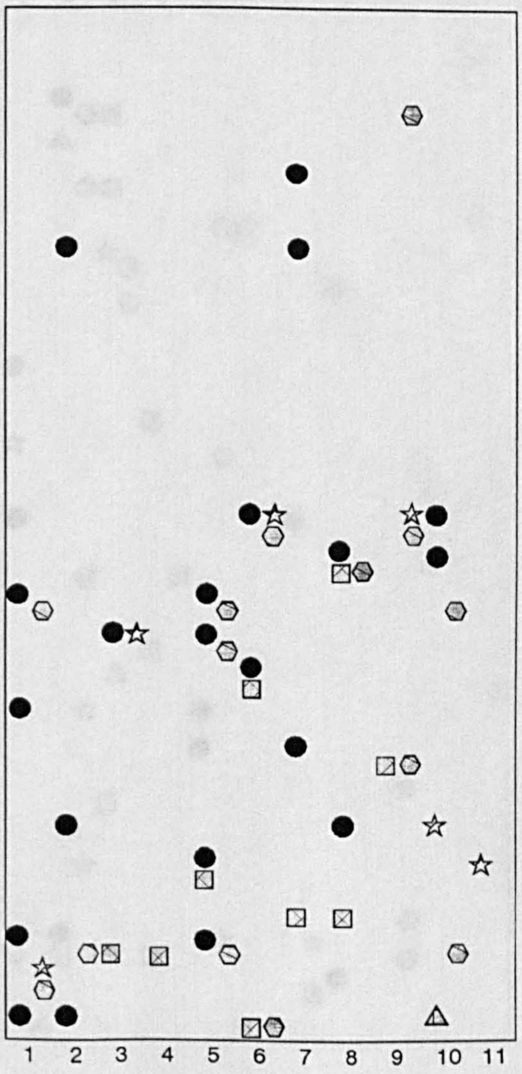
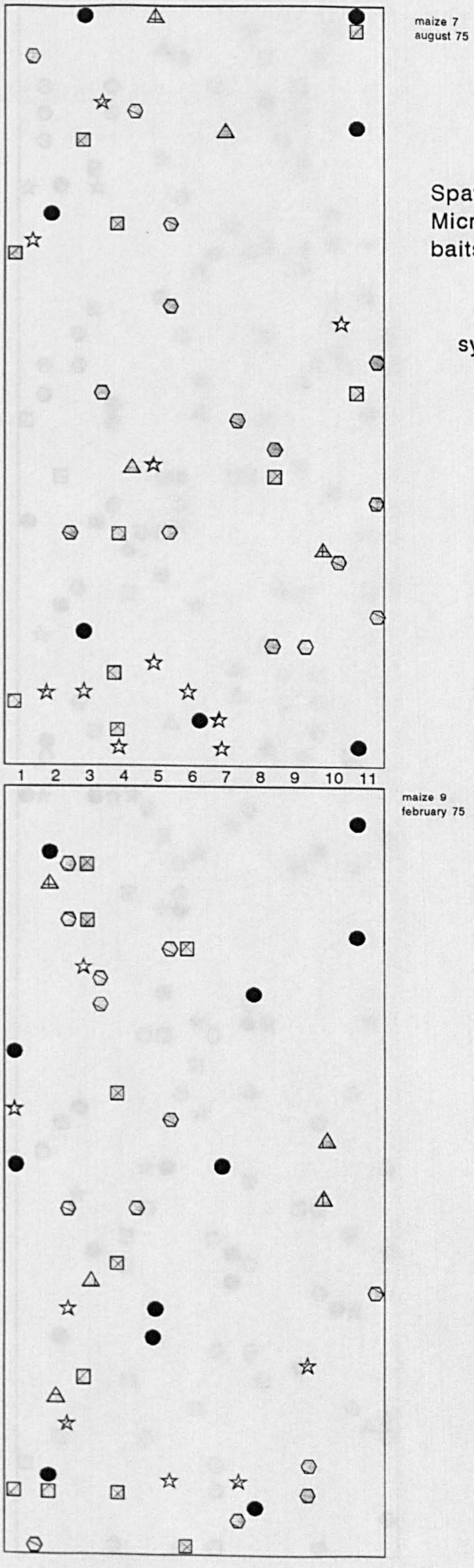
⊠	*M. aluco*
△	*M. n. sp. C*

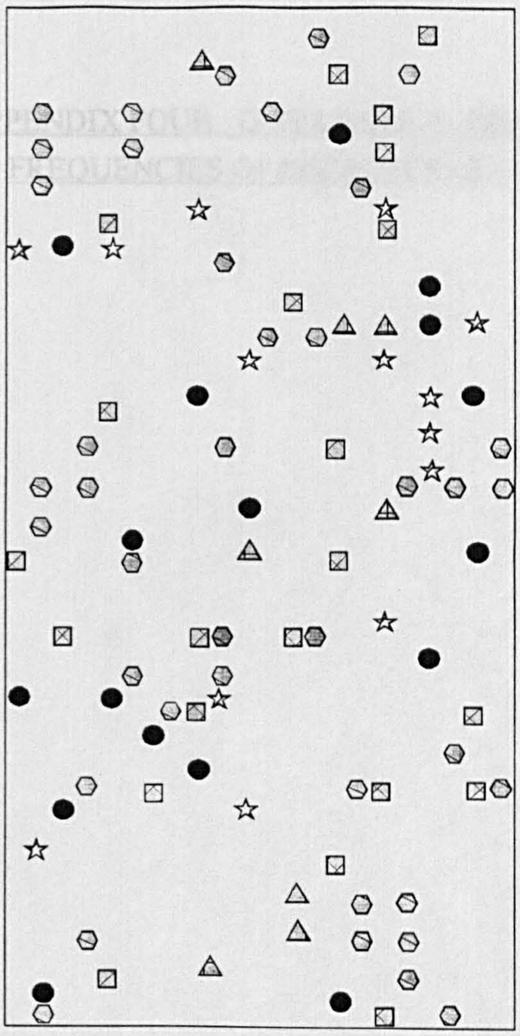


maize 7
may 75



Spatial distribution of Microtermes species foraging on baits.

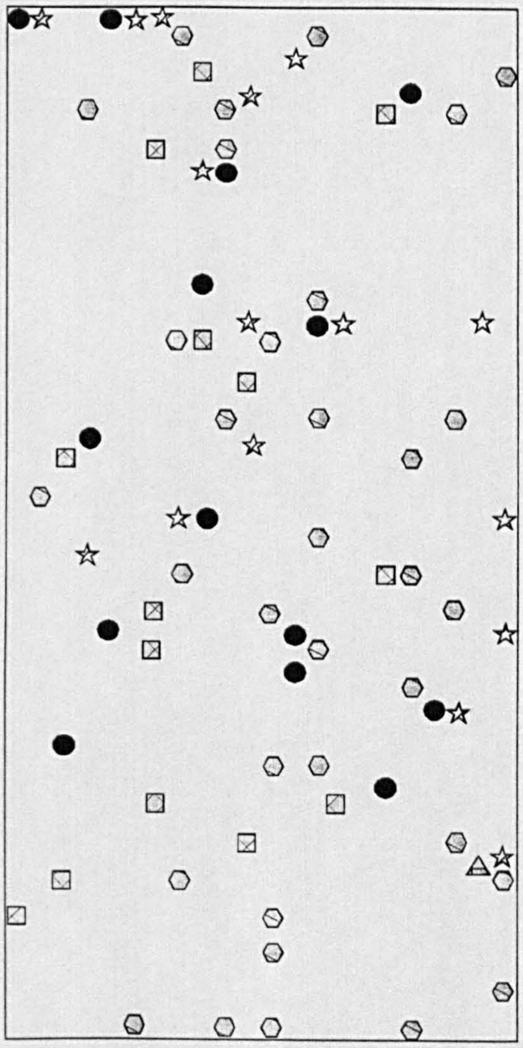
symbol	SPECIES
●	*M. lepidus*
☆	*M. grassei*
⬡	*M. subhyalinus*
⊠	*M. aluco*
△	*M. n. sp. C*



maize 9
june 75

Spatial distribution of Microtermes species foraging on baits.

symbol	SPECIES
●	*M. lepidus*
☆	*M. grassei*
⬢	*M. subhyalinus*
☒	*M. aluco*
△	*M. n. sp. C*



maize 9
august 75

APPENDIX FOUR : G STATISTICS, OBSERVED AND EXPECTED FREQUENCIES OF MICROTERMES FORAGING ON BAITS

Appendix 4a : co-occurrence of Microtermes species on baits. Observed and expected frequencies.

POOL when E<1
frequencies calculated on proportions of baits attacked
ie 1xn
2xn
3xn
4xn
5xn
SUM = N N/297/5

P

df = 1	df = 2	df = 3
3.841	5.991	12
6.635	9.21	11
7.879	10.597	7.8

BUSH 1 MAY 75

	O	E
0	171	169.2611
1	87	95.17376
2	37	26.75761
3	2	5.015174
4	0	0.704995
5	0	0.079282
	297	
mean	0.5622896	
G =		7.595922
df = k-2 =		1

BUSH 12 june 75

	O	E
0	227	228.4017
1	62	59.98428
2	8	7.876724
3	0	0.689545
4	0	0.045273
5	0	0.002378
	297	
mean	0.262626	
G =	na	
df = k-2 =		

BUSH 12 aug 75

	O	E
0	231	231.4986
1	58	57.67979
2	8	7.185698
3	0	0.596792
4	0	0.037174
5	0	0.001852
	297	
mean	0.249158	
G =	na	
df = k-2 =		

BUSH 12 JUNE 74

	O	E
0	254	249.2977
1	34	43.64809
2	9	3.821045
3	0	0.223002
4	0	0.009761
5	0	0.000342
	297	
mean	0.175084	
G =	na	
df = k-2 =		

BUSH 12 DEC 74

	O	E
0	265	247.6246
1	16	45.02266
2	10	4.092969
3	6	0.248059
4	0	0.011275
5	0	0.00041
	297	
mean	0.181818	
G =	na	
df = k-2 =		

BUSH 1 FEB 75

	O	E
0	246	233.8488
1	36	55.90326
2	10	6.682039
3	5	0.532463
4	0	0.031822
5	0	0.001521
	297	
mean	0.239057	
G =	na	
df = k-2 =		

GNUT 2 JUNE 75

	O	E
0	235	234.6375
1	56	55.30178
2	4	6.517044
3	2	0.512001
4	0	0.030168
5	0	0.001422
	297	
mean	0.2356902	
G =	na	
df = k-2 =		

GNUT 2 FEB 75

	O	E
0	238	240.2334
1	55	50.9586
2	4	5.4047
3	0	0.38215
4	0	0.020266
5	0	0.00086
	297	
mean	0.212121	
G =	na	
df = k-2 =		

GNUT 11 JAN 75

	O	E
0	254	250.9822
1	37	42.25289
2	5	3.556641
3	1	0.199587
4	0	0.0084
5	0	0.000283
	297	
mean	0.16835	
G =	na	
df = k-2 =		

GNUT 11 JUNE 74

	O	E
0	273	267.563
1	18	27.92745
2	5	1.457493
3	1	0.05071
4	0	0.001323
5	0	2.76E-05
	297	
mean	0.104377	
G =	na	
df = k-2 =		

GNUT 11 SEPT 74

	O	E
0	238	239.4259
1	54	51.59346
2	5	5.558891
3	0	0.399292
4	0	0.021511
5	0	0.000927
	297	
mean	0.215488	
G =	na	
df = k-2 =		

GNUT 11 JUNE 75

	O	E
0	195	194.9721
1	79	82.05898
2	23	17.2683
3	0	2.422602
4	0	0.254903
5	0	0.021457
	297	
mean	0.420875	
G =	7.237802	
df = k-	1	

GRASS 4 FEB 75

	O	E
0	275	273.0233
1	20	22.98176
2	1	0.967246
3	1	0.027139
4	0	0.000571
5	0	9.61E-06
	297	
mean	0.0841751	
G =	na	
df = k-2 =		

GRASS 4 JUL 75

	O	E
0	164	152.9992
1	78	101.4843
2	46	33.65725
3	9	7.441614
4	0	1.234005
5	0	0.163703
	297	
mean	0.6633	
G =		10.78213
df = k-2 =		2

GRASS 5 JUL 75

	O	P(X)	E
0	127	0.40973	122
1	86	0.365584	109
2	74	0.163097	48
3	9	0.048508	14
4	1	0.01082	3.2
5	0	0.001931	0.6
	297		
mean	0.892256		
G =		22.33242	
df = k-2 =		2	

SWP 8 july 74

	O	E
0	232	234.6375
1	61	55.30178
2	3	6.517044
3	1	0.512001
4	0	0.030168
5	0	0.001422
	297	
mean	0.2356902	
	G =	na
	df = k-2 =	

SWP 10 october 74

	O	E
0	208	204.3828
1	68	76.3855
2	20	14.27406
3	1	1.77825
4	0	0.16615
5	0	0.012419
	297	
mean	0.373737	
	G =	3.63
	df = k-2 =	1

SWP 10 APR 75

	O	E
0	263	263.2048
1	33	32.67979
2	2	2.028779
3	0	0.083965
4	0	0.002606
5	0	6.47E-05
	298	
mean	0.124161	
	G =	na
	df = k-2 =	

SWP 8 JUL 75

	O	E
0	255	237.0196
1	19	53.46907
2	21	6.031023
3	2	0.453511
4	0	0.025577
5	0	0.001154
	297	
mean	0.225589	
	G =	na
	df = k-2 =	

SWP 10 JUL 75

	O	E
0	205	182.275
1	50	88.98949
2	31	21.72302
3	11	3.535172
4	0	0.431481
5	0	0.042131
	297	
mean	0.488215	
	G =	34.7778
	df = k-2 =	1

YAM 3 oct 74

	O	E
0	241	238.6211
1	48	52.22347
2	7	5.71469
3	1	0.416897
4	0	0.02281
5	0	0.000998
	297	
mean	0.2188552	
	G =	na
	df = k-2 =	

YAM 6 aug 74

	O	E
0	215	214.2477
1	69	69.97315
2	11	11.42659
3	2	1.243972
4	0	0.10157
5	0	0.006635
	297	
mean	0.326599	
	G =	0.303
	df = k-2 =	1

YAM 3 APR 75

	O	E
0	228	214.2477
1	43	69.97315
2	24	11.42659
3	2	1.243972
4	0	0.10157
5	0	0.006635
	297	
mean	0.326599	
	G =	23.68168
	df = k-2 =	1

YAM 6 DEC 74

	O	E
0	229	220.0971
1	49	65.95502
2	17	9.88215
3	2	0.987106
4	0	0.07395
5	0	0.004432
	297	
mean	0.299663	
	G =	na
	df = k-2 =	

YAM 3 JUL 75

	O	E
0	245	239.4259
1	42	51.59346
2	8	5.558891
3	2	0.399292
4	0	0.021511
5	0	0.000927
	297	
mean	0.215488	
	G =	na
	df = k-2 =	

YAM 6 JUN 75

	O	E
0	238	216.654
1	31	69.06755
2	23	11.00909
3	6	1.16987
4	0	0.093236
5	0	0.005945
	298	
mean	0.318792	
	G =	47.59469
	df = k-2 =	1

MAIZE 7 july74

	O	E
0	267	262.2119
1	24	32.66613
2	5	2.034759
3	1	0.084496
4	0	0.002632
5	0	6.56E-05
	297	
mean	0.1245791	
	G =	na
	df = k-2 =	

MAIZE 7 APR 75

	O	E
0	262	248.5675
1	2	26.92066
2	11	1.457798
3	2	0.052628
4	0	0.001425
5	0	3.09E-05
	277	
mean	0.108303	
	G =	na
	df = k-2 =	

MAIZE 9 FEB 75

	O	E
0	260	258.7041
1	33	35.71336
2	4	2.465064
3	0	0.113432
4	0	0.003915
5	0	0.000108
	297	
mean	0.138047	
	G =	na
	df = k-2 =	

MAIZE 7 AUG 75

	O	E
0	256	256.9679
1	39	37.2041
2	2	2.693226
3	0	0.129976
4	0	0.004705
5	0	0.000136
	297	
mean	0.144781	
	G =	na
	df = k-2 =	

MAIZE 7 MAY 75

	O	E
0	209	207.8527
1	71	74.18313
2	16	13.23807
3	1	1.574899
4	0	0.140521
5	0	0.01003
	297	
mean	0.356902	
	G =	1.046
	df = k-2 =	1

MAIZE 9 JUN 75

	O	E
0	210	213.8743
1	71	64.38432
2	8	9.691065
3	0	0.97246
4	0	0.073187
5	0	0.004406
	289	
mean	0.301038	
	G =	na
	df = k-2 =	

Appendix 4b: Microtermes foraging on baits; G statistic observed and expected frequencies on baits in quadrats

WET SEASON 1974

YAM 3 WET 74 Oct.

	O	E
0	6	5.9194
1	8	9.989
2	10	8.42822
3	6	4.74087
4	2	2.00005
	32	
mean	1.6875	
	G =	2.85596
	df = k-2	2

GNUT 11 WET 74 sept

	O	E
0	18	16.6014
1	8	10.8947
2	5	3.57481
3	1	0.78199
4		
5		
	32	
mean	0.65625	
G =	1.81769	
df = k-	1	

YAM 6 WET 74 aug

	O	E
0	3	2.97646
1	8	7.0691
2	7	8.39456
3	9	6.64569
4	1	3.94588
5	2	0.13911
6	1	0
7	1	0
	32	
mean	2.375	
	G =	2.19642
	df = k-2	3

GNUT 11 WET 74 aug

	O	E
0	3	5.06314
1	11	9.33516
2	7	8.60585
3	10	5.28901
4	1	2.4379
	32	
mean	1.84375	
G =	8.53549	
df = k-	2	

MAIZE 7 WET 74 july

	O	E
0	9	12.9292
1	18	11.7171
2	4	5.30929
3	1	1.60385
	32	
mean	0.90625	
G =	5.7249	
df = k-	1	

SWP 10 WET 74 sept

	O	E
0	2	2.31807
1	6	6.08494
2	6	7.98648
3	11	6.98817
4	3	4.58599
5	3	2.40764
6	1	1.05334
mean	2.625	
G =	4.4015	
df = k-	4	

SWP 8 WET 74 july

	O	E
0	5	4.90736
1	10	9.2013
2	7	8.62622
3	5	5.39139
4	4	2.52721
5	1	0.9477
	32	
mean	1.875	
G =	6.85109	
df = k-	2	

WOOD 12 WET 74 june

	O	E
0	8	8.3477
1	11	11.2172
2	10	7.53657
3	1	3.37576
4	1	1.13404
5	1	0.30477
	32	
mean	1.34375	
G =	1.70723	
df = k-	2	

DRY SEASON 1974-75

WOOD 1 DS 74-75 feb

	O	E
0	7	5.9194
1	10	9.989
2	7	8.42822
3	3	4.74087
4	4	2.00005
5	1	0.67502
	32	
mean	1.6875	
G =	3.27897	
df = k-	2	

GNUT 2 DS 74-75 feb

	O	E
0	6	5.73728
1	9	9.86096
2	9	8.47426
3	4	4.85504
4	4	2.08615
	32	
mean	1.71875	
G =	3.63426	
df = k-	2	

YAM 6 DS 74-75 feb

	O	E
0	1	3.70427
1	9	7.98733
2	10	8.61134
3	9	6.1894
4	2	3.33647
5	1	1.43885
	32	
mean	2.15625	
G =	7.21164	
df = k-	3	

GNUT 11DS 74-75 jan

	O	E
0	7	7.36682
1	11	10.82
2	8	7.94595
3	4	3.8902
4	2	1.42843
	32	
mean	1.46875	
G =	1.32529	
df = k-	2	

MAIZE 7 DS 74-75 april

	O	E
0	12	10.3889
1	11	11.6875
2	5	6.57421
3	2	2.46533
4	1	0.69337
5	1	0.15601
	32	
mean	1.125	
G =	0.8926	
df = k-	1	

YAM 3 DS 74-75 april

	O	E
0	3	2.97646
1	10	7.0691
2	3	8.39456
3	8	6.64569
4	5	3.94588
5	2	1.87429
6	1	0.74191
	32	
mean	2.375	
G =	6.96703	
df = k-	3	

SWP 10 DS 74-75 april

	O	E
0	12	11.7721
1	11	11.7721
2	8	5.88607
3	0	1.96202
4	0	0.49051
5	1	0.0981
	32	

mean 1
G = 2.00457
df = k- 3

WOOD 12 DS74-75dec

	O	E
0	9	11.0589
1	15	11.7501
2	5	6.24223
3	3	2.21079
	32	

mean 1.0625
G = 3.23006
df = k- 1

PASTURE 4 DS74-75 feb

	O	E
0	16	15.5956
1	10	11.2093
2	5	4.02834
3	1	0.96512
	32	

mean 0.71875
G = 0.76793
df = k- 1

YAM 6 DRY 74/75 dec

	O	E
0	2	2.79613
1	5	6.81556
2	9	8.30647
3	9	6.74901
4	7	4.11268
5		
	32	

mean 2.4375
G = 9.63107

MAIZE 9 DS 74-75feb

	O	E
0	9	9.16815
1	10	11.4602
2	9	7.16262
3	4	2.98442
	32	

mean 1.25
G = 3.39428
df = k- 1

WET SEASON 1975

WOOD 1 WET 75 may

	O	E
0	0	0.70697
1	1	2.69533
2	5	5.13797
3	7	6.52951
4	9	6.22344
5	7	4.74537
6	2	3.01529
7	1	1.64226
	32	

mean 3.8125
G = 18.2472
df = k-2 = 3

GNUT 2 WET 75june

	O	E
0	5	4.4682
1	8	8.79677
2	10	8.65932
3	3	5.68268
4	5	2.79694
5	0	1.1013
6	1	0.36136
	32	

mean 1.96875
G = 3.70013
df = k- 4

PASTURE 4 WET 75 july

	O	E
0	0	0.48589
1	2	2.03468
2	5	4.26012
3	6	5.94641
4	8	6.22515
5	2	5.21356
6	3	3.63863
7	4	2.17668
8	2	1.13936
	32	

mean 4.1875
G = 6.92544
df = k-2 = 5

YAM 3 WET 75 june

	O	E
0	7	5.9194
1	5	9.989
2	12	8.42822
3	7	4.74087
4	1	2.00005
5	0	0.67502
	32	

mean 1.6875
G = 7.39439
df = k- 2

PASTURE 5 WET 75 july

	O	E
0	0	0.14819
1	0	0.79652
2	0	2.14064
3	5	3.83532
4	4	5.15371
5	3	5.54024
6	11	4.96313
7	4	3.81097
8	4	2.5605
9	0	1.52919
10	1	0.82194
	32	

mean 5.375
G = 43.0517
df = k- 3

YAM 6 WET 75 june

	O	E
0	4	4.75638
1	9	9.06684
2	12	8.64183
3	3	5.49116
4	2	2.61688
5	1	0.99769
6	1	0.31697
	32	

mean 1.90625
G = 2.87122
df = k- 2

MAIZE 7 WET 75 aug

	O	E
0	9	7.84194
1	10	11.0277
2	6	7.75387
3	5	3.63463
4	2	1.2778
	32	

mean 1.40625
G = 2.42691
df = k- 2

SWP 8 WET 75 july

	O	E
0	10	9.16815
1	11	11.4602
2	7	7.16262
3	1	2.98442
4	3	0.93263
	32	

mean 1.25
G = 0.68144
df = k- 1

MAIZE 7 WET 75 may

	O	E
0	4	4.06834
1	6	8.39096
2	10	8.65318
3	9	5.94906
4	2	3.06748
5	1	1.26534
	32	

mean 2.0625
G = 4.47391
df = k- 3

SWP 10 WET 75 july

	O	E
0	2	2.04569
1	5	5.62565
2	11	7.73527
3	6	7.09067
4	1	4.87483
5	4	2.68116
6	2	1.22886
7	1	0.48277
	32	
mean	2.75	
G =		7.90958
df = k-2 =		4

GNUT 11 WET 75 june

	O	E
0	1	1.45061
1	3	4.48783
2	9	6.94212
3	7	7.15906
4	8	5.53708
5	2	3.42607
6	0	1.76657
7	1	0.78076
8	1	0.30193
	32	
mean	3.09375	
G =		3.51691
df = k-2 =		4

WOOD 12 WET 75 aug

	O	E
0	3	4.19749
1	10	8.52614
2	7	8.65937
3	7	5.86311
4	5	2.97736
	32	
mean	2.03125	
G =	5.86069	
df = k-	2	

WOOD 12 WET 75 june

	O	E
0	3	4.75638
1	7	9.06684
2	14	8.64183
3	6	5.49116
4	2	2.61688
5		
	32	
mean	1.90625	
G =	7.10924	
df = k-	2	

MAIZE 9 WET 75 june

	O	E
0	1	2.7101
1	9	6.69056
2	6	8.25866
3	7	6.79619
4	8	4.19452
5	1	0.15978
	32	
mean	2.46875	
G =	12.9922	
df =	2	

MAIZE 9 WET 75 may

	O	E
0	2	2.04569
1	7	5.62565
2	4	7.73527
3	8	7.09067
4	6	4.87483
5	5	0.23041
6		
7		
	32	
mean	2.75	
G =		2.11639
df = k-2 =		2

Appendix 4c: G statistics. Observed and expected frequencies of Microtermes foraging on baits: occurence on baits in quadrats

WET SEASON 1974

YAM 3 WET 74 oct
M. aluco

	O	E
0	11	11.772
1	12	11.772
2	7	5.8861
3	2	1.962
	32	
mean	1	
G =	1.4708	
DF = K-	1	

YAM 6 WET 74 aug
M. aluco

	O	E
0	7	5.9194
1	11	9.989
2	6	8.4282
3	3	4.7409
4	3	2.0001
5	2	0.675
	32	
mean	1.6875	
G =	9.5803	
df = k-2	2	

SWP 8 WET 74 july
M. aluco

	O	E
0	15	13.34
1	9	11.672
2	5	5.1066
3	3	1.4894
	32	
mean	0.875	
G =	2.8303	
df = k-2	1	

SWP 10 WET 74 oct
M. aluco

	O	E
0	9	9.7594
1	11	11.589
2	10	6.8812
3	1	2.7238
4	1	0.8086
	32	
mean	1.1875	
G =	2.5942	
df = k-2	2	

SWP 10 WET 74 oct
M. grassei

	O	E
0	17	13.763
1	5	11.613
2	8	4.899
3	2	1.3779
	32	
mean	0.8438	
G =	8.0921	
df = k-2	1	

SWP 10 WET 74 oct
M. subhyalinus

	O	E
0	14	11.41
1	8	11.767
2	6	6.0671
3	3	2.0856
4	1	0.5377
	32	
mean	1.0313	
G =	2.7965	
df = k-2	2	

DRY SEASON 1974-75

WOOD 1 DS74-75
M. subhyalinus

	O	E
0	16	13.763
1	7	11.613
2	7	4.899
3	2	1.3779
	32	
mean	0.8438	
G =	4.2195	
DF = K-	1	

YAM 3 DS 74-75
M. grassei

	O	E
0	15	13.763
1	11	11.613
2	4	4.899
3	1	1.3779
4	0	0.2906
5	1	0.0013
	32	
mean	0.8438	
G =	0.4895	
df = k-2	1	

YAM 3 DS 74-75
M. subhyalinus

	O	E
0	8	9.7594
1	14	11.589
2	7	6.8812
3	2	2.7238
4	1	0.8086
	32	
mean	1.1875	
G =	1.3699	
df = k-2	1	

WET SEASON 1975

WOOD 1 WET 75 may
M. aluco

	O	E
0	10	9.7594
1	13	11.589
2	5	6.8812
3	2	2.7238
4	1	0.8086
5	1	0.0071
	32	
	1.1875	
G =		0.7198
df = k-2		1

WOOD 1 WET 75 may
M. subhyalinus

	O	E
0	0	1.9217
1	8	5.4049
2	6	7.6007
3	6	7.1256
4	8	5.0102
5	4	0.2477
	32	
mean	2.8125	
G =	16.31	
df = k-2	2	

PASTURE 4 WET 75 july
M. subhyalinus

	O	E
0	6	3.4798
1	3	7.7209
2	1	8.5654
3	9	6.3348
4	6	3.5138
5	3	1.5593
6	3	0.5766
7	1	0.1828
	32	
mean	2.2188	
G =	24.781	
df = k-2	3	

PASTURE 5 WET 75 july
M. subhyalinus

	O	E
0	3	2.9765
1	1	7.0691
2	9	8.3946
3	6	6.6457
4	6	3.9459
5	3	1.8743
6	3	0.7419
7	1	0.2517
	32	
mean	2.375	
G =	1.1919	
df = k-2	3	

PASTURE 5 WET 75 july
M. aluco

	O	E
0	2	3.5903
1	8	7.8538
2	10	8.5901
3	7	6.2636
4	4	3.4254
5	1	0.1024
	32	
mean	2.1875	
G =	6.038	
df = k-2	2	

PASTURE 4 WET 75 july
M. aluco

	O	E
0	12	10.389
1	10	11.687
2	5	6.5742
3	4	2.4653
4	1	0.6934
	32	
mean	1.125	
G =	2.197	
df = k-2	1	

PASTURE 4 WET 75 july
M. lepidus

	O	E
0	6	6.5012
1	9	10.361
2	10	8.2566
3	6	4.3863
4	1	1.7477
	32	
mean	1.5938	
G =	2.9759	
df = k-2	2	

YAM 6 WET 75 june
M. lepidus

	O	E
0	13	11.772
1	10	11.772
2	5	5.8861
3	4	1.962
	32	
mean	1	
G =	3.3836	
df = k-2	1	

PASTURE 4 WET 75 july
M. grassei

	O	E
0	12	12.146
1	12	11.766
2	5	5.6993
3	3	1.8404
	32	
mean	0.9688	
G =	1.8049	
df = k-2	1	

MAIZE 9 WET 75 may
M. subhyalinus

	O	E
0	9	5.9194
1	8	9.989
2	5	8.4282
3	6	4.7409
4	2	2.0001
5	2	0.0356
6		
7		
	32	
mean	1.6875	
G =		1.594
df = k-2 =		3

YAM 6 WET 75 june
M. aluco

	O	E
0	16	13.763
1	9	11.613
2	3	4.899
3	4	1.3779
	32	
mean	0.8438	
G =	5.8153	
df = k-2	1	

YAM 6 WET 75 june
M. subhyalinus

	O	E
0	10	11.41
1	15	11.767
2	3	6.0671
3	4	2.0856
	32	
mean	1.0313	
G	5.63	
df	1	

MAIZE 7 WET 75 may
M. subhyalinus

	O	E
0	11	11.059
1	10	11.75
2	9	6.2422
3	2	2.2108
	32	
mean	1.0625	
G =	2.8421	
df = k-2	1	

WOOD 12 WET 75 june
M. aluco

	O	E
0	11	11.059
1	10	11.75
2	9	6.2422
3	2	2.2108
	32	
mean	1.0625	
G =	2.8421	
df = k-2	1	

GNUT 11 WET 75 june
M. aluco

	O	E
0	10	12.531
1	10	11.748
2	7	5.507
3	2	1.7209
4	1	0.4033
5	1	0.0756
6	1	0.0118
	32	
mean	0.9375	
G =	0.0865	
df = k-2	1	

GNUT 11 WET 75 june
M. subhyalinus

	O	E
0	10	10.069
1	12	11.643
2	5	6.7309
3	5	2.5942
	32	
mean	1.1563	
G =	4.1767	
df = k-2	1	

GNUT 11 WET 75 june
M. aluco

	O	E
0	11	0.3679
1	10	0.3679
2	9	0.1839
3	2	0.0613
3	2	1.7209
4	1	0.4033
5	1	0.0756
6	1	0.0118
	26	
mean	1.5385	
G =	158.23	
df = k-2	1	

SWP 10 WET 75 july
M. subhyalinus

	O	E
0	6	6.7076
1	9	10.481
2	11	8.1879
3	5	4.2646
4	1	1.6658
	32	
mean	1.5625	
G =	2.9864	
df = k-2	2	

SWP 10 WET 75 july
M. lepidus

	O	E
0	13	12.146
1	10	11.766
2	7	5.6993
3	1	1.8404
4	1	0.4457
	32	
mean	0.9688	
G =	0.8571	
df = k-2	1	

MAIZE 9 WET 75 june
M. subhyalinus

	O	E
0	8	10.389
1	11	11.687
2	8	6.5742
3	3	2.4653
4	1	0.6934
5	1	0.156
	32	
mean	1.125	
G =	1.7368	
df = k-2	1	