THE INTERACTIONS BETWEEN TERMITE ACTIVITY, AGRICULTURAL PRACTICES AND SOIL CHARACTERISTICS IN KISII DISTRICT, KENYA

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PREFACE

This report deals with a research project which was financed by the Dutch Foundation for the Advancement of Tropical Research (WOTRO). Scientific support and supervision were provided by Dr. W.G.Wielemaker of the Department of Soil Science and Geology and by Prof.Dr. R.H.Cobben of the Department of Entomology both of the Agricultural University, Wageningen, The Netherlands. The proposal for this research was worked out by Dr. W.G.Wielemaker and Ir. P.A. van der Werff, Dept. of Ecological Agriculture. We are very grateful to the late Prof.Dr. J. Bennema of the Dept. of Soil Science and Geology and the late Prof.Dr. J. de Wilde of the Dept. of Entomology for their efforts to secure the finances for the project.

The authors regret the long period of time that has elapsed between the official termination of the project and the issue of the report. The actual writing took mainly place after the project had stopped, and because of other occupations we had progressively less time to devote to the report. But by sacrificing a large part of our free time, we finally managed to complete the job. Drs. Onck is mainly responsible for the sections dealing with soil aspects, while Ir. Kooyman took care of the entomological aspects.

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1 INTRODUCTION

Since Darwin's original study (1881) on the importance of earthworms in soil formation, the action of the soil fauna gradually received more attention. This resulted in a better understanding of its significance, particularly in the breakdown of organic matter and the formation of well structured topsoils in the temperate regions (Kubiena, 1955; Hopp and Slater, 1948; Hoeksema and Edelman, 1960).

In the tropics, where earthworms are less abundant, the attention was directed towards termites. Especially since the 1950's, their contribution to soil formation and their effects on soil fertility became widely discussed (Grassè, 1950; Hesse, 1955; Nye, 1955; Boyer, 1956a; Maldague, 1959). It has been suggested that termites would have similar effects on the soil as earthworms (e.g. Drummond, 1887), but since there are important differences between these two groups, that does not follow so easily.

Regarding their effects on the ecosystem, termites cannot easily be treated as one single group: there are many species of termites, which in their behaviour diverge much more from each other than different species of earthworms do. Moreover, termites are social organisms, usually strongly concentrated in nests, while earthworms behave strictly as individuals. The latter move predominantly in vertical direction, but termites move mainly in horizontal direction. Vertical tunnels are usually only found near nests. Although a relatively permanent system of tunnels radiates in all directions, the members of a nest are active in only one or a few places at any given moment. So they have a very clustered distribution.

Many termite species are active at greater depths than earthworms, where they collect water and building material. They break down organic matter more effectively, aided by microorganisms in their guts or by fungi grown on structures made of 'faecal' pellets (funguscombs). Decomposition of organic matter takes place in the nests and thus mineral nutrients are concentrated and trapped in a few places for at least as long as the nests are active. Earthworms consume organic matter where they find it, so that nutrients are released throughout the soil.

Lee and Wood (1971) present a review of the available literature on the relations between termites and soils. It appears that most work has been done in natural ecosystems and specifically on mound-building species. Termite mounds are a prominent feature in many tropical areas, so it is not surprising that many studies were devoted to their physical and chemical composition as compared with surrounding soils. Many authors reported differences in clay content, pH, organic matter, exchangeable cations and so on (Lee and Wood, 1971; Pomeroy, 1976; Watson, 1976; Miedema and Van Vuure, 1977; Arshad, 1981 and others). However, there is a lack of knowledge about the characteristics of diffuse subterranean nest systems.

The spatial distribution and abundance of termites has often been related to variations in soil type (texture, drainage), vegetation and climate (Pomeroy, 1977; Buxton, 1981a). It has also been noted, that termites are able to modify their habitat to their preferences (Bouillon, 1970; Wielemaker, 1984) thereby affecting local vegetation and microclimate (Glover et al., 1964; Arshad, 1982).

As far as the agricultural aspects of termite activity are concerned, attention has mainly been given to the damage they cause to crops both in the field and in storage, as well as to wooden structures (Harris, 1961; Sands, 1973). Recently, important work has been done on species diversity and densities of termites under different types of landuse (Wood et al., 1977; Wood et al., 1982) and on the consumption of litter by termites (Buxton, 1981b; Collins, 1981a,b). But little has been done to investigate the contribution of termites to the formation and maintenance of soil structure.

The balance between the biotic and abiotic components of the soil can easily be disrupted by human activities such as agriculture. In the temperate regions it has been found, that modern methods often adversely affect the soil fauna (Aritajat, 1977; Abbott et al., 1979), which may lead to degradation of the soil. Also in the tropics, agriculture is being intensified and modern methods introduced, which already leads to such problems as physical degradation, loss of fertility and erosion (Aina, 1984). If, as Wielemaker (1984) concludes for West Kenya, termites are important for the formation and maintenance of a good soil structure, these problems could partly be avoided by maintaining and perhaps even enhancing termite activity. Recently, the importance of soil biological processes for the fertility of tropical soils has been stressed (Swift, 1984). It was concluded that more research is needed about the effects of the soil fauna on soils, esp. soils under cultivation.

In 1983, a study was initiated in Southwest Kenya to investigate some of these effects. This study attempts to answer the following questions:
1. What is the relation between the distribution and species diversity of termites and the spatial variations in ecological conditions?
2. To what extent is the activity of termites affected by farming practices, and how does this reflect on soil characteristics?

In Chapter 2, the relevant features of the study area are described. Chapter 3 deals with the distribution of the termite species present in the area in relation to some ecological and geographical factors, and Chapter 4 with their impact on the micromorphology of the soil.

When the proposers of this study presented their plan, they stressed the importance of experiments. Experimental plots were to be prepared on four different soil types in order to study the effects of several treatments, like ploughing, hoeing and compaction, on the soil and on the termite populations. However, during the initial description of the first set of experimental plots it soon became clear, that the time needed for this had been seriously underestimated. So we decided to carry out a comparative survey of farmer's fields in order to study the long-term effects of tillage and type of crop on the soil and the termite populations. The field experiments are described in Chapter 5. The next chapter deals with

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the comparative survey of farmer's fields planted with various crops in two small areas.

The effects of termite building activities were investigated separately and the results are presented in Chapter 7. In the same chapter some additional experiments are described. Food preference experiments were carried out to get a clearer understanding of the distribution of the various termite species. Two other experiments served to study the construction of termite tunnels and the fate of excavated soil. In the last chapter the role of termites in soil formation and maintenance is discussed in the light of our findings.

2 STUDY AREA

2.1 LOCATION AND EXTENT

The study area is part of the Kisii District (Nyanza Province, Southwest Kenya), roughly bounded by latitudes 34°40′ and 35°00′ E, and longitudes 0°30′ and 0°45′ S (Fig. 2.1.). It is entirely covered by the map sheets 130/1 Oyugis and 130/2 Kisii, scale 1:50 000 (Survey of Kenya). Within this area, which measures approximately 775 km², a few representative key areas have been selected and investigated.

The Kisii District has a humid climate and good soils with a high agricultural potential. Most of the original vegetation has been cleared and the area is under intensive cultivation to support a rapidly growing population. The average population density for the district is 395 per km², but in the central part this figure

Fig.2.1 Map of Kenya with location of study area.

reaches 765 per km^2 (Kenya population census, 1979). As arable land is becoming increasingly scarce, intensification of agriculture is likely to continue in the future.

2.2 GEOLOGY

The geology of the Kisii area has been described by Huddleston (1951). From the original data, a simplified map has been compiled by Wielemaker and Boxem (1982), which will serve as a basis for this chapter (Fig. 2.2.).

The Kisii area consists chiefly of basic, intermediate and acid volcanic rocks of Precambrian age. These formations can be divided in three major systems according to age and position in the field :

1. In the western part of the area, generally below altitudes of 1500 m, the rocks of the **Nyanzian** System occur. This system consists mainly of rhyolites, andesites, dolerites and basalts, with interbedded metamorphosed coarse sediments. Locally, boulder conglomerates and grits of the **Kavirondian** System are found in association with Nyanzian strata. Both the Nyanzian and Kavirondian Systems are between 2600 and 3000 million years old (Saggerson, 1969).

STRATIGRAPHY	ROCK TYPE		STRATIGRAPHY	ROCK TYPE	
Tertiary		nephelinites, nepheline basalts	Nyanzian		upper andesites
Precambrium			Nyanzian		rhyolites
Bukoban		rhyolites and tuffs	Nyanzian		andesites and dacites
Bukoban		felsites and andesites	Nyanzian		basalts
Bukoban		quarzites and cherts	Intrusives		
Bukoban		basalts	Post-Kavirondian		dolerites and lamprophyres
Kavirondian		conglomerates	Post-Kavirondian		Wanjare granites and quarzdiorites
			Post-Nyanzian		Kitere and Oyugis granites
					faults

Fig.2.2 Geology of the study area (After Wielemaker and Boxem, 1982)

2. **Precambrian intrusives** occur at several places in the study area, but are most pronounced in the Nyanzian System. For the present research, only the Wanjare granite intrusion is important. It occupies a slightly elevated area that attains a maximum height of 1650 m.
3. In the eastern part, where the Kisii highlands are situated, the rocks of the **Bukoban** System are exposed, at altitudes from 1500 to just over 2100 m. This system consists of a succession of basalts, quartzites and cherts, generally below 1800 m, and is covered by felsites, andesites and rhyolites. The age of the basalts is approximately 670 million years (Saggerson, 1969). The highest parts of the area are composed 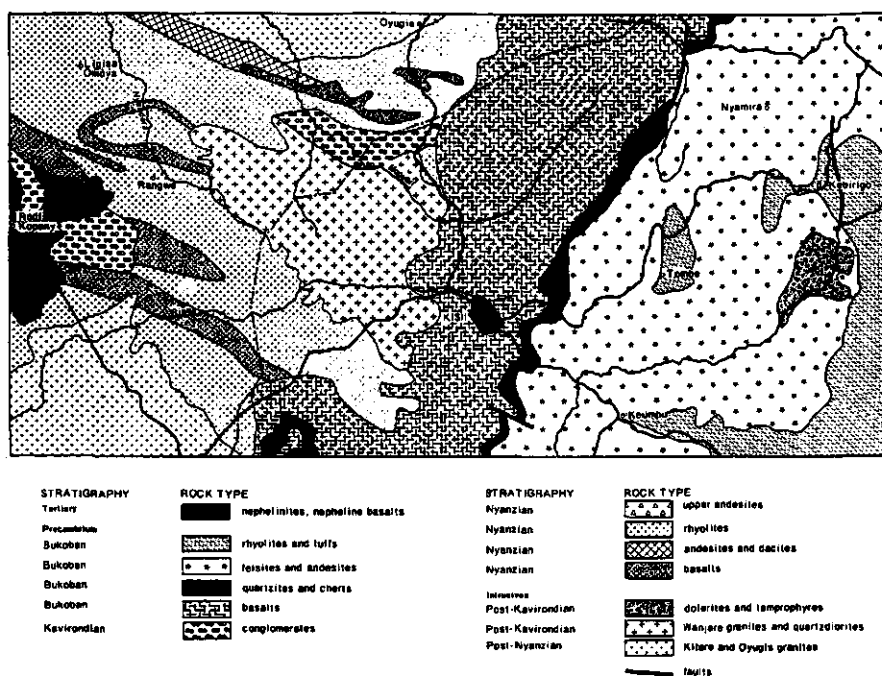of rhyolites and rhyolitic tuffs. The quartzites appear as a very prominent escarpment, that traverses the area from north to south.

With the exception of some basalts in the extreme west, Tertiary or younger formations have not been recorded. In Quaternary times, volcanic ash deposits have covered the Kisii area (Wielemaker, 1984). At present, remnants of these deposits occur in some wide and flat-bottomed valleys. The ash has been incorporated to some extent in older soil material through the action of the soil fauna. This accounts for the relatively high natural fertility of the, otherwise deeply weathered, Kisii soils (Wielemaker, 1984).

2.3 GEOMORPHOLOGY

On the whole, the Kisii area features a hilly to rolling landscape, consisting of more or less flat-topped ridges and generally V-shaped valleys. Altitudes increase in easterly direction from 1350 to about 2130 m, and the relief becomes more hilly. Wielemaker and van Dijk (1981) identified several erosion surfaces, and distinguished four upland levels. As far as possible, their terminology will be adopted (Fig. 2.3.).

The Kisii area can be broadly divided into three adjacent zones with different relief and with a NE-SW orientation:
1. The eastern zone, with an elevation between 1700 to 2130 m, is predominantly composed of ridges of rhyolite and associated tuffs, the so-called **Keroka Uplands**. Their gently sloping summit levels are probably remnants of a tilted Cretaceous peneplain. The slopes are generally steep (15-20 %) and single with a clearly convex margin to the gently sloping ridge crest.
   The lower parts of this zone, with altitudes of 1700-1950 m, form the **Magombo Uplands**, developed in felsites and andesites. The Magombo uplands are associated with wide, flat-bottomed valleys in which marshy conditions exist. The Keroka and Magombo Uplands are strongly dissected, and have a hilly to rolling topography.
2. The quartzite escarpment, with an elevation of about 1800 m, forms the boundary between the eastern zone and the central zone or **Kisii Uplands**. The area consists mainly of Bukoban basalts and Post-Kavirondian intrusives, and attains altitudes of 1450-1800 m. The area is strongly dissected

Fig.2.3 Geomorphology of the study area (After Wielemaker and Boxem, 1982)

Legend:
- hills
- minor scarps
- footslopes
- Keroka erosion surface (rolling to hilly), 1800-2150m
- Magombo erosion surface (undulating to rolling), 1700-1950m
- Kisii erosion surface (rolling) 1450-1800m
- Rongo erosion surface (undulating to rolling), 1200-1500m
- plains and bottomlands
- bottomlands

by V-shaped valleys, and has a rolling topography. Apart from some isolated hills, which represent outliers of the eastern uplands, a summit level of 1600-1700 m can be recognized in the field. It is regarded as a remnant of the Kisii erosion surface, probably of Tertiary age. This surface is partly preserved in the higher parts of the Wanjare area (Kebuye Range). The ridge consists of quartz diorite and is part of the divide between the drainage basins of the Gucha and the Mogusii rivers, the main rivers in the Kisii District.

3. A knickline marks the transition of the Kisii Uplands to the **Rongo Uplands**. The latter show an undulating to rolling topography, formed by parallel, flat-topped ridges developed in rocks of the Nyanzian System. The ridges may carry a thick ironstone cap and are locally covered with riverine deposits.

2.4 CLIMATE

The Kisii area has a cool to warm, humid tropical high altitude climate, with an average annual precipitation of 1600 to more than 2000 mm. The climate is one of the wettest in Kenya, because of convergence of the easterlies and the daily lakewinds, which causes the air to rise and leads to heavy showers, especially in the afternoon. There are no pronounced wet and dry seasons in most of the area. Maximum rainfall occurs from March to May and only January and February are commonly considered 'dry'. Average annual evaporation ranges from around 2000 mm at an altitude of 1500 m to 1650 mm at 2100 m.

The regional variation of evaporation follows an opposite trend to that of precipitation. In the western part, low rainfall coincides with high evaporation, while the eastern highlands are characterised by high rainfall and relatively low evaporation figures. The ratio between average annual precipitation and average annual potential evaporation (r/Eo) is used for the distinction of so-called agro-climatic zones (Sombroek et al., 1982). A further division of these zones is based on the average annual temperature, which depends largely on the altitude of the site (Table 2.1.). The boundaries of the agro-climatic zones are shown in Fig. 2.4.

Table 2.1. Boundary criteria for agro-climatic zones (After Sombroek et al., 1982).

Moisture availability		Temperature		
zone	ratio r/Eo	zone	mean annual temperature °C	altitude m
I	>0.80	6	14–16	2100–2400
II	0.65–0.80	5	16–18	1800–2100
III	0.50–0.65	4	18–20	1500–1800
IV	0.40–0.50	3	20–22	1200–1500
V	0.25–0.40	2	22–24	900–1200

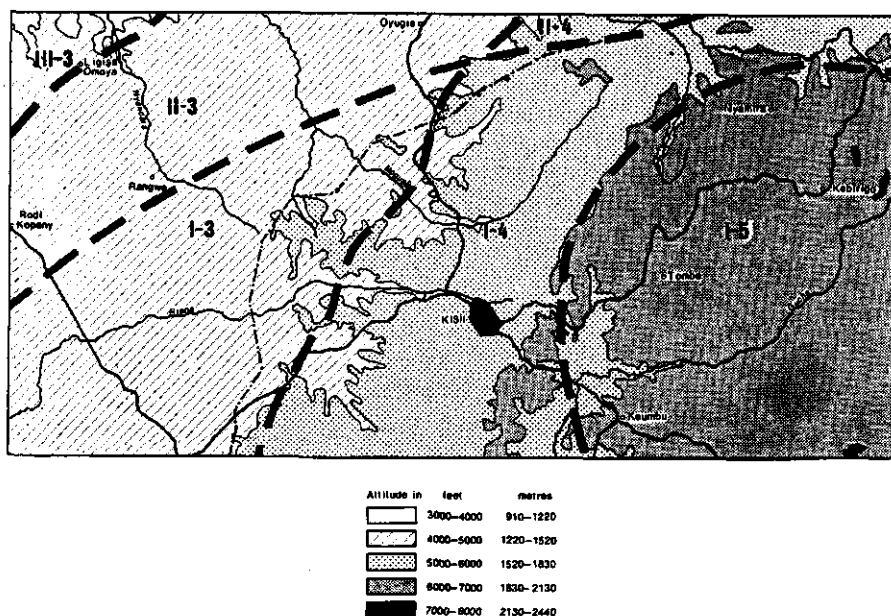| Altitude in	feet	metres
	3000–4000	910–1220
	4000–5000	1220–1520
	5000–6000	1520–1830
	6000–7000	1830–2130
	7000–8000	2130–2440

Fig.2.4 Altitude and approximate boundaries of the agroclimatic zones of the study area (Modified after Sombroek et al., 1982)

The temperatures at different altitudes are roughly as follows (Sombroek et al., 1982).

Table 2.2. Mean annual temperatures at various altitudes in the Kisii District.

altitude	1300 m	1600 m	2130 m
mean annual temperature (°C)	21.8	19.6	16.4
mean max. temperature (°C)	27.8	26.0	22.8
mean min. temperature (°C)	15.6	13.5	9.8

The Kisii District belongs to agro-climatic zones I 5, I 4, and I 3. To a large extent, the boundaries between these zones coincide with those of the eastern, central and western Uplands respectively (Fig 2.4.).

2.5 VEGETATION

Before 12000 B.P., when the climate was cool and dry, forests were not very extensive. Most of the study area probably had a savanna vegetation. During the subsequent wet period forests covered the area again, but later on the vegetation became more open, esp. in the lower parts of the area.

Until a century ago, the ridges at higher altitudes were densely forested. West of the escarpment there was woodland giving way to grassland dominated by *Loudetia* and *Hyparrhenia* with woody patches. A dense forest was situated in the Wanjare area. In poorly drained valleys and plains, trees and bushes were probably confined to large termite mounds, as is often still the case today. Common tree species in the area almost certainly included: *Albizia gummifera, A. zygia, A. coriaria, Antiaris toxicaria, Casearia battiscombei, Chlorophora excelsa, Croton megalocarpus, Erythrina abyssinica, Fagara macrophylla, Ficus capensis, Grewia trichocarpa, Harungana madagascarensis, Markhamia platycalyx, Prunus africana, Strombosia scheffleri* and *Teclea nobilis*. Of these *Albizia, Croton* and *Markhamia* are still relatively common. Many imported trees are planted in the area, the most important of which are: *Eucalyptus saligna, Acacia mearnsii* and *Sesbania sesban*. The original vegetation has now virtually disappeared.

2.6 LAND USE

The introduction of agriculture in western Kenya is estimated at around 250-300 AD (Soper, 1969, in: Morrison and Hamilton, 1974). Habitation started along the shores of Lake Victoria and the low hills surrounding it. In the study area, permanent habitation started a few centuries ago when groups of people belonging to the Gusii tribe were driven from the lowlands by the invading Luo (Ochieng', 1974). Originally, the Abagusii were pastoralists, but because of the climate and vegetation and because of cattle rustling by neighbouring tribes, they were forced to turn increasingly to sedentary agriculture. However, it was

only in this century, that the fast growth of the population caused the clearing of nearly all natural forest, which became restricted to some rocky outcrops and very steep slopes.

Because of the high population density, almost all the land is used for agriculture. Cattle grazing is now mainly confined to poorly drained valleys and plains and places with very shallow soil. Crops are grown partly for subsistence and partly for cash. In the eastern uplands, the main cash crop is tea. Pyrethrum, which used to be important in the 1970's, has declined because of low prices and delayed payments by the produce board. In the central uplands, coffee is an important cash crop, but because of delayed payments, it now faces competition by bananas. The area under tea is being increased despite the fact that conditions are not optimal. In the western uplands, mainly subsistence crops are grown, but sugar-cane is on the increase and also groundnuts grow well there.

Subsistence crops grown in the study area are maize, beans, potatoes, sweet potatoes, bananas and, more to the west, finger-millet and sorghum become more important. Fertilizers and pesticides are almost exclusively used with cash crops, though the use of fertilizers in other crops is increasing. Heavy machinery is not used by the common farmer, cultivation and weeding being done with hoes. Where plots are big enough and not too steep, ox-ploughs may be used. Growing population pressure will lead to still smaller plots and possibly to an increase in the acreage under subsistence crops. Therefore it is unlikely, that farmers will be able to invest in mechanization or even in more fertilizer and pesticides in the near future.

2.7 SOIL FAUNA

Termites (Isoptera) are the main component of the soil macrofauna. They occur almost everywhere in the study area, except in permanently waterlogged places. Few species can maintain nests in cultivated plots, so nests are usually found outside those plots. Foraging, however, takes place everywhere. Termites are the most important diggers in the soil because of their habit of constructing foraging tunnels and soil sheetings. Some 17 species were collected: 1 wood-feeding species, 9 wood-and-litter-feeding species and 7 humus-feeding species. They will be treated in some detail in chapter 3.

Ants (Formicidae) are also abundant. In poorly drained areas, they may be more abundant than termites. The nest heaps of *Myrmicaria eumenoides* (Gerstäcker) are a prominent feature in pastures. Also common are *Camponotus sp.*, *Anochetus sp.* and a number of very small species (e.g. *Paratrechina spp.*). The digging activity of ants can be considerable (Van der Werff, 1978), but is usually much less than that of termites, because they do not construct foraging tunnels and they do not go as deep as termites.

Dungbeetles (Scarabaeoidea) are common where dung is produced. In some pastures, their burrows may reach densities of $20/m^2$. Most are dug directly beneath dung pads. They are 5-12 mm in diameter and may go down to over 1

m deep. At the bottom end, they contain one or more balls of dung each with a larva. The soil from the burrows is deposited on the soil surface. Their effect on the soil can locally be compared with that of ants, but is usually much less.

Rainworms (Annelida) are not very common in the study area and most species are small (25-60 mm). Their population density usually does not exceed ca. 20/m^2, so their effect on the soil is very small.

Mole rats (*Tachyoryctes sp.*) are common in well-drained, not too shallow soils. They feed on plant roots and construct tunnels of about 12 cm in diameter mainly in the upper 30 cm of the soil. Excess soil is deposited in heaps on the soil surface.

Locally two larger mammals are active in the soil. Especially in the central and western uplands, signs of aardvark (*Orycteropus afer*) activity were frequently observed. This animal lives in large burrows and excavates termite mounds and subterranean nests during the night. Though they are able to displace massive amounts of earth, their effect on the soil is only locally important. In some places holes of porcupines (*Hystrix galeata*) were seen, but they do not dig as much as aardvarks do.

2.8   SOILS

The soils in the Kisii area have recently been mapped by Wielemaker and Boxem (1982). This paragraph contains a brief review of the most important soil types.

Most of the Kisii area consists of well drained, deep to very deep, reddish brown, friable clayey soils with a high biological activity. Although they have a rather uniform appearance, differences exist in chemical and physical properties, depending on such factors as volcanic ash enrichment, parent rock and local topography. A relatively small part of the area consists of Planosols, Vertisols and Lithosols. These belong to completely different groups of soils, which have not been considered in this study.

In the eastern uplands (**Keroka** and **Magombo Uplands**), the dominant soils are Nitosols and Phaeozems. They have properties associated with the presence of volcanic ash, such as dark colours, low bulk density and high silt content. On the stable, gently sloping parts, Luvic Phaeozems (USDA: Typic Paleudoll) occur. They are well-drained, very deep, friable, clayey soils with a deep humic topsoil. Humic Nitosols (USDA: Typic Palehumult) occur where the topsoil lacks the requirements for a mollic epipedon, usually because of lower base saturation. A low base saturation is common in soils with volcanic ash admixtures because of the pH-dependant charge of the clay fraction (Mohr et al., 1972). The soils have a moderate, fine angular to subangular blocky structure with shiny ped faces, a friable consistency, and clay contents of 60-80 %.

In the **Kisii Uplands**, the influence of volcanic ash is less conspicuous and the chemical properties of the soils are mainly determined by the underlying rock (Wielemaker and Boxem, 1982):

- Soils developed on basalt are mainly Humic Nitosols (USDA: Typic Palehumult). Basically, they can well be compared with soils in the eastern uplands, but because of the lower volcanic ash content, they have a lower silt content, a higher bulk density and higher base saturation. The soils have a moderate to strong, fine angular blocky structure, and a high clay content. Nitic properties (shiny ped faces, polyhedral structure) are generally very well developed in the argillic B-horizon.
- Soils developed on intermediate and acid rock are generally well-drained, very deep friable clayey soils with an acid humic (umbric) or humic (mollic) topsoil. Clay contents range from 50-60 % on intermediate and 30-45 % on acid parent rock. The soils have a weak to moderate, very fine subangular blocky structure and nitic properties are not pronounced. Clay minerals are dominated by kaolinite, and the soils have a low natural fertility. Although Humic Nitosols occur in places, the majority of the soils can be classified as Humic Ferralsols (USDA: Typic Haplohumox and Typic Umbriorthox). Textural differentiation in the profile is gradual and cutans are not always visible.

The **Rongo Uplands** have predominantly shallow soils with well-developed argillic B horizons and a moderate to strong angular to subangular blocky structure. Clay contents are generally below 50 %. Depending on the presence of a humic topsoil, they can be classified as Chromic (or Orthic) Luvisols and Luvic Phaeozems. On granitic parent material, Humic Ferralsols occur that are similar to those in the Kisii Uplands.

3 TAXONOMY AND GEOGRAPHICAL DISTRIBUTION OF TERMITES

3.1 INTRODUCTION

In the study area, 17 species of termites were found all belonging to the family Termitidae (Table 3.1.). Three species belong to the subfamily Apicotermitinae, five to the Termitinae and the rest to the Macrotermitinae. The genera of the last two subfamilies were identified with Bouillon & Mathot (1965), but those of the Apicotermitinae were identified with Sands (1972b). The species of *Cubitermes* were identified with Williams (1966), the *Pseudacanthotermes* species with Sjöstedt (1926) and the remaining species by comparison with museum specimens. Identifications were checked by J.P.E.C.Darlington and R.K.N.Bagine of the National Museums of Kenya and by S.Bacchus of the Termite Identification Unit of the Tropical Development and Research Institute in London. However, many identifications are uncertain because of the bad state of the termite taxonomy. Material has been deposited at the National Museums of Kenya, Nairobi, the British Museum (Nat.Hist.), London, and the Department of Entomology in Wageningen, The Netherlands.

3.2 APICOTERMITINAE

In the study area, all apicotermitine termites belong to species lacking a soldier caste. Identification of these species involves dissection of the enteric valve of the worker, which is very time-consuming. Since these termites did not seem to be very important for the rest of our work, it was decided not to invest too much time in establishing their taxonomic status.

Judging from the size of the workers, three types of Apicotermitinae could be distinguished. These types may each contain more than one species, but each type is probably confined to one genus: in order of decreasing size most likely to *Astratotermes, Astalotermes* and *Adaiphrotermes*.

Apicotermitinae are confined to the upper 20-30 cm of the soil profile, where they consume soil with partly decomposed organic matter. Their exact food requirements are not known. It is reported, that they ingest appreciable amounts of inorganic particles (Lee & Wood, 1971), but it seems unlikely that they eat soil indiscriminately. Probably they choose organic-rich soil components, as Okwalol (1980) found for *Cubitermes* species (Termitinae), which have comparable food requirements.

The nests are loose systems of tunnels with widenings where the queen, the king, the eggs and the larvae are kept. There is no well-defined nest boundary. We even got the impression that the nests were not always permanent, but that a colony could move to another spot, esp. when the nest was disturbed. The

Table 3.1. List of termite species found in the study area and their nesting and feeding habits.

	Nesting[a]	Feeding[b]	Altitude[c] range (m)	Pasture[d]	Cultivated plots[d]			
					Perennial crops[e]		Annual crops[e]	
					nests	foraging	nests	foraging
Apicotermitinae								
Astratotermes sp.	S,(N)	S	w.a.	++	++	++	+	+
Astalotermes sp.	S,N	S	w.a.	+++	++	++	+	+
Adaiphrotermes sp.	S,N	S	w.a.	++	+	+	(+)	(+)
Termitinae								
Cubitermes ugandensis Fuller	M	S	w.a.	++	-	-	-	-
Cubitermes testaceus Williams	M	S	w.a.	+++	-	(+)	-	(+)
Basidentitermes amicus Harris	S,N	S	<1800	+++	-	(+)	-	(+)
Promirotermes gracilipes Schmitz	S,N	S	<1800	+	-	-	-	-
Microcerotermes parvus (Haviland)	S,M.N	W	<1650	+	-	-	-	-
Macrotermitinae								
Macrotermes michaelseni (Sjöstedt)	M	W,B,D,(G)	<1500	+++	++	++	++	++
Pseudacanthotermes spiniger (Sjöstedt)	M	W,B,L,(G,D)	<1700	+++	++	++	+	++
Odontotermes amanicus Sjöstedt	S+vo	W,B(G,D)	w.a.	+	+	+	+	+
Odontotermes kibarensis (Fuller)	S(+vo)	W,B,L,G,D	w.a.	+	++	++	++	++
Odontotermes tanganicus Sjöstedt	S(+vo)	B,G,D	>1800	++	(+)	++	-	++
Odontotermes nolaensis Sjöstedt	S+ch	B,(G,D)	<1700	+++	-	-	-	-
Odontotermes fulleri (Emerson)	S+ch	W,B,D,(G)	<1800	+++	-	-	-	-
Microtermes cf. vadschaggae (Sjöstedt)	S,(N)	W,B,R,(L)	<1900	+	++	++	+++	+++
Microtermes sp.								

[a] S = subterranean, M = mound building, N = associated with nests of other species, vo = ventilation openings without chimneys, ch = ventilation openings with chimneys, (between brackets): infrequent occurrence).

[b] S = soil, W = wood, B = woody litter, L = leaf litter, G = dry grass, D = dung, R = roots.

[c] w.a. = whole area

[d] +++ = very common, ++ = common, + = not common, (+) = one or two records

[e] Perennial crops: coffee, tea, bananas. Annual crops: maize, beans, sorghum, potatoes.

queens that were found were always relatively mobile.

Apicotermitinae were found in all habitats in the study area, but they seemed to be most abundant in not too shallow, well-drained soils with a relatively high organic matter content. At poorly drained places or where the soil is shallow, they are practically confined to mounds of other termites. *Adaiphrotermes* was most commonly found in the nests of other termites, even under otherwise favourable conditions. One or more species were found in the walls of most nests of Macrotermitinae, not only in the outer walls but usually also in the walls of chambers and ventilation shafts, in which case they could occur at depths of more than 1 m. Sometimes they were encountered in large mounds of *Cubitermes* species, but then only in the periphery.

In general, Apicotermitinae are easily disturbed by tillage, but some Kisii types can adapt to tillage by hand. In the study area, *Astalotermes* was the most common type in cultivated plots followed by *Astratotermes*, while *Adaiphrotermes* was hardly found in this habitat. In mechanically ploughed plots, Apicotermitinae were usually absent. All 3 types were often found together in pasture.

3.3 TERMITINAE

3.3.1 General

Five Termitinae species were found. They were identified as *Cubitermes ugandensis* Fuller, *C.testaceus* Williams, *Basidentitermes amicus* Harris, *Promirotermes gracilipes* Schmitz and *Microcerotermes parvus* (Haviland), but the last three species' names are uncertain.

3.3.2 Cubitermes

The *Cubitermes* species, which are humivorous, are common in uncultivated plots which are not too wet, esp. in pastures. They do not occur in cultivated plots. The two species can often be found together in the same field, but *C.testaceus* seemed to be more common in drier places with shallow soils and in places with many trees or dense scrub than *C.ugandensis*. Both species are mainly active in the upper 10-20 cm of the soil.

They build dome-shaped nest-mounds, those of the bigger *C.ugandensis* being the larger of the two. Typical sizes for *C.ugandensis* mounds were: diameter ca. 60 cm and height 30-50 cm and for *C.testaceus*: diameter ca. 45 cm and height 15-35 cm. A mound consists of a central cluster of small chambers surrounding the queen's cell. The walls of the chambers are plastered with faeces. In the case of *C.ugandensis*, the mound is usually capped with a layer of soil of varying thickness, but such a cap is usually absent from *C.testaceus* mounds.

3.3.3 Other Termitinae

B.amicus and *P.gracilipes* are also humivorous. They were only found in well-drained grass-fields with a relatively dark A-horizon. The former species is much more common than the latter. Its nest-system resembles that of Apicotermitinae,

but is more compact and the chambers are easier to recognize. The nests can either be found under grass between 5 and 30 cm below the surface or associated with mounds of *Pseudacanthotermes* or *Cubitermes*. This species was never found at altitudes above 1800 m.

P.gracilipes was rarely encountered. Nests were always found in mounds of *Pseudacanthotermes* or *Cubitermes*. They resemble *Cubitermes* nests, but are much smaller (diam. < 20 cm). This species does not occur above 1800 m. Both *Basidentitermes* and *Promirotermes* are active in the upper 150 mm of the soil. *M.parvus* is a wood-feeder and therefore occurs only where trees or shrubs are present. Like the other four Termitinae, this species was not found in cultivated plots. It builds spherical or ovoid nests of carton just under the surface, often near a tree-trunk or a dead stem. They were also found in association with *Cubitermes*. The species is only present in the lower parts of the area, the highest altitude recorded for a nest being 1630 m.

3.4 MACROTERMITINAE

3.4.1 General

The remaining species found in the study area all belong to the Macrotermitinae. The genera *Macrotermes, Pseudacanthotermes, Odontotermes* and *Microtermes* were identified. They all grow fungus in their nests on a substrate of masticated plant material. The first three genera build relatively compact nests consisting of a large number of fungus-chambers surrounding the queen's cell and nursery. The amount of metabolic heat is such, that ventilation shafts are needed to control the nest temperature. These shafts are either open to the outside air or run under a thin, porous wall.

A permanent system of underground tunnels radiates from the nest in all directions to the foraging areas. With some species, a large number of permanent foraging holes give access to the surface. Other species rarely forage on the surface. Litter, dead wood and grass, dung and decaying roots are cut into small fragments. Some species store these fragments in the nest or in special storage pits, others process them immediately. In all cases, the material is masticated and passes the alimentary canal. It is not turned into real faeces, however, but formed into pellets which are used to construct fungus combs. The fungus (usually a *Termitomyces*-species) breaks down the material and is in turn eaten by the termites. In this way a nitrogen-rich food is produced from nitrogen-poor sources.

3.4.2 Macrotermes

The genus *Macrotermes* is represented by only one species: *M.michaelseni* (Sjöstedt). Within Kisii District, only a few nests of this species were found, i.e. in the west and southwest near the border with South Nyanza District. In the latter district, the species is very common. It builds large, closed, irregularly dome-shaped mounds on a wide variety of soil-types and under different drai-

Fig.3.1.a. Nest of *Macrotermes michaelseni*.

Fig.3.1.b. Cross section through the same nest. a = royal chamber, b = nursery, c = chamber with funguscomb, d = ventilation tunnel

nage conditions. In poorly drained places, a mound can be over 2 m high with a diameter of up to 5 m. On well-drained soils, mounds are usually about 1-1.5 m high and roughly 2 m in diameter.

Fig. 3.1.b. shows a section through a *M.michaelseni* mound. The ventilation shafts do not open to the outside air, but run close beneath the outer casing of the mound, which allows exchange of gases. This species maintains foraging holes at the end of the underground tunnels, which are closed when not in use.

M.michaelseni mounds are abundant in South Nyanza District, but beyond

the border with Kisii District they disappear almost immediately. The soils at the two sides of the border are not different and also other natural factors do not change abruptly. The only apparent difference is that the two sides are occupied by different tribes. The Luo of South Nyanza usually leave large mounds intact in the farms, though new ones can only develop in uncultivated plots or plots which are left fallow for at least 5 years. In Kisii District, these mounds used to be more abundant, as we were told by old people, but when the farms became increasingly smaller, the mounds were removed. However, this explanation is not completely certain, since our informants were not always able to distinguish between *Macrotermes* and *Pseudacanthotermes*.

M.michaelseni collects mainly litter and dead grass from the surface, but also many types of dead wood, incl. wooden posts, wooden parts of houses and thatched roofs. They forage on the surface, often under cover of earthen runways or sheetings which protect them against desiccation and predators. Normally, crops are unaffected, but under dry conditions and when alternative food is scarce, crops like maize and cotton may be attacked. Young trees may be killed as well.

3.4.3 Pseudacanthotermes

The genus *Pseudacanthotermes* is also represented by one species: *P.spiniger* (Sjöstedt), which is very common in the western part of the area up to 1700 m. Fig. 3.2.b. shows a section through a typical nest. The actual nest or habitacle is subterranean. On top of it there is usually a conical ventilation mound, which contains only empty chambers and passages. In the cool climate of the Kisii hills the ventilation mound may reach a height of ca. 1 m. In the hot parts of South Nyanza District the mound may grow into a chimney-like structure of over 2 m high closed at the top. Nests are mainly found outside cultivated plots, because on farms, the conical mounds are regularly destroyed. Apparently, this species is not easily disturbed, because the mounds are rebuilt every time.

Material washed from the ventilation mound by rain, collects at its foot. After a number of years, the ground level around the mound is noticeably raised. If the same site is reinvaded several times by *P.spiniger*, the rise can result in a lenticular mound with one or more conical ventilation mounds on top. Often, *Odontotermes* species contribute as well to the rise in ground level through excavation of chambers and ventilation shafts. A large lenticular mound in which no previous *Odontotermes* activity could be determined, measured roughly 8 m across with a height of ± 75 cm. On its top, it carried two conical mounds both belonging to the same *P.spiniger* nest.

Mounds occur in a wide variety of habitats: well-drained and poorly drained, with deep and rather shallow soils, open and heavily shaded. Where the soil is poorly drained or too shallow, the nest is largely above surrounding ground level. At altitudes above 1400 m, nests were often found rather deep under the surface and often had small ventilation mounds. This is probably in response to lower environmental temperatures which could also be the explanation for the absence of the species above 1700 m.
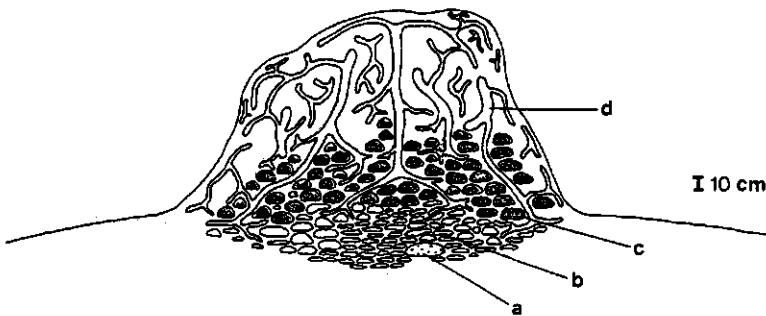
20

Fig.3.2.a. Conical mound of *Pseudacanthotermes spiniger*

Fig.3.2.b. Cross section through the same nest. a = royal chamber, b = chamber with funguscomb, c = ventilation tunnel, d = empty chamber

P.spiniger is a very efficient forager of all kinds of litter both at and below the surface. Only tea leaves were hardly taken. Crops that are in good condition, were never found to be attacked by this species, but sugar-cane and cassava cuttings which have not yet properly established themselves, are often attacked. The species does not seem to attack wooden structures. At times of high humidity, columns of workers and soldiers were often observed day and night. When it was dry, they constructed covered runways. These runways do not seem to be needed as protection against predators, the large number of small soldiers present in the foraging parties being able to handle them.

3.4.4 Odontotermes

Five *Odontotermes* species were identified: *O.amanicus* Sjöstedt, *O.kibarensis* (Fuller), *O.tanganicus* Sjöstedt, *O.nolaensis* Sjöstedt and *O.fulleri* (Emerson). These identifications must be considered tentative, however, pending a revision of the East-African species of this genus, which is taken care of by R.K.N.Bagine at the National Museums of Kenya in Nairobi.

All five species construct subterranean nests with ventilation shafts (fig. 3.3.). The shafts either open flush with the soil surface or at the top of low chimneys. The openings can be partly or completely closed, when the temperature drops too much. The number of openings depends on the size of the nest.

These species do not seem to maintain permanent foraging holes. In fact, none was regularly seen foraging at the soil surface. Only workers of *O.kibarensis* were sometimes seen foraging in grass at night after a rainy day. Covered runways were never observed, only soil sheetings covering dead grass, branches and other food items. Apparently, food is detected from below the soil surface, which could explain the fact that small bits of litter were not often attacked.

Fig.3.3 Cross section through nest of *Odontotermes fulleri* a = royal chamber, b = chamber with funguscomb, c = ventilation shaft, d = chimney, e = ventilation opening

Only after a long dry period, when the grass-shoots started dying, workers emerged and started covering the grass with sheetings before consuming it. Often, food items were entered from below and hollowed out from inside, whereby no sheetings were constructed.

O.fulleri is common in the western and southwestern parts of the area below ca. 1800 m. *O.nolaensis* was only found in the north up to ca. 1700 m. These two species can be distinguished by their size and the shape of the soldiers' heads. Other differences were not observed, although the nest components (chambers, tunnels etc.) of *O.nolaensis* seem to be larger. The ventilation shafts of these two species open at the top of low chimneys. In the study area, these were regularly destroyed by people and cattle, so that an average height could not be determined; the maximum height recorded was 41 cm. There is much variation in the diameter of the ventilation shafts. Deep in the nest they start narrow (ca. 5 cm) and upwards they join forming wider shafts. At ground level, they are between 10 and 30 cm in diam., but at the top of a chimney they are narrower.

The nests of these two species are relatively compact, and near the upper boundary of their area of distribution they are situated between 1 and 2 m below the surface. At lower altitudes, the nests are generally closer to the surface. In response to lower temperatures, these species apparently move deeper into the soil. In the hills of Kisii District, both species always occur in deep, well-drained soils. Nests were never observed in cultivated fields, but they are common in pasture. These two species are often associated with lenticular mounds like the ones described in chapter 3.4.3., which may measure up to 20 m in diameter and ca. 1.5 m in height. Often, *P.spiniger* is also present in these mounds, so it is not possible to say which species is the main builder. One mound dissected by us, appeared to be full of chambers of *O.fulleri* and *P.spiniger*, most with fungus combs. These observations support the theory of Darlington (1985) that lenticular mounds, which are found at many places in Kenya, are built by termites and not by fossorial rodents as proposed by Gakahu and Cox (1984).

In South Nyanza District, *O.fulleri* also occurs in poorly drained plains, where the species either constructs nests in mounds of *Macrotermes* or *P.spiniger*, or builds low mounds of its own. In the latter case, the chambers always start close to the surface.

O.fulleri and *O.nolaensis* consume all kinds of litter, dung and large pieces of wood, but were never seen attacking wooden structures or thatched roofs. Crops are hardly affected.

The remaining three *Odontotermes* species are more common in the higher parts of the area and nests can be found under both poorly and well-drained conditions, sometimes even in cultivated plots. *O.amanicus* and *O.kibarensis* were found throughout the study area, but *O.tanganicus* occurs only above 1800 m. They are all absent from shallow, rocky soils. Under poorly drained conditions, they build low mounds. Mounds of *O.kibarensis* can reach a height of >1.5 m and a diameter of 3-4 m, esp. at lower altitudes, but mounds of the other two species are smaller. These mounds are often overgrown with dense

Fig.3.4 Fungus comb of *Odontotermes tanganicus*

scrub and trees. The smaller mounds at higher altitudes usually have no ventilation openings.

The examined nests of *O.tanganicus* were quite compact and were surrounded by a ring of ventilation shafts of which some penetrated the mound. The openings were small (2-3 cm). The nests were not very deep, even in deep soils. The upper chambers were never found more than 20 cm below the surface. A full-grown fungus comb consisted of two separate layers, the whole structure being dome-shaped and oval, with a flat or slightly domed bottom and placed on short legs (fig. 3.4.).

Nests of *O.amanicus* and *O.kibarensis* are more loosely structured. Chambers are scattered through the soil, but more or less concentrated along ventilation shafts, which open flush with the soil surface. The shaft openings of *O.amanicus* are much wider (c. 10 cm) than those of the latter species (5-7 cm). The fungus-combs of *O.kibarensis* are of about the same size as those of *O.tanganicus*, though somewhat flatter. Seen from above, they have a more closed appearance (fig. 3.5.). Those of *O.amanicus* look like those of *O.tanganicus*, but have larger openings.

These three species consume a wide variety of dead plant material: wood and leaf litter, dung, bark of trees and also wooden structures and thatched roofs. *Odontotermes* species are often reported as pests (e.g. Wood et al., 1980), but no references have been found on the species described in this report. Damage to herbaceous and cereal crops appears to be serious only where these crops

Fig.3.5 Fungus comb of *Odontotermes kibarensis*

grow under suboptimal conditions. In the study area they are not attacked, but woody crops, e.g. coffee, are affected, when the termites strip the bark and cut thin branches in the process. They can also attack recently planted cuttings of sugar-cane and cassava, but where they occur together with *P.spiniger*, the latter species is a more serious pest in that respect.

3.4.5 Microtermes

Microtermes species are very common below 1900 m. In cultivated plots, they are by far the most common termites. The genus is represented by at least two species, one of which is very similar to *M.vadschaggae* (Sjöstedt). The other species could not be identified. In the samples it was often difficult to determine the species because of lack of the soldier caste, so in this report they will be treated together.

Microtermes species are strictly subterranean. A nest consists of a great number of chambers more or less randomly distributed through a large volume of soil. In the study area, chambers were found between 10 cm and 2 m below the surface, but > 80 % were between 10 and 50 cm. The area occupied by a single colony is not known for any *Microtermes* species. Bigger (1966) estimated the radius of a nest of *M.albopartitus* in Tanzania at 20 feet (area ca. 117 m^2) with 431 fungus combs. However, it is not clear how he arrived at this figure. Josens (1977), working in Ivory Coast, found an area of 240 m^2 and 560 fungus combs per nest of *M.toumodiensis*, which is certainly an overestimate of the area

and an underestimate of the number of fungus combs, since he dug only to 25 cm. In Nigeria, Johnson, according to Wood (1981), found two queens (unnamed) in 104 pits of 2×1 m^2 and 1 m deep, which gives an area of 104 m^2 per colony.

In our project, two queens were found in 255 pits of 0.5×0.5 m^2 and 0.5 m deep, which gives an area of about 32 m^2. In 2500 cores of 8 cm diam. and 40 cm deep (total area 12.57 m^2) no queen was found. Since estimates based on two queens are not very accurate, the following observation probably gives a better estimate. Five pits of 0.5 m deep were dug in a maize-field, four with a diameter of 10 m and one with a diameter of 8 m. In each of the first four pits, one queen was found and none in the last pit. This gives an area of 91 m^2 per colony. The numbers of funguscombs found in the pits were: 713, 634, 612, 581 and 416, which is 8.12/m^2 or 739/colony. The average dry weight of a funguscomb in the study area was ca. .5 g, so one colony would contain ca. 370 g d.w. of funguscombs. The population density of *Microtermes* in a nearby maize-field was estimated at 1469 workers and 115 soldiers per m^2. A colony would thus have about 134,000 workers and 10,000 soldiers.

Microtermes species do not construct covered runways nor do they have permanent foraging holes. Even a large part of their underground tunnels does not seem to be permanent, esp. not in the upper 20-30 cm. According to Wood and Johnson (1978) foraging takes place both at the surface, mainly on wood and occasionally on dead grass and leaf litter, and underground on roots. *Microtermes* species are reported as, often serious, crop pests (Agarwala & Sharma, 1954; Harris, 1961; Bigger, 1966; Wood et al., 1980), but only slight damage was observed in the study area. They were often observed in dry stalks of grain crops and dry stems of crops like beans and groundnuts. In the last crop the dry pods may be attacked as well. Young, vigorous crops were never seen attacked. Tunnelling in stalks can lead to lodging and subsequent attack by other termites, fungi, etc., but when such stalks are removed within a few days, loss of ears will be small. Damage to wooden structures does occur, but is negligible compared to damage by *Odontotermes* and *Macrotermes.*

4   EFFECTS OF TERMITES ON THE MICROSTRUCTURE OF SOILS.

4.1   INTRODUCTION

Many studies have been published which deal with the ability of termites to alter the physical and chemical composition of soil material, particularly through the construction of mounds (Lee and Wood, 1971). Some attention was also paid to the classification of micro-structures in termite mounds (Sleeman and Brewer, 1972), but relatively little is known of the effects that subterranean termites have on the structure and physical properties of the soil.

The fungus-growing Macrotermitinae are the dominant termites in the study area. They comprise the species *Pseudacanthotermes spiniger*, *Microtermes* and *Odontotermes spp.*; their taxonomy and geographical distribution was treated in Chapter 3. Humus-feeding termites (Termitinae, Apicotermitinae) occur abundantly in the Kisii area but seem to be less important for the reworking of soil material.

4.2   METHODS

Sampling sites were chosen in three agroclimatic zones with different termite populations. Differences in geology made it impossible to select identical soils in each zone and the examined soil profiles thus differ in more aspects than just biological activity. The sampling sites were all situated on flat or gently inclined upper slopes, and they were under traditional cultivation, so that differences due to topography and human activity were avoided. The major characteristics of the sites are given in Table 4.1.

Table 4.1. Locations and characteristics of sampling sites.

profile nr.	1	6	8
site	Wanjare	Kisii	Tombe
soil classification			
USDA Soil Taxonomy	Haplohumox	Paleudoll	Palehumult
FAO/Unesco	Humic Ferralsol	Luvic Phaeozem	Luvic Phaeozem
termite species*	P + M + O	O + M	O
agroclimatic zone	13	14	15
altitude (m)	1530	1700	2025
rainfall (mm)*	1700–1800	1800–1900	2000–2100
temperature (°C)*			
maximum	26.4	25.4	23.4
minimum	14.0	12.8	10.5

* P = *Pseudacanthotermes spiniger*, M = *Microtermes*, O = *Odontotermes spp.*
* annual average
(Climatic data from Wielemaker and Boxem, 1982)

On each site, one soil profile was studied and sampled for micromorphological examinations. Eight large (10 × 15 cm) and five small (5 × 5 cm) thin sections were prepared from undisturbed soil samples, using standard procedures. The soil fabric was described according to Brewer (1964). A point counting method was applied to estimate the area fractions of biologically reworked material on the thin sections (magnification of 125).

Two core samples (100 cc) were taken at intervals of 10 cm in each profile for physical analyses. Field descriptions of soil profiles and analytical data are given in Appendix 1, the analytical methods in Appendix 2. Soil classification is according to FAO/Unesco (1974) and USDA Soil Taxonomy (Soil Survey Staff, 1975).

4.3 RESULTS

4.3.1 Morphology of termite structures

Field observations suggest that the workers of the different genera have a more or less similar building behaviour. Rounded pellets, generally smaller than 1 mm, are carried in the mandibles through cavities and foraging tunnels and are carefully set together in a distinct pattern. A drop of saliva is usually added as a cement to increase the stability of the structure. Humivorous termites also use oral pellets as building material but they stabilize their structures with faecal droppings that are produced and slightly modelled at the building site. Micromorphological examination pointed out that the size and structural arrangement of channels and associated fill is characteristic for each species.

The foraging tunnels of *Microtermes* are the most abundant in the Kisii soils; they measure 0.8-1.2 mm and follow a seemingly random course through the soil profile. Tunnels were generally observed down to depths of several meters. Because of their uniform size and the presence of slightly compacted walls, these tunnels could easily be identified in the field and in thin sections (Fig. 4.1). Most channels contained single, oral pellets of 20-50 µm, composed of dark brown or reddish brown material, with the same colour as the surrounding soil. Backfilled termite channels were classified as matric ortho-aggrotubules (Brewer, 1964).

The channels of *P.spiniger* resemble those of *Microtermes*, but are somewhat larger, associated with the bigger size of the workers. The channels measure 1.2-1.6 mm in diameter and contain single oral pellets with a diameter of 80-120 µm (Fig. 4.2). They occur throughout the entire soil profile, and even extend into the regolith. As with *Microtermes*, the channel walls are compacted and they seem to be plastered with clay. The dark brown to dark reddish brown, isotropic pellets consist of mineral and organic soil material, but do not seem to contain faecal material. The colour of the pellets is about the same as that of the surrounding soil, but some dark coloured pellets, observed in deeper soil horizons, witness transport by termites. Pellets are first arranged into arches (Fig. 4.3) cemented with saliva. These arches seem not very stable as they were

Fig.4.1 Cross-section through channel of *Microtermes*

only observed in 'fresh' channels. Where *P.spiniger* is active, the soil matrix was sometimes entirely composed of pellets, so that individual aggrotubules could no longer be identified.

Channels of *Odontotermes* spp. are least abundant and show a considerable range in diameter from 2-5 mm (foraging tunnels) to over 20 cm (ventilation shafts). Foraging tunnels were recognized in only a few thin sections. As with *P.spiniger*, the channel walls are compacted and slightly plastered. Single oral pellets measure 100-500 μm in diameter, depending on species, but due to their limited occurrence they could not always be identified beyond doubt.

Backfilled tunnels of humus-feeding termites (Fig. 4.4) were mainly observed in thin sections from humic topsoils. They are 2-5 mm wide and composed of laminae (40-80 μm thick) of welded pellets, with a semi-elliptical arrangement (striotubules: Brewer, 1964). The tunnel fill is composed of soil plasma and skele-

Fig.4.2 Cross-section through channel of *Pseudocanthotermes spiniger*

Fig.4.3 Oral pellets of *Pseudacanthotermes spiniger*

Fig.4.4 Backfilled channel of humivorous termite; approximate contour indicated by drawn line

ton grains, mixed with excrements. The general appearance of excrements of humivorous termites is very much like normal soil (Lee and Wood, 1971), so that the presence of such burrows can often only be inferred from the typical isolated openings (mamillated vughs) between the laminae. A lenticular fabric was found in backfilled tunnels of Apicotermitinae. This fabric is composed of lens-shaped nodules with differences in color and composition. Dark coloured parts seem to consist of soil plasma and excreta, and the lighter parts mainly of skeleton grains. Similar structures were reported from nests of *Microcerotermes* (Sleeman and Brewer, 1972).

4.3.2   *Microstructure of selected profiles*

Table 4.2. shows the area fractions of biologically reworked soil and termite

Table 4.2. Area fractions of termite-made pellets and tunnels in thin sections from selected profiles.

Profile	Depth	single pellets	welded pellets	total	tunnels
1	5– 20	0.16	0.06	0.22	0.03
	40– 45	0.17	0.06	0.23	0.07
	90– 95	0.33	0.02	0.35	0.02
	130–135	0.15	0	0.15	0.05
6	5– 10	0.04	0.08	0.12	0.02
	20– 25	0.04	0.06	0.10	0.02
	40– 45	0.04	0.04	0.08	0.05
	80– 95	0.03	0.03	0.06	0.03
	140–145	0.02	0.01	0.03	0.04
8	15– 30	0.04	0.14	0.18	0.07
	50– 65	0	0.03	0.03	0.06
	90–105	0	0.03	0.03	0.06
	140–145	0	0.03	0.03	0.06

made tunnels in each soil profile. A distinction was made between single (oral) pellets and welded (faecal) pellets. Single pellets occur as loose backfill material in termite tunnels and as matrix material in the topsoil. Deeper in the soil, the pellets occur in compacted clusters, but generally still with recognizeable outlines. Welded pellets, produced by humivorous termites, occur particularly in humic topsoils.

Profile 1 is dominated by the pellets of *Microtermes* and *P.spiniger*. Biological activity is so high, that many termite channels and associated fill are disrupted, leaving parts of the compacted tunnel walls behind in the soil matrix. Plasmic fabric is isotic to undulic due to organic matter and coatings of sesquioxides. Ferri-argillans occur in termite-made channels penetrating the regolith at depths of 2 m or more. Most of the soil pores are compound packing voids: they form a continuous porous phase between the loosely packed termite pellets. Termite-made channels are found throughout the soil. Most of them are made by *Microtermes* and *P.spiniger*. Planes and other physicogenic voids are absent except for some curved micro-fissures that occur in the compacted walls of former termite channels. In the deeper horizons, where the pellets are more closely packed, they are separated by mamillated vughs. The stability of the pellets seems to be quite high, as there are no signs of dispersion.

Profile 6 also contains termite-made structures, but the proportion of biologically reworked material is clearly lower than in profile 1. The area fraction of single pellets is generally below 0.05, which is attributed to the absence of *P.spiniger* in this area. Welded pellets are however more numerous than in profile 1. Most pellets seem to have a lower stability than those from profile 1. They show signs of dispersion and many have merged together. Particularly in the subsoil, the soil fabric is dominated by physicogenic peds. The soils in this basalt area are characterised by a moderate, fine, subangular to angular blocky struc-

ture with shiny ped faces. This structure is associated with a high clay content (> 60 %) and the presence of expanding-lattice clay minerals. A weakly developed lattisepic fabric in the B horizon, appearing as a reticulate pattern of birefringent streaks, confirms the occurrence of moderate swelling of the soil. A similar fabric was observed in compacted pellet structures, suggesting that compression is also responsible for the degradation of pellets. Termite-made channels, most of them made by *Microtermes*, are found at all depths. Ferri-argillans occur at a depth of about 150 cm. They are mainly associated with channels and tubules. Papules (pieces of oriented clay) were found throughout the profile: those in the B horizon might be attributed to swelling and shrinkage, but the papules in the topsoil are small enough (20-40 μm) to have been transported by termites.

Thin sections from profile 8 also have low amounts of termite made-pellets. Most of them are welded faecal pellets, made by Apicotermitinae. Although *Odontotermes* occurs in the Tombe area, its activity is only modest. Part of the soil fabric is composed of compacted pellet structures, which resemble those of profile 6. The pellets are subject to degradation (compression, dispersion) and they have partly merged together. Termite-made channels are found throughout the soil profile. Because of its high humus content, the topsoil has an undulic plasmic fabric. The soil fabric gradually becomes lattisepic at a depth of about 70 cm, which corresponds with the presence of shiny, blocky peds observed in the field. Ferri-argillans occur in channels and pedotubules, at depths between 100-150 cm. The uniform distribution of papules and skeleton grains (volcanic minerals) suggests biological homogenization of the soil.

4.3.3 Physical soil properties

Results of physical soil analyses, averaged for topsoil (0-50 cm) and subsoil (60-110 cm) are given in Table 4.3. Three classes of equivalent pore sizes were distinguished, viz. 2.8-0.5 mm, 0.5-0.2 mm and < 0.2 mm (capillary pores); they drain at matrix suctions corresponding with pF 0, pF 0.75 and pF 1.15, respectively.

Total pore space increases gradually with increasing altitude, particularly in the topsoil. This is largely due to the increasing volume of capillary pores, and attributed to the increase in organic matter content of the soil. In profile 1, noncapillary porosity increases in the subsoil, but in profile 6 and 8 it decreases. This is caused by essential differences in the structure of the B-horizon. The oxic B horizon of profile 1 has a weak, fine subangular blocky structure, while the soils at higher altitudes feature well developed argillic horizons with expanding lattice clays and angular blocky peds. These structural differences make it very difficult to assess the influence of termite activity on pore size distribution. A comparison of profile 6 and 8 suggests that decreasing termite activity results in a reduction of non-capillary porosity.

Differences in hydraulic conductivity seem to be connected with soil structure, pore size distribution and humus content. No evidence is found for a lower conductivity due to decreasing termite activity.

Table 4.3. Porosity, hydraulic conductivity and organic carbon content of soils on sampling sites.

Profile nr.	1	6	8
Location	Wanjare	Kisii	Tombe
Altitude (m)	1530	1700	2025
Topsoil (0–50 cm)			
total pore space (vol. %)	52.9	60.7	63.6
pores <0.2 mm	47.0	47.0	51.7
pores 0.2–0.5 mm	1.2	3.0	2.3
pores 0.5–2.8 mm	4.7	10.7	9.6
Ksat (cm/day)	67	377	130
% C	2.1	2.3	3.7
Subsoil (60–110)			
total pore space (vol. %)	59.6	56.4	60.7
pores <0.2 mm	46.7	46.8	51.5
pores 0.2–0.5 mm	0.6	1.4	1.1
pores 0.5–2.8 mm	12.3	8.2	8.1
Ksat (cm/day)	192	158	192
% C	0.8	0.9	1.4

So, in spite of the decreasing importance of termite activity towards higher altitudes, there is no substantial evidence to suggest that this results in less desirable soil properties. The potential effects of burrowing termites on the soil are obliterated by the presence of deep humic topsoils at higher elevations.

4.4 CONCLUSIONS

1. The burrowing of termites results in the formation of a soil structure composed of oral and faecal pellets, whereby each species produces a more or less characteristic gallery fill.
2. The most active termite species in the Kisii area are *P.spiniger* and *Microtermes* spp. Their gradual disappearance towards higher altitudes, associated with lower soil temperatures, is one of the reasons for the decrease of single pellets in the soil. Because of the increasing importance of Apicotermitinae at higher elevations, associated with the presence of deep humic topsoils, the amount of welded, faecal pellets increases simultaneously.
3. Loosely arranged single pellets occur as backfill material in termite tunnels, and as matrix material in the top-soil. They are composed of mineral and organic soil material. Micromorphological evidence for active enrichment with excreta was only found in the burrows of humus-feeding termites. A loose pellet structure is maintained by the continuous burrowing of termites, especially in the topsoil. Deeper in the soil profile, the pellets occur in a more densely packed, but still very porous matrix. Here, the formation of pellets takes place at a slower rate, and the pellets are subject to degradation.
4. Termite-made tunnels occur in all soils. The relatively low numbers recorded

in soils at Wanjare are attributed to the intense and continuous burrowing of termites which disrupts abandoned tunnels.

5. The decay of pellet structures is mainly affected by the stability of the soil material. Moderate swelling and dispersion of the clay in profiles 6 and 8 control the stability of the pellets. The prominence of pellet structures thus depends on the balance between the rate of formation and the intensity of degradation processes. The most stable and well developed pellet structures were observed in the Wanjare area, where the combination of high termite activity (*P.spiniger*) and very stable soil material (red, clayey Haplohumox) is present. Subterranean termites are generally absent from areas with strongly swelling and unstable clays (Lee and Wood, 1971). The moderately swelling clay of the Nitosols in the study area probably represents an intermediate situation, where termites are able to construct and rearrange pellets, but where the pellets are subject to degradation. The balance between the formation and decay of pellet structures might be delicate in these soils, and affected by human activities.

6. The existence of compacted pellet structures in the Tombe area does not agree with the low present-day activity of termites. It is possible however, that termites (particularly *Odontotermes* spp.) were more numerous in the past and disappeared from this area after it was brought under cultivation in the 1940's (Uchendu and Anthony, 1975). This would also explain the uniform distribution of papules and volcanic ash minerals in the soil.

7. There is no straightforward relationship between the decrease in termite activity towards areas of higher altitude and variations of physical soil properties. This is attributed to the increasing importance of humic topsoils, associated with lower soil temperatures, and to differences in type of soil structure.

5 FIELD EXPERIMENT

5.1 EXPERIMENTAL PLOTS

To study the interaction between soil tillage, termite activity and soil characteristics, a number of experimental plots was prepared at the Nyanza Agricultural Research Station (NARS), about 2 km from Kisii Town at an altitude of between 1700 and 1740 m. For many years, these fields had been used for growing maize during the 'long rains' and beans during the 'short rains'. At the beginning of each growing season, the fields had been ploughed to a depth of 0.3-0.4 m and subsequently harrowed.

The experiment was started in January 1984. Each plot was subjected to one of three treatments: ploughing, hoeing or compaction of the soil. Soil compaction was achieved by repeatedly driving a tractor over the plot during wet weather. Additional treatments were given to some plots. Half of each 'hoe plot' was sprayed with aldrin to stop termite activity (0.5 % watery suspension at the rate of 0.25 l/m²). At the beginning of each growing season, half of each 'compaction plot' was covered with a mulch of maize stalks and dry grass to enhance termite activity.

All plots were planted with maize during the 'long rains'. During the 'short rains' soya-beans were planted except on the compaction plots. After two seasons under maize, the compaction plots did not support a reasonable crop anymore, so they were left fallow after that. All plots were weeded with hoes twice during each growing season. On the compaction plots, weeds were not dug out, but since the soil had to remain compacted, they were scraped off with sharpened hoes, which did not disturb more than the upper 5 cm of the soil. Harvesting was done by hand on all plots. During the experiment, no pesticides were used apart from those mentioned.

5.2 SAMPLING AND ANALYSIS TECHNIQUES

5.2.1 Termite populations
There has been much debate over the question of how to sample termites, esp. subterranean species (e.g. Lee and Wood, 1971; Sands, 1972a). However, the best technique for sampling all kinds of termites still has to be devised. Probably a combination of techniques is the best. In our project we initially decided to use pit sampling. We expected that both *Microtermes* spp. and humivorous termites could be sampled satisfactorily in this way. Other species would either be overestimated or underestimated depending on whether they happened to be foraging or not at the time of the sampling.

So in the autumn of 1983, before the experiment was started, 20 sampling pits of 0.5×0.5 m² and 0.5 m deep were excavated at random on each of the

nine experimental plots. Termites were collected from the pits by breaking up the soil clods over a paper bag. Funguscombs were collected as well. In the laboratory, the termites were separated from the earth by hand. Each sample was counted and identified as to species and caste composition. Funguscombs were dried in an oven at 105°C for 24 h and weighed.

The final sampling of the termite populations, which started in mid-April 1985, was not carried out in sampling pits, because that had proved to be too time-consuming and the proportion of termites missed too large. Instead, a specially developed auger (Fig. 5.1.) was used. From each plot 100 soil cores of 0.4 m deep were taken at random. The cores were immediately broken up and termites collected by hand. Funguscombs were counted fully even when only parts of them were recovered from the cores. For that reason, in calculating densities of funguscombs, the effective radius of the auger was assumed to be the actual radius plus the average radius of a funguscomb (40 + 12.5 mm). In Chapter 6 the results of auger sampling are compared with pit sampling.

5.2.2 Soil characteristics

Bulk density, porosity and soil moisture retention (pF) were determined on soil core samples (100 cm³) taken from depths of 5 and 50 cm in sampling pits. Soil moisture retention was determined gravimetrically after equilibration of the soil core samples at pF values between 0 (saturation) and 2 on a sandbox (Stakman et al., 1969). The results were converted to volume % pore space, using equivalent pore diameters (EPD), in the relation:

$$d = \frac{2.8}{a}$$

Fig.5.1 Auger used in sampling termites

In this formula d is the equivalent pore diameter (in mm) of a cylindrical pore with the same capillary tension (a, in mbar) as the actual, irregularly shaped pore. Particularly for clayey soils, this conversion is not entirely correct because many pores have a composite pore morphology (e.g. necks), but it enables a rapid, indicative comparison of a large number of samples. Three classes of EPD were distinguished, viz. 2.8-0.5 mm, 0.5-0.2 mm and <0.2 mm.

Some other physical soil characteristics, such as aggregate stability (raindrop tests, dry and wet sieving), aggregate size distribution and penetration resistance, were also studied, but when the preliminary results were discouraging, further tests were cancelled.

Immediately after the preparation for the first growing season, another set of soil cores was taken from each plot and analysed. A last set was taken during the final sampling, on which occasion core samples were taken from depths of 5, 20 and 50 cm. Bulk density, porosity and soil moisture retention were determined as before. Additionally, unsaturated hydraulic conductivity was determined using a laboratory stand with which the flow rate could be registered at various suctions (Appendix 2).

5.2.3 Biopores

During the final sampling of the experimental plots, the number and size of tubular soil pores (biopores) was estimated for each sampling pit at depth intervals of 10 cm. Because of the smeary character of the soil, the pores could not be studied in situ. Therefore, a fresh surface was obtained by carefully pressing a soil tin (5 × 5 cm) into the wall of the pit at the desired depths. The estimation of soil pores was thus done on a vertical surface of 0.25 dm^2, with the use of a simple 10x hand lense and metal wire gauges with various diameters. Pore sizes were grouped in three classes, viz. fine (0.5-0.9 mm), medium (1.0-1.5) and large (1.6-3.0 mm). The number, size and morphology of termite tunnels were also recorded. In most cases, termite tunnels could easily be distinguished from other biopores because of their specific shape.

5.3 RESULTS AND DISCUSSION

5.3.1 Termite populations

Table 5.1. presents the population densities of the various termite species before and after the experiment. Unfortunately, a hoe plot and a compacted plot were lost, because they were accidentally ploughed before the final sampling had taken place.

When the sampling was in process, the weather became extremely wet. The plots sampled during the wet period yielded very few termites. From other observations, we had also got the impression that heavy rain reduces termite activity. Therefore, the plots concerned were sampled again during drier weather. The results (Table 5.2.) confirmed our impression. The dry-weather figures were used in Table 5.1. There was not enough time to sample all three plough plots, so

Table 5.1. Average population densities of adult termites in the experimental plots at the NARS ($m^{-2} \pm$ s.e.).

		Plough plots	Hoe plots		Compaction plots	
			no aldrin	aldrin	no mulch	mulch
Microtermes	initial	101 ± 31	129 ± 44	103 ± 7	119 ± 113	114 ± 37
(termites)	final	71 ± 13	148 ± 55	0	169 ± 22	131 ± 12
Microtermes	initial	6.4 ± 1.8	3.5 ± 0.9	3.7 ± 2.0	3.2 ± 2.0	7.0 ± 3.4
(fungus)	final	2.9 ± 1.7	5.2 ± 1.7	0	3.5 ± 1.2	1.2 ± 1.2
Apicoter-	initial	115 ± 103	85 ± 73	40 ± 21	62 ± 62	17 ± 17
mitinae	final	0	0	0	72 ± 72	0
Odontotermes	initial	16 ± 7	16 ± 0	7 ± 6	7 ± 7	323 ± 318
kibarensis	final	1 ± 1	0	0	26 ± 26	237 ± 99

Table 5.2. Comparison of sampling results during very wet weather and during relatively dry weather on three fields at the NARS ($m^{-2} \pm$ s.e.).

Plot	Weather	Microtermes	Apicotermitinae	O. kibarensis
hoe	wet	0	0	0
(no aldrin)	dry	93 ± 60	0	0
hoe	wet	44 ± 34	0	0
(aldrin)	dry	0	0	0
plough	wet	24 ± 24	0	2 ± 2
	dry	84 ± 42	86 ± 55	139 ± 81

one was left out. This means that the figures obtained before the experiment are each based on three plots and those obtained after the experiment on two plots.

The *Microtermes* spp. were only affected by the aldrin treatment. Both aldrin plots yielded no termites when sampled during the relatively dry period. One of these was also sampled during very wet weather and then two cores contained termites at depths of 30-40 cm. On other occasions, termites were found in the aldrin plots too but always deeper than 30 cm. Apparently, the aldrin was only or mainly active in the upper part of the soil. The average weight of a *Microtermes* funguscomb was found to be ca. 0.5 g with a range of 0.1 to 3.4 g.

Before the experiment, all plots but two yielded Apicotermitinae. However, in most plots more of these termites were found towards the edges of the fields. Since the auger, used in sampling after the experiment, sampled a smaller surface area, it may just have missed the few concentrations of Apicotermitinae present, so that after the experiment very few were found. Statistical analysis of the samples showed that the populations of these termites were more aggregated than those of *Microtermes*. The sample data of all species could be fitted to negative binomial distributions with various values for the dispersion parameter k. For the Apicotermitinae, k was smaller than for the *Microtermes* species.

It was expected that *Odontotermes kibarensis* would be attracted by mulch. However, the estimate of the average population density in the compaction plots with mulch did not increase. This may be explained by the fact that one of the samples taken before the experiment contained an extremely large number of *O.kibarensis*. The compaction plots without mulch contained few *O.kibarensis* both before and after the experiment, while one of the mulched plots showed an increase from $5 \pm 1/m^2$ to $306 \pm 234/m^2$ and the other one contained many termites of this species both before (641 ± 404) and after (167 ± 167) the experiment. Moreover, during our visits to the plots we noticed, that *O.kibarensis* was more active on the mulched plots than on the other plots. All taken together, it seems that this species is attracted by large amounts of litter. Apparently, the compactness of the soil does not influence its activity.

5.3.2 Soil characteristics

A correct interpretation of the soil analytical data from the experimental plots is difficult to make, as cultivation itself has a strong effect on physical soil properties which may mask or counteract the influence of the soil fauna. After tillage, the larger clods accumulate at the surface, which results in a decrease of the smaller size aggregates (Fig. 5.2.). Upon further cultivation (harrowing), or after rainfall, the fresh clods break down into smaller aggregates. These events have important consequences for soil porosity and permeability. Therefore, differences between experimental plots should not be regarded as entirely caused by differences in the activity of the soil fauna.

Fig.5.2 Aggregate size distribution (cumulative) of surface samples from experimental plots at the NARS

Table 5.3. Average porosity (vol %) and standard error of soil samples from experimental plots at the NARS.

Depth (cm)		PLOUGH plots	HOE plots		COMPACTION plots	
			no aldrin	aldrin	no mulch	mulch
5–10	before	55.0 ± 0.5*			54.0 ± 0.9	54.2 ± 0.6
	after	59.6 ± 0.7*	57.4 ± 0.7*	58.4 ± 0.4*	53.0 ± 0.7	54.3 ± 0.8
	final	56.9 ± 0.5*	58.3 ± 0.4	59.8 ± 0.5	53.2 ± 0.6	53.1 ± 0.5
20–25	final	55.4 ± 0.4*	53.3 ± 0.7	56.5 ± 0.5	52.2 ± 0.6	50.7 ± 0.7
50–55	before	51.2 ± 0.6*			56.8 ± 1.2	57.1 ± 1.3
	after	54.7 ± 0.6*	54.5 ± 0.4*	56.1 ± 0.6*	54.0 ± 0.6	57.1 ± 1.0
	final	55.8 ± 0.4*	52.8 ± 0.7	56.9 ± 0.4	55.9 ± 0.6	53.9 ± 0.7

N = 20, except*: N = 40.
before = before first treatment
after = after first treatment
final = after completion of the experiments.

Porosity

Because of their favourable structure, the soils have a rather high average total porosity, even in the upper B horizon (50-55 cm). On the experimental plots, even compaction by tractor wheels did not have a significant effect on total soil porosity.

When several pore size classes are distinguished, however, the effect of com-

Fig.5.3 Moisture characteristic of soils at the NARS

paction by tractor wheels becomes noticeable (Table 5.4). The distribution of equivalent pore size classes is also shown in a graph (Fig. 5.4.). Pores wider than 200 μm decreased in number shortly after compaction and the smaller pores increased. Stimulation of termite activity on the mulched parts did not seem to have any positive effect on the total porosity of the soil (Table 5.3). The main reason is that the larger voids, such as biopores, contribute very little to total porosity (Table 5.4). This is confirmed by the moisture retention curves of the examined soils (Fig. 5.3.; after Wielemaker and Boxem, 1982). It appears that much soil water is bound between clay particles (adhesion), and only a small portion of all moisture is retained in capillary voids. Most of the soil water is therefore released at a tension above pF 3, which corresponds with an EPD (equivalent pore diameter) of 2.8 μm. Pores smaller than 10 μm account for about 85 % of the total pore volume. The high micro porosity of the soils is caused by a high clay content, a high organic matter content and the presence of sesquioxides coating the clay particles.

Table 5.4. Average porosity, in equivalent pore size classes (vol%), and standard error of soil samples from experimental plots at the NARS.

EPD (mm)	Depth (cm)		PLOUGH plots	HOE plots		COMPACTION plots	
				no aldrin	aldrin	no mulch	mulch
2.8–0.5	5–10	before				1.9 ± 0.5*	0.9 ± 0.1*
		after	3.5 ± 0.6	2.0 ± 0.4	3.6 ± 0.4	0.7 ± 0.2*	0.9 ± 0.1*
		final	1.2 ± 0.1*	1.2 ± 0.1	1.4 ± 0.2	1.3 ± 0.1	1.3 ± 0.1
	20–25	final	1.0 ± 0.1*	0.9 ± 0.1	1.1 ± 0.1	1.2 ± 0.2	1.3 ± 0.2
	50–55	before				1.5 ± 0.3*	1.4 ± 0.3*
		after	1.8 ± 0.2	2.1 ± 0.3	2.3 ± 0.2		
		final	1.2 ± 0.1*	1.1 ± 0.1	0.8 ± 0.1	1.4 ± 0.3	1.3 ± 0.1
0.5–0.2	5–10	before				1.5 ± 0.2*	1.1 ± 0.2*
		after	1.5 ± 0.2	1.0 ± 0.2	1.4 ± 0.2	0.4 ± 0.1*	0.4 ± 0.1*
		final	2.8 ± 0.3*	2.6 ± 0.4	3.7 ± 0.5	1.0 ± 0.1	1.3 ± 0.1
	20–25	final	1.3 ± 0.1*	1.3 ± 0.1	1.2 ± 0.1	0.8 ± 0.1	1.4 ± 0.2
	50–55	before				1.2 ± 0.2*	1.2 ± 0.2*
		after	1.1 ± 0.1	1.0 ± 0.1	1.1 ± 0.2		
		final	1.8 ± 0.2*	1.1 ± 0.1	1.4 ± 0.1	1.2 ± 0.2	2.0 ± 0.2
<0.2	5–10	before				42.5 ± 1.6*	40.2 ± 0.6*
		after	43.4 ± 1.5	38.9 ± 1.7	41.5 ± 1.3	46.8 ± 1.2*	48.1 ± 1.0*
		final	46.9 ± 0.5*	46.3 ± 1.1	49.1 ± 0.6	42.1 ± 1.3	37.3 ± 0.8
	20–25	final	47.4 ± 0.6*	43.9 ± 1.4	49.5 ± 0.5	43.1 ± 1.3	36.7 ± 0.9
	50–55	before				42.4 ± 1.3*	41.3 ± 1.2*
		after	42.8 ± 1.5	36.4 ± 0.8	42.3 ± 1.4		
		final	46.0 ± 0.6*	41.3 ± 1.3	48.4 ± 0.7	43.5 ± 1.2	36.3 ± 0.7

N = 20, except *: N = 10; ★: N = 40
before = before first treatment
after = after first treatment
final = after completion of the experiments

At the end of the experimental period the pore size distribution has recovered. Nevertheless, on the mulched parts, the volume of intermediate pores (200-500 µm) seems slightly higher and the volume of smallest pores (< 200 µm) slightly lower in comparison with the bare parts. This can be explained by assuming that biopores collapse when the soil fauna is suppressed. Under such conditions, the number of large soil pores decreases in favour of the smaller size classes. Increased biological activity will have a reverse effect. The renewal of pore systems by termites, and the associated repacking of soil particles will result in less micropores and a higher number of macropores.

The initial effect of ploughing is an increase in total soil porosity which is lost again in the course of time (Table 5.3). Ploughing produces large clods at the soil surface, which increases the abundance of large inter-aggregate pores. Later, the clods break down under the impact of rain and the larger pores become clogged. As a result, the total volume of pores smaller than 500 µm increases again (Table 5.4).

Changes in soil porosity in the hoe plots show basically the same trends as in the plough plots. The average total porosity remained fairly stable from the start to the end of the experiments, but the proportions of large and finer pores varied. The volume of pores >0.5 mm was relatively large immediately after cultivation, but it decreased in the course of time.

Fig.5.4 Equivalent pore size distribution in soil samples from experimental plots at the NARS from depths of 5, 20 and 50 cm.
I = before the experiment, II = after the experiment
a = plough plot, b = hoe plot, c = hoe plot with aldrin, d = compaction plot, e = compaction plot with mulch

The application of aldrin on the hoe plots strongly reduced the activity of termites in the topsoil (Section 5.3.1.), but this hardly affected the volume of large soil pores (Table 5.4). Contrary to expectations, we even recorded slightly higher total porosities on the aldrin-treated than on the untreated plots. Part of the differences is explained by the higher initial values measured on the aldrin-treated plots. For a better impression of soil porosity, however, the various pore size classes have to be considered. A comparison of initial and final porosities of the hoe plots indicates both a stronger decrease of large pores (> 500 µm) as well as a stronger increase in smaller pores in aldrin-treated parts. As on the compaction plots, the volume of smaller pores tends to increase under conditions unfavourable to termite activity. This adds some weight to our suggestion that this may be caused by the collapse of biopores. Unfortunately, physical measurements do not discriminate between termite-made tunnels and other large soil pores.

Hydraulic conductivity
The hydraulic conductivity of a pore increases exponentially with increasing pore size. Soil water permeability is therefore determined by the abundance of large, continuous soil pores. When a saturated soil becomes unsaturated, the largest pores are emptied first and no longer contribute to water-flow. Hydraulic conductivity thus decreases rapidly with increasing soil moisture tension ($=$ lower moisture content). An increase in the number of termite made tunnels (> 1 mm wide) should thus be reflected by a clearly higher saturated hydraulic conductivity.
The average hydraulic conductivity (cm/day) of soil core samples from the

Table 5.5. Average hydraulic conductivity (cm/day) at low moisture tensions (pF) and standard error of soil samples from experimental plots at the NARS.

pF	Depth (cm)	PLOUGH plots (N = 15)	HOE plots		COMPACTION plots	
			no aldrin (N = 10)	aldrin (N = 6)	no mulch (N = 15)	mulch (N = 15)
0	5–10	34.2 ± 3.1	26.2 ± 2.6	52.8 ± 3.0	23.5 ± 5.4	10.9 ± 1.2
	20–25	33.9 ± 2.3	33.4 ± 2.4	48.0 ± 2.4	22.5 ± 5.3	11.5 ± 1.4
	50–55	36.0 ± 3.6	29.5 ± 2.9	50.4 ± 5.6	22.7 ± 4.6	8.8 ± 1.3
0.7	5–10	23.4 ± 2.6	15.1 ± 2.5	37.2 ± 2.9	16.1 ± 3.7	5.6 ± 0.6
	20–25	24.2 ± 1.9	24.9 ± 2.2	33.6 ± 2.4	11.7 ± 2.8	7.3 ± 1.0
	50–55	25.4 ± 3.4	20.2 ± 2.8	38.9 ± 4.9	11.2 ± 1.9	5.9 ± 0.6
1.0	5–10	17.6 ± 2.0	11.1 ± 2.0	26.4 ± 2.4	8.5 ± 2.1	4.2 ± 0.7
	20–25	15.4 ± 2.0	16.4 ± 2.2	21.6 ± 3.2	8.0 ± 1.8	5.4 ± 1.0
	50–55	17.1 ± 2.7	12.6 ± 1.9	27.4 ± 3.5	7.3 ± 1.2	3.4 ± 0.5
1.2	5–10	9.9 ± 1.6	6.2 ± 1.0	18.0 ± 2.5	4.3 ± 1.0	2.2 ± 0.3
	20–25	8.8 ± 1.1	9.8 ± 1.4	13.2 ± 2.2	4.4 ± 1.1	3.7 ± 0.6
	50–55	10.0 ± 1.8	7.1 ± 1.4	14.4 ± 2.3	3.6 ± 0.6	2.4 ± 0.5

Fig.5.5 Average hydraulic conductivity of topsoil samples (0-5 cm) from experimental fields at various moisture tensions.

experimental plots at various soil moisture tensions is given in Table 5.5. Hydraulic conductivity was only determined at the end of the experiment period. As the variations in the upper 50 cm all show the same trend, only the results of the samples from 0-5 cm are shown in a graph (Fig. 5.5.).

All studied soils had a high hydraulic conductivity. Rather low values were recorded in the compaction plots, which is obviously caused by the decrease of large pores after artificial compaction. Hydraulic conductivity was about twice as high in the bare parts as in the mulched parts. In the cultivated plots the highest values were recorded in aldrin treated parts, followed by the ploughed plots and finally the hoe plots. These measurements correspond with the observed differences in microporosity and suggest that termite activity adversely affects hydraulic conductivity of the soil. To explain this, we regard the conductivity in relation with moisture content.

At low matric suctions, a linear relationship exists between soil moisture tension, expressed on a logarithmic pF-scale, and hydraulic conductivity (Fig 5.5.). As argued before, permeability depends mainly on the larger pore size classes,

but it appears that low values for hydraulic conductivity (< 10 cm/day) are only reached around pF 1.2 (15 mbar). This figure corresponds with an EPD of about 200 µm, which suggests that there are sufficient pores in the range 200-500 µm to conduct water downwards. Probably, the larger pores such as termite tunnels normally remain air-filled after rainfall and thus do not contribute to water flow.

To study the practical importance of termite tunnels for moisture transport, a number of infiltration tests were done with methylene blue as a tracer. This dye has strong adhesive properties, and stains the walls of soil pores and other flow paths until the dyed water is absorbed into dry, fine porous peds (Bouma and Dekker, 1978). This method is particularly useful to detect 'short-circuiting' phenomena in soils, whereby excess water moves through large vertical pores without wetting the soil inside the peds. Our observations, however, suggest that short-circuiting does not occur in the studied soils. Irrespective of the quantities of dyed water, or the way of application (spraying, ponding), practically all the dye was filtered out on the surfaces of the finer aggregates in the upper 5 cm of the soil. Hardly any stained bands or pores were observed below. This indicates that infiltration proceeds mainly through (capillary) sorption and with a gradually and evenly advancing wetting front. Although most termite tunnels are > 1 mm wide and theoretically increase the permeability of the soils, it seems that water flow in the studied profiles is principally through the fine, porous and stable matrix of the soil mass. Termites that repack soil particles to make room for tunnels and chambers in fact reduce the volume of small pores and therefore reduce lower hydraulic conductivity.

The effects of termites on physical soil properties such as porosity, bulk density, moisture retention, permeability etc., have been subject to much debate. Termites exploit large foraging areas, and their effects on the soil are not confined to the limits of their actual nests. In most studies, however, conclusions are based on comparisons between termitaria (mostly mounds) and adjacent soils, which gives only a very simplified picture. Few studies consider the importance of foraging tunnels. Maldague (1964) reported a porosity of 58 % in forest soils with a high termite population, compared with 48 % in adjacent fallow land, and attributed the difference to termites. This needs not necessarily be correct, as forest clearing and subsequent cultivation may have altered the soil structure. In western Texas, Spears et al. (1975) found that termites (*Gnathamitermes tubiformans*) increase capillary pore space and reduce non-capillary pore space, through the excavation of tunnels, and by repacking of soil particles. Aina (1984) did similar experiments with earthworms in forest soils and cultivated soils in Nigeria. In both cases he recorded a significant decrease of infiltration rate and porosity (esp. pores > 60 µm) after treatment with aldrin.

5.3.3 Biopores
Physical analysis of soil samples produced scanty evidence of soil properties being influenced by increased or decreased termite activity. Therefore, micro-

morphological field studies were initiated. Cross-sections of termite tunnels are generally round to elliptic and feature smooth, plastered walls. They often contain concentrations of oral pellets. The size, direction and morphology of termite tunnels often indicate the species building the tunnel (Chapter 4). The tunnels made by other members of the soil meso-fauna (e.g. micro-arthropods, earthworms) are usually smaller than termite tunnels and do not have plastered walls. Root-channel sections are usually round, they may contain (decomposed) plant tissue and they do not have plastered walls. So, in most cases the various tunnels can be distinguished by studying the soil profile with a simple hand lense. It is not always possible to determine the origin of tunnels beyond doubt: growing root tips have may penetrated a termite tunnel and altered its appearance.

Most of the termite-made tunnels at NARS could be attributed to *Microtermes*. They have a random orientation pattern with a slight domination of horizontally extended tunnels. Diameters range between 0.8 and 2.0 mm, but some 60 % of all tunnels measure between 1.0 and 1.2 mm.

Odontotermes species construct various types of tunnels. The main foraging tunnels are flat and straight, 10-20 mm wide and only a few mm high. Their orientation is nearly always oblique, under an angle of 30-60 degrees with the surface. Much smaller (secondary) foraging tunnels are 2-5 mm wide, but mostly between 3.0 and 3.5 mm. Reddish spots on the tunnel walls indicate active plastering with clay from the subsoil.

Tunnels made by humus-feeding termites (mainly Apicotermitinae) were encountered least frequently. They are generally funnel shaped and have a width between 2.0 and 3.0 mm.

The recorded average density of termite tunnels and of other biopores in the various plots is shown in Table 5.6. The results are grouped with respect to

Table 5.6. Average density of termite tunnels and other biopores (per dm^2) and standard error in the topsoils (0–50 cm) of experimental plots at NARS.

Plot nr.	N	Treatment	Biopores			Termite made tunnels
			large (1.6–3.0)	medium (1.0–1.5)	fine (0.5–0.9)	
1A	60	hoe	2.3 ± 0.41	28 ± 2.8	55 ± 5.7	2.6 ± 0.50
1B	60	hoe + Aldrin	1.4 ± 0.33	27 ± 2.4	71 ± 7.0	1.5 ± 0.34
1E	60	hoe	1.8 ± 0.35	16 ± 1.6	56 ± 5.2	2.2 ± 0.46
1F	60	hoe + Aldrin	2.3 ± 0.36	18 ± 1.7	60 ± 6.4	1.1 ± 1.36
2A	120	plough	1.7 ± 0.25	21 ± 1.4	62 ± 5.1	1.8 ± 0.29
2B	120	plough	1.9 ± 0.26	18 ± 1.2	64 ± 5.2	1.8 ± 0.28
3C	60	compaction	2.0 ± 0.47	18 ± 2.2	77 ± 8.7	2.1 ± 0.52
3D	60	comp. + mulch	1.8 ± 0.44	21 ± 2.0	95 ± 9.4	3.0 ± 0.60
3E	60	compaction	3.3 ± 0.50	23 ± 2.2	42 ± 3.9	1.8 ± 0.43
3F	60	comp. + mulch	2.3 ± 0.45	26 ± 2.7	50 ± 6.2	1.9 ± 0.37

the position of the plots in the field. Plot 1A and 1B are adjacent plots, just as 1E/F, 2A/C, 3C/D and 3E/F.

The variation in the composition of macropores within plots was considerable: despite the large number of observations, the standard error amounts to about 10 %. Therefore, the differences between treatments are generally not statistically significant, so that only certain trends can be indicated, such as a slight increase in medium and fine pores in the mulched plots. It does not seem likely, that the problems of high standard errors can be overcome by increasing the sampling density.

The variations in the number of termite tunnels are even more pronounced: the standard error is about 20 % at $N = 60$ and still 15 % at $N = 120$. Nevertheless, some interesting trends appear from the recorded densities. The majority of the termite tunnels that were counted, belong to the 'medium' size class (1.0-1.5 mm), but their contribution to biopores in this class appears to be modest. Roughly 5-10 % of the medium pores in the topsoil consisted of tunnels that were clearly made by termites.

Prior to our experiment, all the fields at NARS used to be ploughed mechanically twice a year, which seems to have kept the number of termite tunnels down to a level of around 1.8 per dm^2. The return to traditional cultivation practices (hoe) leads to a resumption of termite activity, reflected by an increase in the number of termite-made tunnels. The 'untreated' hoe plots had an average tunnel density of around 2.4 per dm^2, but the application of aldrin led to lower figures. The results of the compaction plots are somewhat confusing. Realising however, that 3C and 3D are adjacent plots, just as 3E and 3F, one might suspect that plot combination 3C/D had a higher initial faunal activity than 3E/F. This is confirmed by field observations. On the whole, compaction by tractor wheels does not seem to disturb termite activity. The application of a mulch layer increased the number of tunnels on both plots.

Table 5.7 presents the average density of termite tunnels and other biopores at different depths in the soil. The density and origin of the termite-made tunnels are shown in Fig. 5.6.

The number of termite tunnels in the upper 50 cm increased with depth. At around 40 cm, the soil becomes more compact, so that pores are less easily destroyed. Ploughing and the use of insecticides seemed to have some effect in the upper 30 cm, but termite activity was definitely not wiped out. The effects of compaction were also slight and noticeable only in the upper 10 cm. Differences occur with respect to the origin of termite tunnels (Fig. 5.6). The untreated hoe plot represents the situation under traditional soil management and can be regarded as a reference. Apicotermitinae were particularly susceptible to tillage operations, because they live in the upper few centimeters of the soil. Their tunnels were only incidentally observed on the hoe plots, and not at all on the plough plots. Although Apicotermitinae did occur on the compaction plots (Section 5.3.1.), their tunnels were not found. This was probably caused by the extremely aggregated distribution of these species.

Odontotermes species are also affected by intensive cultivation, although to

Table 5.7. Average density of biopores and termite tunnels (per dm²) and standard error in experimental plots at the NARS.

Pore size	depth (cm)	PLOUGH plots	HOE plots		COMPACTION plots	
			no aldrin	aldrin	no mulch	mulch
LARGE	5	1.5 ± 0.4	2.4 ± 0.7	2.0 ± 0.5	3.2 ± 0.8	3.2 ± 0.9
(1.6–3.0 mm)	10	1.9 ± 0.5	2.0 ± 0.7	1.4 ± 0.5	2.2 ± 0.8	2.8 ± 0.9
	20	1.6 ± 0.3	1.6 ± 0.6	1.2 ± 0.5	1.0 ± 0.5	1.0 ± 0.5
	30	1.1 ± 0.3	2.7 ± 0.7	2.4 ± 0.7	2.4 ± 0.9	2.0 ± 0.6
	40	2.4 ± 0.5	1.9 ± 0.6	2.3 ± 0.7	3.8 ± 1.0	1.8 ± 0.7
	50	2.4 ± 0.5	1.6 ± 0.8	1.8 ± 0.6	3.4 ± 0.9	1.6 ± 0.9
MEDIUM	5	6.9 ± 0.8	9.0 ± 1.8	8.6 ± 1.4	7.0 ± 0.8	9.4 ± 2.6
(1.0–1.5 mm)	10	8.3 ± 0.8	14.0 ± 2.0	9.2 ± 1.7	9.4 ± 1.4	10.8 ± 1.6
	20	15.8 ± 1.7	17.2 ± 3.1	16.0 ± 1.9	11.6 ± 1.8	18.2 ± 3.6
	30	25.3 ± 2.4	26.3 ± 3.8	31.0 ± 4.1	29.0 ± 2.4	32.2 ± 4.6
	40	32.2 ± 1.9	29.9 ± 3.4	33.7 ± 3.0	33.8 ± 3.6	36.6 ± 3.5
	50	29.8 ± 1.9	39.7 ± 7.2	37.3 ± 3.3	31.2 ± 3.8	32.0 ± 3.4
FINE	5	13.7 ± 1.5	25.6 ± 5.9	13.6 ± 2.4	23.8 ± 3.3	28.6 ± 5.8
(0.5–0.9 mm)	10	20.2 ± 2.3	32.4 ± 4.7	25.0 ± 3.9	24.4 ± 3.2	25.2 ± 4.8
	20	43.5 ± 4.5	45.4 ± 6.0	51.2 ± 6.9	36.0 ± 6.0	48.6 ± 6.0
	30	95.0 ± 9.0	64.2 ± 9.3	82.0 ± 8.4	78.8 ± 13.5	106.0 ± 13.8
	40	99.8 ± 9.1	78.5 ± 7.7	114.9 ± 11.1	98.6 ± 14.6	100.2 ± 19.7
	50	106.1 ± 8.3	98.9 ± 12.7	112.7 ± 10.2	94.2 ± 12.8	127.4 ± 19.7
TERMITE	5	1.0 ± 0.3	1.0 ± 0.6	0.2 ± 0.2	0.6 ± 0.6	0.8 ± 0.4
tunnels	10	0.6 ± 0.2	2.4 ± 0.7	0.2 ± 0.2	0.8 ± 0.4	1.2 ± 0.7
	20	1.3 ± 0.5	1.8 ± 0.7	1.4 ± 0.5	2.8 ± 1.0	1.8 ± 0.5
	30	1.9 ± 0.5	2.5 ± 0.9	1.8 ± 0.8	2.2 ± 0.7	4.0 ± 0.9
	40	3.2 ± 0.5	4.2 ± 0.9	2.5 ± 0.7	2.0 ± 0.9	2.8 ± 0.9
	50	2.9 ± 0.6	2.7 ± 1.0	2.0 ± 0.7	3.4 ± 1.1	4.2 ± 1.3

a lesser extent. The decrease in *Odontotermes* tunnels in the topsoil of the plough plot and the aldrin plot agrees with the estimates of population density (Section 5.3.1.). *Microtermes* was relatively unaffected by cultivation practices. The ratio of *Microtermes* to *Odontotermes* tunnels was highest in the ploughed fields, especially in the topsoil. It increased roughly from 3 on the hoe plot to 6 in the plough plot. On the aldrin plot the number of *Microtermes* tunnels has declined, which is also supported by population figures.

The data from Table 5.7 show that the average density of non-termite pores also increases with depth. Most of the differences between treatments did not reach even the 10 % level of probability (by Student's t-Tests) so that only some trends could be recognized.

It seems that the application of mulch on the compaction plots had stimulated the biological activity in the soil, judging from a slight but consistent increase in medium and fine biopores.

Data from the aldrin plots suggest a reduction of large pores (upper 30 cm), medium pores (upper 20 cm) and fine pores (upper 10 cm). Below these depths, the situation changes and the pores become more numerous than on the untreat-

Fig.5.6 Origin and average numbers of termites tunnels per dm² in topsoils (0-50 cm) at the NARS

ed hoe plots. Again, the differences are not statistically significant, but they are in conformity with the findings on the distribution of termite tunnels. It seems as if the application of insecticides caused the migration of the soil fauna (including termites) to slightly deeper parts of the soil. This behaviour is quite common for termites during dry weather conditions (Lee and Wood, 1971). A temporary migration of faunal activity might also take place, when other kinds of unfavourable conditions exist.

In the upper 10 cm of the plough plots, we recorded fewer termite tunnels than on the hoe plots, which is in accordance with the smaller number of fine and medium biopores. It is possible that the soil fauna had moved deeper, but there is no evidence to support this.

There are several plausible explanations for the similarity of trends observed in termite-made pores and other biopores:
— On the whole, termites and the other soil meso- and macrofauna may respond in the same way to cultivation practices. The relation between termites and the diversity of the soil fauna is still poorly understood, but there are indications that the two are closely linked (Wielemaker, 1984).

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– Part of the 'non-termite biopores' may originally have been constructed by termites and subsequently occupied by other soil fauna or plant roots. Robinson (1958) found that termite tunnels even improve the growth of roots in the soil. In such cases, the morphology of the tunnels can be altered beyond recognition.

6 SURVEY OF FARMER'S FIELDS

6.1 Selection of farmer's fields

Fields were selected in two areas: a rather flat hill-crest near Igonga in Wanjare Location (altitude 1530 m) and the area surrounding the Nyanza Agricultural Research Station (NARS) between 1700 and 1740 m. Each field had been under the same crop and had received the same tillage for at least 5 years. In both areas five fields were chosen each with a different crop: either pasture, maize, coffee, tea or bananas, which were the main crops in both areas.

The pastures had been grazed by cattle and they represented a more or less natural situation. The maize-fields had been cultivated in the traditional way (Section 5.2.1.). For coffee, tea and bananas, fields were chosen which had a good permanent cover of the soil and which were regularly weeded. The fields in Wanjare were all situated on the same well drained, very deep, friable, clayey soils, classified as Typic Haplohumox and Typic Umbriorthox (Soil Survey Staff, 1975). The fields near the NARS were also on well drained, very deep, friable clayey soils, but these were classified as Orthoxic Palehumult. None of the fields was mulched, but crop residues were generally left on the field. Banana 'stems' were often removed to be fed to cattle. Pesticides were used with coffee and tea, but these were sprayed on the trees and, as far as we could assess, had no effect on termites.

In every field the following observations were done:
- species composition and population density of termites
- soil profile characteristics
- construction of termite tunnels in unstructured soil columns
- consumption of litter by termites

6.2 Species composition and population density of termites

6.2.1 Methods

The sampling procedure was essentially the same as the one used in the final sampling of the experimental plots (Section 5.2.1.). However, to save time, the samples were not taken at random but in a grid of 10×10 with distances between samples of 2 m in one direction and 3 m in the other. This procedure was compared with sampling at random on several fields, but no significant differences were found. Three fields were sampled with both sampling pits and the auger to compare the results.

6.2.2 Results

The results of the sampling on the farmer's fields are presented in Table 6.1. When plotting the number of *Microtermes* funguscombs against the number

Table 6.1. Mean numbers of termites/m² ± s.e. in various farmer's fields in Wanjare Location (W) and near the Nyanza Agricultural Research Station (N), Kisii.

		Maize	Coffee	Bananas	Pasture	Tea
WOOD-FEEDERS						
Microceroter-	W	0	0	0	324 ± 117	0
mes parvus	N	0	0	0	0	0
WOOD-AND-LITTER-FEEDERS						
Microtermes	W	1594 ± 428	1000 ± 310	606 ± 218	177 ± 58	776 ± 191*
(two species)	N	1363 ± 601*	1188 ± 290	211 ± 79	187 ± 133	159 ± 18*
Microtermes	W	8.1 ± 3.3	8.1 ± 3.0	4.0 ± 1.5	2.3 ± 1.6	1.2 ± 1.2
(fungus)	N	10.4 ± 3.2*	9.2 ± 3.1	1.6 ± 1.2	3.5 ± 2.0	1.8 ± 0.6*
Pseudacanthotermes	W	70 ± 32	42 ± 17	244 ± 123	886 ± 341	173 ± 90
spiniger	N	0	0	0	0	0
Odontotermes	W	260 ± 177	+	+	+	0
amanicus	N	40 ± 40	+	+	+	0
Odontotermes	W	+	+	+	+	+
kibarensis	N	69 ± 69*	54 ± 52	736 ± 342	+	92 ± 92*
Odontotermes	W	0	0	0	44 ± 21	0
fulleri	N	0	0	0	12 ± 9	0
Total wood-and-	W	1924 ± 526	1042 ± 285	850 ± 255	1107 ± 354	949 ± 237
litter-feeders	N	1472 ± 630*	1242 ± 292	947 ± 391	199 ± 133	251 ± 109*
HUMUS-FEEDERS						
Astratotermes spp.	W	98 ± 49	73 ± 25	+	312 ± 76	0
	N	±	181 ± 177	371 ± 164	177 ± 124	0
Astalotermes spp.	W	285 ± 111	87 ± 31	92 ± 46	80 ± 36	61 ± 28
	N	±	20 ± 20	656 ± 248	756 ± 231	306 ± 159
Adaiphrotermes spp.	W	0	109 ± 56	145 ± 98	945 ± 234	202 ± 113
	N	0	58 ± 52	598 ± 221	744 ± 294	1028 ± 580
Cubitermes	W	0	0	0	8 ± 8	0
testaceus	N	0	0	0	200 ± 191	0
Cubitermes	W	0	0	0	0	0
ugandensis	N	0	0	0	+	0
Basidentitermes	W	0	0	0	94 ± 59	0
amicus	N	0	0	0	1932 ± 456	0
Promirotermes	W	0	0	0	48 ± 42	0
gracilipes	N	0	0	0	0	0
Total humusfeeders	W	382 ± 123	269 ± 88	237 ± 107	1487 ± 265	263 ± 92
	N	0	259 ± 185	1627 ± 366	3810 ± 645	1334 ± 421
Total abundance	W	2306 ± 547	1311 ± 296	1087 ± 265	2918 ± 521	1212 ± 254
	N	1472 ± 630*	1501 ± 359	2574 ± 595	4009 ± 650	1585 ± 311
Total number of	W	7	8	8	13	6
species found	N	6	7	7	11	5

* = based on two fields, ★ = deviant figure (see text), + = not recorded on sampling field, but observed on nearby fields.

Fig.6.1 Relation between the number of *Microtermes* adults and funguscombs in farmer's fieldsM = maize, B = bananas, C = coffee, T = tea, G = pasture

of *Microtermes* adults, one would expect a linear relationship. Fig. 6.1. shows that this is true for most fields, except for one banana field and the tea field in Wanjare. Just before sampling, this banana field had been weeded and the dead plants had been left on the field, which probably attracted the large number of *Microtermes*, and incidentally also the large number of *P.spiniger*, from outside the field. Since another banana field had been sampled as well, the aberrant field was omitted. The reason for the high density of *Microtermes* in the tea field is not clear, but the field was included, because no other tea fields were sampled in Wanjare. In other calculations and comparisons, the population density of *Microtermes* in this tea field will be assumed to be $160/m^2$ (about equal to the tea fields near the NARS).

The results indicate that *Odontotermes fulleri*, *Microcerotermes parvus*, *Cubitermes testaceus*, *C.ugandensis*, *Basidentitermes amicus* and *Promirotermes gracilipes* occur only in pasture. Also on other occasions, these species were never encountered outside pasture, except one record of *B.amicus* in a fallow maize field. *O.amanicus* was most often encountered in pasture, but also several times under maize, coffee and bananas. This species is less common in both areas than *O.kibarensis* and *O.fulleri*. *O.kibarensis* does not seem to have a clear preference for one crop. It is usually absent from pasture in areas where *O.fulleri* occurs, maybe because of competition. The banana field near the NARS yielded a large number of *O.kibarensis* compared to the other fields, but since the sampling method used is not reliable for this species (Section 5.2.1.), no significance can be attached to the difference. The same thing applies to *P.spiniger*, which appears to be equally common under all crops studied except tea, under which the species was rarely found. The large number recorded in the sampled tea field must be due to the presence of a nest in one corner of the field.

The *Microtermes* species show the same order of preference in both areas:

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maize, coffee, bananas, pasture, tea. In the case of pasture maybe the word 'preference' should not be used. It is likely that the low density of *Microtermes* in pasture is caused by competition of the many other termite species in this habitat. The densities under maize and coffee were significantly higher than under bananas, pasture and tea (t-test: $p < 0.01$). The banana field in Wanjare supported a relatively large *Microtermes* population. Since our experiments (Section 7.4.) indicate that *Microtermes* is not particularly fond of banana leaves, the reason for this abundance is probably that this field was weeded less rigorously than the banana field near the NARS.

In Wanjare, the Apicotermitinae were most common in pasture, while the densities under the other crops were all the same. Near the NARS, however, they were as common under bananas and tea as in pasture, but virtually absent from maize. Possibly, different apicotermitine species occur in the two areas. The high density in the NARS banana field might also have been caused by the fact that litter was not removed from the field but collected in trash lines and left to rot. These trash lines attracted many Apicotermitinae as well as *O.kibarensis*.

In Table 6.2., sampling with the auger is compared with pit sampling in three fields in Wanjare. *Microtermes* and Apicotermitinae numbers were clearly underestimated by the sampling pits. These termites are easily overlooked, especially in a large quantity of soil. The funguscombs of *Microtermes* seem to have been underestimated by the auger, but actually the difference is only significant in the banana field. *P.spiniger* is not easily missed, so the two methods sample this species equally well. The same will probably be the case for *Odontotermes* species, which are equally conspicuous.

Table 6.2. Comparison of two sampling methods in three
fields in Wanjare (mean numbers/m² and standard error).

	Pits	Auger
Microtermes-termites		
coffee	351 ± 87	1000 ± 310
bananas	583 ± 176	610 ± 218
maize	405 ± 111	1594 ± 428
Microtermes-fungus combs		
coffee	12.8 ± 1.8	8.1 ± 3.0
bananas	9.4 ± 2.3	4.0 ± 1.5
maize	14.4 ± 2.2	8.1 ± 3.3
Apicotermitinae		
coffee	78 ± 27	269 ± 88
bananas	55 ± 15	253 ± 110
maize	204 ± 70	376 ± 123
P. spiniger		
coffee	62 ± 28	42 ± 17
bananas	95 ± 43	244 ± 123
maize	263 ± 140	70 ± 32

Table 6.3. Population desities of various termite species in maize fields at various altitudes (mean numbers/m² ± s.e.).

Site	Altitude (m)	Micro-termes	Apico-termitinae	Odonto-termes	Pseuda canthotermes
Igonga	1530	1594 ± 428	376 ± 123	260 ± 177[a]	70 ± 32
Kisii Town	1690	762 ± 257	2 ± 2	80 ± 65[a]	0
NARS	1715	1964 ± 565	0	137 ± 82[k]	0
Bobaracho	1830	179 ± 76	10 ± 10	0	0
Keumbu	1920	84 ± 84	12 ± 12	0	0
Birongo	1995	0	361 ± 160	63 ± 42[t]	0
Tombe	2060	0	352 ± 132	0	0

[a] = amanicus, [k] = kibarensis, [t] = tanganicus

Table 6.3. shows that *Microtermes* is less common above 1800 m and even disappears at higher altitudes. The increase of Apicotermitinae from ca. 1700 m upwards might be attributed to the darker soils at those altitudes, which contain more organic matter. On the other hand, even at Igonga, where the soil is not rich in organic matter, these termites were common under maize, though different species may be involved.

6.2.3 Discussion

These results show that the type of crop grown in a field has a marked effect on its termite fauna. In all cultivated fields studied near Kisii, species diversity was about the same, but abundance differed. Wood-feeders were absent everywhere. In Wanjare, wood-and-litter-feeders were more abundant than humus-feeders, but there was a decreasing trend from maize through coffee and bananas to tea. Near the NARS, however, humus-feeders were more abundant than wood-and-litter-feeders under bananas and tea. Generally, the more intense the cultivation of a field was the less the abundance of humus-feeders. In the case of wood-and-litter-feeders, one has to distinguish between the *Microtermes* species, which nest in the fields, and the other species, which generally nest outside the fields. The *Microtermes* species tend to increase in abundance with increasing intensity of cultivation. The other species' nests often disappear from cultivated fields and *O.fulleri* and *O.nolaensis* rarely forage on such fields. The remaining species are largely indifferent to cultivation as far as foraging is concerned. They forage where sufficient litter is available, except when this litter is less palatable, as seems to be the case with tea leaves and perhaps banana leaves (Section 7.4.2.).

The effect of clearing and cultivation on the termite fauna has been studied by several investigators (Sands, 1965; Wood & Lee, 1971; Wood et al., 1977, 1982; Collins, 1981a). It is apparent from these studies that clearing of the natural vegetation causes a sharp decline in the number of species. Subsequent cultivation further reduces the number of species. In our study area hardly any natural vegetation was left, so only a comparison between cultivated and uncultivated land could be made.

Our results can best be compared with those of Wood et al. (1977), who examined the effect of clearing and cultivation on termite populations in woodland near Mokwa, Nigeria. They found the same difference between pasture and cultivated fields. They recorded 20 species in pasture and 4-8 species under maize. Our figures are very similar. In Kisii District, all 17 identified species can be found in pasture (three of these, *Macrotermes michaelseni, Odontotermes nolaensis* and *O.tanganicus*, are not included in Table 6.1.) and 8 species (incl. *O.tanganicus*) occur under maize. There is a difference between Mokwa and Kisii in the abundances of the various species. In Kisii District as a whole, humus-feeders are by far the most abundant group of termites, followed by wood-and-litter-feeders, while wood-feeders are least abundant. Under maize, wood-feeders are absent and wood-and-litter-feeders are much more abundant than humus-feeders. Near Mokwa, wood-and-litter-feeders are the most abundant, while the other two groups are equally but much less abundant. Under maize, wood-feeders are very abundant, but that is solely due to a species of *Amitermes*, a genus which does not occur in western Kenya. Near Mokwa too, wood-and-litter-feeders are more abundant under maize than humus-feeders. The abundance of *Microtermes* species was much higher near Mokwa than near Kisii. That may be because there are five species near Mokwa against two in Kisii District and/or because of the higher altitude of the latter area. In fact, in the eastern part of the district, above 1900 m, no *Microtermes* could be found.

6.3 SOIL PROFILE CHARACTERISTICS

6.3.1 Methods
In each field, except the tea field, a soil profile was described according to FAO guidelines (FAO, 1967) and classified according to the USDA Soil Taxonomy (Soil Survey Staff, 1975). Samples were taken at intervals of 10 cm, for physical and chemical analysis. Field descriptions of soil profiles and analytical data are given in Appendix 1, the analytical methods in Appendix 2. From each profile, four undisturbed soil samples were collected at intervals of 40 cm for the preparation of thin sections. A point count method was applied to quantify micromorphological phenomena in the thin sections. The obtained sets of data were examined for evidence of the effects of termite activity on soil materials (Table 6.4.). The upper 140 cm of the soil was considered, except for the maize field where gravel started at a depth of 130 cm. The analysis results were grouped under different headings (soil texture, soil structure and soil fertility) (Table 6.5.).

6.3.2 Results

Soil texture
All examined soils had a rather homogeneous, clayey texture without clear signs of clay translocation. Wielemaker (1984) attributes the homogeneous soil

Table 6.4. Soil profile characteristics in farmer's fields at Wanjare.
Maize field

Depth (cm):	0–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150
% clay	48	47	60	57	55	61	49	(17)
% 0.42–0.21 mm/tot · sand	25	23	19	15	17	17	11	(13)
M 50 (sand, mm)	0.29	0.30	0.31	0.29	0.28	0.27	0.30	(0.08)
% aggr. < 0.42 mm	60	23	21	29	46	47	41	(14)
bulk density (g cm^{-3})	1.17	1.21	1.29	1.04	1.04	1.08	1.20	(1.49)
total porosity (vol%)	54.9	53.5	50.4	60.0	60.0	58.5	53.8	(42.7)
Ksat (cm day^{-1})	134	38	29	223	223	130	86	(176)
% carbon	2.6	2.3	1.5	0.9	0.8	0.7	0.8	(0.3)
(CEC (mmol/kg soil)	162	143	140	128	126	121	115	(94)
exch. Ca	37	31	59*	21	17	11	1	(<1)
exch. Mg	12	12	12	10	7	7	3	(3)
Base saturation (%)	31	31	64*	24	19	15	8	(3)
Termite pellets	[0.21	]	[0.22	]	[0.35	]	[0.15	]
Termite tunnels	[0.03	]	[0.07	]	[0.02	]	[0.05	]

* unreliable results

Banana field

Depth (cm):	0–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150
% clay	54	64	63	67	66	65	71	63
% 0.42–0.21 mm/tot · sand	31	21	20	18	18	18	15	15
M 50 (sand, mm)	0.25	0.33	0.30	0.25	0.24	0.31	0.23	0.32
% aggr. < 0.42 mm	36	30	36	49	44	42	33	52
bulk density (g cm^{-3})	0.99	1.11	1.08	1.12	1.01	1.08	1.22	1.27
total porosity vol%	61.9	57.3	58.5	56.9	61.2	58.5	53.1	51.2
Ksat (cm day^{-1})	166	194	90	224	605	497	130	223
% carbon	3.1	1.6	1.0	0.9		0.8		0.6
CEC (mmol/kg soil)	179	139	158	138		121		116
exch. Ca	66	35	14	8		5		7
exch. Mg	20	13	5	2		2		2
Base saturation (%)	50	35	13	8		6		8
Termite pellets	[0.17	]	[0.38	]	[0.27	]	[0.25	]
Termite tunnels	[0.04	]	[0.05	]	[0.02	]	[0.01	]

texture and the very gradual transition between soil horizons in Kisii to bioturbation by termites. The range in clay content within the profiles (parameter A) was 14 % under maize, 17 % under bananas, 13 % under coffee and 10 % under grass. In view of the generally poor accuracy of texture analyses on low-activity clays (Soil Survey Staff, 1975) these results indicate a very close similarity of texture profiles. Therefore, these figures do not suggest a more intense bioturbation under one crop or another. Relatively strong textural changes were found in cultivated fields, notably under maize and banana, at the transition from Ap horizon to deeper soil layers. Less intensively cultivated soils show a more

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Table 6.4 (continued)
Coffee field

Depth (cm)	0–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150
% clay	54	56	58	62	63	67	62	61
% 0.42–0.21 mm/tot · sand	36	31	27	22	24	21	25	17
M 50 (sand, mm)	0.26	0.29	0.30	0.32	0.31	0.29	0.32	0.37
% aggr. < 0.42 mm	34	36	37	38	36	33	34	38
bulk density (g cm^{-3})	1.08	1.08	1.23	1.14	1.10	1.17	1.15	1.23
total porosity (vol%)	58.5	58.5	52.7	56.2	57.7	55.0	55.8	52.7
Ksat (cm day^{-1})	153	96	90	212	264	223	193	128
% carbon	2.8	1.9	1.0		0.7		0.6	0.6
CEC (mmol/kg soil)	144	161	139		141		129	129
exch. Ca	47	70*	46		37		35	33
exch. Mg	20	17	13		10		14	15
Base saturation (%)	48	54*	42		33		38	37
Termite pellets	[0.31		] [0.26		] [0.41		] [0.30		]
Termite tunnels	[0.05		] [0.04		] [0.03		] [0.06		]

* unreliable results

Grass field

Depth (cm):	0–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150
% clay	56	58	62	63	64	66	64	66
% 0.42–0.21 mm/tot · sand	29	22	24	24	21	19	18	17
M 50 (sand, mm)	0.29	0.29	0.30	0.30	0.31	0.33	0.34	0.35
% aggr. < 0.42 mm	42	56	60	60	58	55	57	64
bulk density (g cm^{-3})	1.06	1.16	1.06	1.07	1.11	1.13	1.20	1.28
total porosity (vol%)	59.2	55.4	59.2	58.8	57.3	56.5	53.8	50.8
Ksat (cm day^{-1})	274	158	104	353	324	346	324	410
% carbon	3.2	2.5	1.5	1.1		0.7	0.7	0.6
CEC (mmol/kg soil)	174	126	132	136		112	129	105
exch. Ca	56	20	22	13		12	16	11
exch. Mg	19	7	3	2		< 1	3	< 1
Base saturation (%)	47	27	22	13		13	15	10
Termite pellets	[0.26		] [0.40		] [0.36		] [0.35		]
Termite tunnels	[0.01		] [0.07		] [0.05		] [0.02		]

gradual increase in clay content from the A to the B horizon.

Parameter B deals with the particle-size fraction of 0.42-0.21 mm, expressed as percentage of total sand. Studies on soil translocation (Section 7.1.) revealed that termites move fine grained material from the deeper parts of the soil to the soil surface. The fraction of 0.42-0.21 mm appeared to be preferentially transported by termites. Termite activity would thus result in a decrease of this fraction in the subsoil and enrichment in the topsoil. However, we found that the differences between topsoil and subsoil values (parameter B) of the various fields are of the same order of magnitude. Similarly, no significant differences were

Table 6.5. Summary of soil characteristics

Attribute	Para-meter	Value			
		Maize	Banana	Coffee	Grass
Soil texture	A	14	17	13	10
	B	14	16	19	12
	C	0.29	0.28	0.31	0.31
	D	38	40	36	57
	E	123	266	170	287
Soil structure	F	55.9	57.3	55.9	56.4
	G	0.23	0.27	0.32	0.34
	H	0.04	0.03	0.04	0.04
Soil fertility	I	134	142	141	131
	J	20	23	40	21
	K	9	7	15	5
	L	21	20	40	21

A variation in clay %
B variation in fraction 0.42–0.21 mm, as a % of total sand
C average median diameter of the sand fraction (M 50), in mm
D average % aggregates < 0.42 mm
E average saturated hydraulic conductivity (cm/day)
F average porosity (vol. %)
G average area fraction of termite-made pellets
H average area fraction of termite tunnels
I average CEC (mmol/kg soil)
J average exchangeable calcium content (mmol/kg soil)
K average exchangeable magnesium content (mmol/kg soil)
L average base saturation (%, by sum of cations).

found between the average median diameters of the sand fraction (parameter C) in soils from the various fields.

Soil structure

Soil structure was studied with physical and micromorphological methods. Termites contribute to aggregate formation by breaking up larger peds during the process of tunnelling and by cementing soil particles together into soil crumbs. Termite activity thus affects porosity, hydraulic conductivity, and the amount of fine aggregates in the soil. Examination of thin sections showed indeed that termite-made aggregates ('pellets') are abundant in soils of the Wanjare area (Chapter 4).

The average weight % of soil aggregates of < 0.42 mm (parameter D) was highest under grass, whereas the other fields showed little difference. Regardless of the high clay contents, all profiles had a high to very high hydraulic conductivity in the A and lower B horizon. Average hydraulic conductivity (K_{sat} in cm day^{-1}) was used as a further indication of termite activity (parameter E). On the whole, the highest conductivity values were measured in the grass field and the banana field followed by the coffee and the maize field in decreasing order.

In cultivated fields, particularly under maize, the conductivity of the upper B horizon was quite low, suggesting that some structure deterioration may have taken place.

The average porosity of the soil (parameter F) appeared to be remarkably similar in the various fields. The area fractions of termite-made pellets (parameter G) and termite tunnels (parameter H) were estimated by micromorphological methods, and averaged for the entire profile. Differences between fields were only small, particularly the occurrence of termite-made tunnels. Samples from the grass field and the coffee field contained the largest amounts of pellets. Values for the banana field were slightly higher than for the maize field, but because the deepest sample from the maize field contained part of a gravel layer this difference was not considered significant.

Soil fertility

In Chapter 7 we shall discuss the influences that termites have on the properties of soil material through the addition of saliva and faeces. Increased levels of CEC, exchangeable Ca and Mg and % base saturation were commonly found in termite-modified soil materials.

A comparison of the analysis results shows that average CEC (parameter I) is equally low in all fields. The average levels of exchangeable Ca and Mg (parameter J and K) are highest under coffee, just as the % base saturation (parameter L). The differences in exchange characteristics are only small among the remaining fields. Exchangeable Ca is low (20-50 mmol/kg) in all topsoils and very low (< 20 mmol/kg) in subsoils. Similarly, exchangeable Mg is low (5-15 mmol/kg) in the topsoil and very low (< 5 mmol/kg) in the subsoil.

6.3.3 Conclusions

Termite sampling showed high population densities of termites in maize fields in comparison to fields with other crops. By means of a comparative soil survey we intended to find evidence for differences in soil characteristics caused by variations in termite activity. However, only very small differences in soil conditions were noted among the fields considered in this study. All soils had gradual transitions between soil horizons and gradually increasing clay contents, without clear signs of clay illuviation. The strongest increase in clay content was recorded in the topsoil of the maize field, which suggests that some structure deterioration has taken place. This is also indicated by relatively low values for hydraulic conductivity.

Wielemaker (1984) has demonstrated that continued termite activity shifts the median of the sand fraction to lower values. We found that termites indeed enrich the topsoil with fine sized particles. However, average grain diameters did not differ significantly among the fields, nor could we detect systematic differences in the enrichment of topsoils.

Differences in soil structure also apeared to be very small among the fields. Highest hydraulic conductivity and highest content of fine aggregates were recorded under grass. Among the cultivated fields, relatively large amounts of

fine aggregates were found in the upper 10 cm of the soil under maize. Comparison with the abundance of termite-made pellets suggests, that this is not caused by increased termite activity. Micromorphological observations indicated in fact a very similar degree of biological reworking in all soils studied.

No evidence was found for improved soil fertility in plots with large termite populations. Apparently, chemical enrichment of soil materials by termites is not strong enough to have a measurable effect. This seems to confirm the results of our investigations on the significance of foraging sheetings for the fertility of the soil (Section 7.2.). Although some enrichment my take place, the chemical properties of termite-modified soil are largely similar to those of the original soil material.

An important conclusion that can be drawn from this study is that changes in termite population density and activity do not necessarily have measurable effects on soil characteristics. In the Wanjare area this is probably due to the particularly stable soil structure. Many authors have attributed the favourable structure of such clay-rich Oxisols to the occurrence of very stable, sand-sized granules that are coated with amorphous iron and aluminium oxides (Sanchez, 1976). Wielemaker (1984) has shown that the quality of a certain soil as a habitat for termites depends largely on the stability of its structure. Soils in the Wanjare area apparently offer excellent habitat conditions, so that termites do not have to modify the soil structure to suit their demands. Consequently, changes in termite activity, associated with certain farming practices, probably have only marginal implications for the structure of these soils.

6.4   CONSTRUCTION OF TERMITE TUNNELS IN UNSTRUCTURED SOIL COLUMNS

6.4.1   Methods
The subterranean activity of termites under various kinds of land use, was studied in an experiment with unstructured soil columns. For this purpose, small pits (diam. 25 cm, depth 50 cm) were excavated and filled with soft, yellowish loamy material. This material occurs in a deep pallid zone on granite intrusions, just above the partially weathered parent material. It is composed of de-ironated kaolinitic clay and quartz sand, and locally used for the plastering of houses (vernacular name: 'ekebuse'). Because of its light colour and lack of biopores, termite-made tunnels show up clearly in this material.

In each of the selected farmers' fields, three columns were made and examined after 20, 30 and 50 weeks respectively. At 10 cm below the soil surface 35 g of chopped maize stalks were added to the columns to attract foraging termites. Unfortunately, some columns were destroyed in the course of the experiment because of unforeseen tillage of the land.

6.4.2 Results

Small earthworms were often the first soil animals to enter the soil columns, but they hardly attacked the applied mulch. Their tunnels have a diameter of 0.8-1.0 mm and usually occur throughout the entire soil column. They were neither lined with clay nor back-filled with soil. Termite-made tunnels, on the other hand, were always found close to the mulch layer and were mostly lined with clay. The colour of linings and gallery-fill suggests that they are composed of topsoil material (*Microtermes, P.spiniger*) or of subsoil material (*O.kibarensis*) or of excreta (Apicotermitinae, *Cubitermes*). The thickness of the linings ranges from less than 0.5 mm (*Microtermes*) to 2-4 mm (*P.spiniger, O.kibarensis,* humivorous termites) and even up to 8 mm (*M.michaelseni*). The plastering of

Fig.6.2 Backfilled channel of *Pseudocanthotermes spiniger* in column experiment

tunnel walls and the occasional backfilling of tunnels thus results in a thorough mixing of soil constituents (Fig. 6.2.). In some cases, 'ekebuse' material was incorporated in the soil, some 10-15 cm away from the column.

The numbers of termite tunnels recorded in the soil columns are shown in Table 6.6. In the Wanjare area, the activity of termites was most pronounced in the maize field, which can be attributed to the high population density in this field (Section 6.2.2.). The lowest activity was recorded in the banana field, which seems in line with our findings on the formation of soil sheetings (Section 7.2.). This observation is however contested by population data (Table 6.1.) and the results of consumption tests (Table 6.7.). The reason for this discrepancy is not known.

Unlike *P.spiniger* and *Microtermes*, the foraging activity of *O.kibarensis* and most humus-feeding termites is severely depressed by tillage. This explains the relatively abundant occurrence of these species in fields with low-intensity cultivation (tea, coffee) and pasture. The absence of *P.spiniger* from the tea and coffee fields is attributed to the small amount of plant litter returned to the soil surface and to the low palatability of this litter.

Most soil columns were visited by one or two species, but the one under pasture contained tunnels of *Microtermes*, *P.spiniger* and several humus-feeding species (*Cubitermes*, Apicotermitinae). A high species diversity appears to be characteristic for pasture (Section 6.2.2.).

At NARS, the highest values were obtained in uncultivated fields. *O.kibarensis* was particularly active in the banana field, where much litter was available at the time. This corresponds well with previous observations on the population density and activity of this species. In the coffee field, *Microtermes* and Apicoter-

Table 6.6. The number and origin of termite channels in soil columns under different crops, after 20, 30 and 50 weeks.

Site		Wanjare					NARS		
Species	Weeks	Maize	Coffee	Banana	Pasture	Tea	Maize	Coffee	Banana
Micro*	20	22	0	0	14	2	0	15	0
	30	6	12	0	8	6	0	4	0
	50	n.d.	4	0	0	0	n.d.	n.d.	n.d.
Pseuda*	20	2	0	0	0	0			
	30	5	0	0	0	0		NOT PRESENT	
	50	n.d.	0	1	3	0			
Odonto*	20						1	0	16
	30		NOT PRESENT				0	1	6
Other*	20	0	0	0	1	1	0	7	0
	30	0		0	5	2	0	4	0
	50	0	2	0	7	2	n.d.	n.d.	n.d.

* Micro = *Microtermes* Pseuda = *P.spiniger* Odonto = *O.kibarensis*
Other = humus feeding termites (mainly *Apicotermitinae*)

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mitinae were the main active species. Despite the occurrence of *Microtermes* in the maize and banana fields at NARS, their tunnels were not found in the soil columns. Because of the abundant supply of available plant litter the added pieces of maize probably did not attract these termites.

In order to study differences in termite activity at different altitudes, some more farmer's fields were included in this experiment. The number and origin of termite tunnels observed in soil columns are given in Table 6.7. Near Oyugis, just outside the Kisii District, *M.michaelseni* and *P.spiniger* are the dominant species. Five weeks after the soil columns were dug in, already 7 large *M.michaelseni* tunnels (diam. 7-10 cm) were excavated and most of the mulch was consumed. An appreciable quantity of soil was thereby brought into the soil column.

At Igonga, *P.spiniger* was largely responsible for the mixing of soil and 'ekebuse' material. Tunnels (diam. 3-10 mm) and chambers (diam. 15 cm) plastered with clay, were found throughout the soil column. After 30 weeks, all mulch had been consumed. At higher altitudes, humus feeding termites (Apicotermitinae) become dominant. Their tunnels extended only incidentally into the clay columns as they do not feed on fresh plant litter. Even after 30 weeks there were no signs of consumption and no soil material was brought into the column.

6.4.3 Discussion

The excavation and plastering of foraging tunnels by termites eventually causes a thorough mixing of soil materials. The species composition of the termite population determines to a large extent the rate at which this happens. Under natural conditions, the species composition is governed by climate, vegetation and soil properties, but in cultivated land it is also affected by tillage operations and crop characteristics. The results of experiments with unstruc-

Table 6.7. The number and origin of termite tunnels in soil columns in maize fields at various altitudes.

Species Site	Altitude	Weeks	Macro	Pseuda	Micro	Odonto	Other
Oyugis	1350 m	5	7	0	0	0	0
		20	0	6	0	0	0
		30	1	0	0	0	0
Igonga	1530 m	20		2	22	0	0
		30		5	6	0	0
NARS	1715 m	20			0	1	0
		30			0	0	0
Naikuro	1930 m	20	NOT PRESENT			0	2
		30				0	0
Tombe	2060 m	20					0
		30					0

Macro = *M. michaelseni*, Pseuda = *P. spiniger*, Micro = *Microtermes sp.*, Odonto = *Odontotermes spp.*, Other = humus-feeding termites.

tured soil columns demonstrate the effect of natural and human-induced variations in termite activity.

M.michaelseni and *P.spiniger* are the most effective species in terms of litter consumption and soil homogenization. Their occurrence in the Kisii area seems to be governed by altitude (Chapter 3). *Odontotermes* spp. are less important, partly because their nest density is lower and partly because they are susceptible for tillage. The other species (*Microtermes*, humivorous termites) are even less important for the mixing of soil, although their tunnels may be quite abundant. In the area around Tombe, the termite population is entirely composed of humus-feeding species which do not attack fresh litter. This may have important consequences for the accumulation and the distribution of organic matter in the soil.

6.5 CONSUMPTION OF LITTER

6.5.1 Methods
Litter, collected from the selected farmer's fields except from pasture, was cleaned and dried in an oven at 105°C for 24 h. Bags of 20 × 20 cm were filled with a known amount of litter (c. 25 g d.w.) and replaced in the fields. Ten bags were placed at the surface and ten bags at 10 cm below the surface. The bags at the surface were made of so-called 'coffee-wire', a kind of square wire-gauze with a mesh-width of 4 mm. The other bags were made of plastic-coated cotton mosquito-netting with a mesh-width of ca. 1.2 mm preventing access of *P.spiniger* and *Odontotermes* spp. Unfortunately, no metal gauze could be obtained, when the litterbags were prepared. As we already feared, the cotton proved not resistant against the termites that had to be kept out, so a number of bags were partly destroyed and the contents eaten.

After one week 3 bags from the surface and 3 bags from below were removed at random. After two weeks this procedure was repeated and after four weeks the remaining bags were removed. The litter was carefully cleaned and dried at 105°C for 24 h and finally weighed.

6.5.2 Results and discussion
In Table 6.8. the consumption from the litterbags in the farmer's fields is shown. Litterbags disappeared from many fields, especially near the NARS. Where this had happened, figures were recalculated to ten bags. Near the NARS proper guarding was not possible, so the experiment was terminated after three weeks. The figures for these fields were recalculated to 4 weeks.

Since the sites on which this litter was introduced, were not cleared and since this litter had the same composition as the original litter, it may be assumed that the rate of removal of the original litter was the same. On the maize field in Wanjare, the measurements were made immediately after the harvest and after the preparation for sowing, which is the time of maximum amount of litter. During the first three months of the growing period, litter production is minimal,

Table 6.8. Total consumption (grams) after 4 weeks from 10 litterbags each containing ca. 25 d.w. of litter on various farmer's fields.

	Microtermes spec.		Pseudacanthotermes spiniger		Odontotermes amanicus		Odototermes kibarensis	
	O	S	0	S	0	S	0	S
Maize-W	0.00	34.16 (3.3)	76.84 (5)	166.67 (6.7)	62.50 (2.5)	0.00	–	–
Maize-N	15.96 (6)	24.92 (6)	–	–	–	–	2.52 (2)	41.44 (2)
Coffee-W	10.64 (4)	34.16 (4)	59.80 (3)	116.20 (2)	–	–	–	–
Coffee-N	28.84 (6.7)	75.60 (8.9)	–	–	–	–	73.64 (3.3)	12.88 (1.1)
Bananas-W	36.12 (6)	47.04 (6)	30.80 (2)	37.43 (4)	–	–	–	–
Bananas-N	36.12 (6)	59.64 (6.7)	–	–	–	–	51.37 (3)	27.78 (1.1)
Tea-W	103.32 (9)	89.04 (6)	7.84	82.06 (4)	–	–	–	–

Between brackets: number of bags attacked. For fields from which bags were removed by people, figures were recalculated to ten bags.
O = on surface, S = below surface, W = Wanjare, N = NARS.

so that the termites continue collecting the litter produced in the previous months, though the removal rate decreases, partly because the amount of litter decreases and partly because of the often heavy rain during this period. When 80-90 % of the litter is removed, the remaining is scattered in pieces too small to attract termites any longer. On the other fields, litter production is more constant throughout the year with a small drop during the wet seasons, and 30-50 % is removed by termites. On the tea fields, the tea leaves remain largely untouched.

For *Microtermes* the amount removed from the bags shows a significant negative correlation (P < 0.05) with population density, correlation coefficients being -0.72 for above-ground consumption and -0.70 for underground consumption. A possible explanation is the following. *Microtermes* species are recorded as feeding on roots (Wood and Johnson, 1978). In maize fields, where these species are very common, there are many dead roots in the soil, because harvest takes place twice a year. Compared to that the amount of litter introduced was probably too small to be especially attractive to *Microtermes*. In fields with permanent crops the amount of dead roots is much less, so extra litter is more likely to be attacked. In the tea field, the effect was even stronger, because the introduced litter contained only few tea leaves (which proved unattractive in food choice tests; section 7.4.), and may therefore have been extra attractive.

For *P.spiniger* the correlations are -0.82 and -0.80 and for *O.kibarensis* 0.65 and 0.50 resp., but in these cases the number of observations is too small for the correlations to be significant. No plausible explanation can be offered for a negative correlation in the case of *P.spiniger*.

7 ADDITIONAL ANALYSES AND EXPERIMENTS

7.1 MOUNDS

7.1.1 Introduction

In the Kisii area, termite mounds are built by workers of the species *Macrotermes michaelseni, Pseudacanthotermes spiniger, Cubitermes ugandensis* and *C.testaceus*. Mound samples were analysed and compared with samples from adjacent soil profiles to asses the effects of various species of termites on soil materials. A subterranean nest of *Odontotermes fulleri* was included in this study.

All Macrotermitinae construct funguscombs from masticated organic material, which has been kept in the crop for some time. These funguscombs support certain species of fungi (*Termitomyces*) that are able to attack cellulose and lignin and make it digestible to the termites. Little is known about the chemical composition of funguscombs, although they represent an important stage in the breakdown of the organic matter collected by termites. In this chapter, the possible role of funguscombs in the supply of nutrients to the soil is briefly discussed.

7.1.2 Materials and methods

M.michaelseni mounds are large, domed structures, normally over 1.5 m high, and with a base diameter of 1.5-3.0 m (Fig. 3.1.). A mound was chosen located in a sorghum field 2.5 km south of Oyugis at an altitude of 1425 m. The soil is a moderately deep, gravelly clayey Oxic Tropudalf on weathered Precambrian rhyolite.

P.spiniger builds domed or broad stemmed mounds (Fig. 3.2.) with a height of 0.3-2.0 m and a base diameter smaller than 1 m. The investigated *P.spiniger* mound was located in a maize field at Wanjare, 7 km north-west of Kisii Town, at 1530 m altitude. The soil is a dark reddish brown, very deep, clayey Typic Haplohumox. The mounds of *M.michaelseni* and *P.spiniger* have a rather similar architecture. They are both composed of a central part with numerous cavities that are connected by a network of tunnels and a compact protective outer wall. The habitacle (or hive) is situated below the original soil level. It consists of brood chambers with funguscombs and the royal chamber.

In an adjacent pasture, a *C.testaceus* mound and a subterranean *O.fulleri* nest were selected. Mounds of *C.testaceus* are low (less than 30 cm), domed structures , with a simple architecture of chambers separated by thin walls with connecting openings. The nest of *O.fulleri* is characterized by a cluster of bun-shaped fungus chambers at a depth of 80-120 cm with an elaborate system of ventilation shafts and foraging tunnels.

Composite samples were taken from each termite nest as well as from the area immediately adjacent to the mound. The wall and the interior part of the larger mounds (*M.michaelseni, P.spiniger*) were sampled separately. The nest of *O.fulleri* was sampled in between the fungus chambers, in the central part

Tabel 7.1. Physical and chemical properties of termite mounds and adjacent soil.

Sample depth/ Material	Size fractions (weight %)			pH (H₂0)	C%	N%	C/N ratio	P total (g/kg)	CEC	Exchange characteristics (mmol/kg soil)			
	Clay	Silt	Sand							Ca²⁺	Mg²⁺	K⁺	Na⁺
P. spiniger													
interior mound	75.3	9.5	15.2	5.3	1.5	0.15	9.9	0.57	147	41	25	1	1
outer wall	74.0	9.1	16.9	5.4	1.5	0.13	11.4	1.18	151	36	19	3	1
5– 10 cm	48.2	21.8	30.0	5.6	2.6	0.21	12.4	0.65	162	37	2	1	1
20– 30 cm	47.4	20.0	32.6	5.4	2.3	0.17	13.3	0.57	143	31	12	1	1
40– 50 cm	59.6	15.0	25.4	5.3	1.5	0.11	13.5	0.61	140	59	12	7	12
60– 70 cm	**56.7**	**12.4**	**30.9**	**5.5**	**0.9**	**0.09**	**10.2**	**0.48**	**128**	**21**	**10**	**1**	**1**
100–110 cm	**61.0**	**9.4**	**29.6**	**5.5**	**0.7**	**0.07**	**10.4**	**0.48**	**121**	**11**	**7**	**1**	**1**
120–130 cm	**48.7**	**13.0**	**38.3**	**5.3**	**0.8**	**0.07**	**11.6**	**0.57**	**115**	**1**	**3**	**3**	**2**
140–150 cm	17.2	12.6	70.2	5.1	0.3	0.02	15.5	0.65	94	1	3	1	1
C. testaceus													
mound	64.7	25.0	10.3	5.2	3.6	0.31	11.6	0.79	16.2	6.4	2.1	0.2	1
O. fulleri													
hive	72.1	11.8	16.2	6.1	0.6	0.08	7.9	0.65	15.6	6.6	2.2	0.5	0.2
5– 10 cm	**55.9**	**11.3**	**32.8**	**5.4**	**3.2**	**0.25**	**12.8**	**0.48**	**17.4**	**5.6**	**1.9**	**0.4**	**0.3**
20– 30 cm	**57.5**	**9.6**	**32.9**	**4.9**	**2.5**	**0.18**	**13.6**	**0.35**	**12.6**	**2.0**	**0.7**	**0.4**	**0.3**
40– 50 cm	62.0	10.0	28.0	5.0	1.5	0.10	15.0	0.31	13.2	2.2	0.3	0.4	tr
60– 70 cm	63.1	10.9	26.0	5.0	1.1	0.09	12.1	0.31	13.6	1.3	0.2	0.2	tr
110–110 cm	**66.4**	**7.3**	**26.3**	**5.1**	**0.7**	**0.07**	**10.1**	**0.35**	**11.2**	**1.2**	**tr**	**0.1**	**0.2**
120–130 cm	**63.8**	**7.8**	**28.4**	**4.8**	**0.7**	**0.07**	**9.9**	**0.39**	**12.9**	**1.6**	**0.3**	**tr**	**tr**
140–150 cm	66.1	9.4	24.5	5.0	0.6	0.05	12.0	0.31	10.5	1.1	tr	tr	tr
M. michaelseni													
interior mound	45.5	30.7	23.8	6.9									
outer wall	43.1	33.4	23.5	6.7	1.7								
0– 15 cm	63.7	18.7	17.6	5.7	2.3								
15– 30 cm	**60.4**	**22.2**	**17.4**	**6.0**	**1.8**								
30– 55 cm	55.1	25.2	19.7	6.4	0.5								
55– 70 cm	44.0	21.0	35.0		0.6								

Note: Estimated depth of collection in **bold** print.

of the nest system. All soil samples were analysed at the Dept. of Soil Science and Geology (Agricultural University, Wageningen). The composition of funguscomb material was determined at the National Agricultural Laboratories (Nairobi). For laboratory methods, reference is made to Appendix 2. Soil classification was done according to U.S.D.A. Soil Taxonomy (Soil Survey Staff, 1975).

7.1.3 Results

Physical differences between mound and soil material

Table 7.1. shows the physical and chemical characteristics of termite nests and adjacent soil profiles for each of the species studied. No chemical data are available for the *M.michaelseni* mound. Comparison of the colours of the mounds with those of adjacent soil indicated that, except for *C.testaceus*, subsoil material was used for construction of the mounds. The depth of collection can also be established by comparing the textural composition of mound soil with that of adjacent soils. Our observations suggest that building material is mostly collected at a depth of 80-120 cm, unless the soil is shallow, as was the case with the *M.michaelseni* mound. *C.testaceus* collects soil in the upper 25 cm of the profile.

There is a tendency towards higher proportions of clay and lower proportions of sand in termite-modified soil in comparison with unworked soil (Table 7.1.). The magnitude of the differences between mound material and unmodified soil is highest in mounds of *C.testaceus* and *P.spiniger*. Relatively much coarse material was found in the mound of *M.michaelseni*, probably because of the gravelly clay subsoil and the ability of this species to move large particles to the soil surface. So in this exceptional case, mound soil was coarser textured than adjacent topsoil.

A comparison of the composition of the sand fractions of mound soil and adjacent soil demonstrates that termites prefer medium and fine sand above coarse sand for the construction of their mounds, and consequently change the grain size distribution of the soil materials (Table 7.2.). *M.michaelseni* and *P.spiniger* prefer to move particles of 150-420 µm, while the much smaller workers of *O.fulleri* accumulate grains of 50-210 µm. This is in accordance with our observations on foraging sheetings (Section 7.2.). Relative to the soil composition, the *C.testaceus* mound has a low proportion of particles of 105-850 µm and higher proportions of material < 105 µm and > 850 µm. Stoops (1964) attributed this decrease of intermediate fractions to the fact that such particles are too large to be swallowed and carried in the crop, and too small to be carried piece by piece in the mandibles.

Chemical differences between mound and soil material

Mounds of *P.spiniger* and *C.testaceus* contain more organic carbon and total nitrogen than unworked subsoil material because of the admixture of faeces (*C.testaceus*) or saliva (*P.spiniger*) during construction of the mound. The sub-

Table 7.2. Composition of the sand fractions of termite structures and adjacent soil.

Sample depth/ Material	Fractions (µm)					
	50–105	105–150	150–210	210–420	420–850	850–2000
M. michaelseni						
interior mound	31.8	15.5	12.9	17.6	11.0	11.2
outer wall	32.5	16.6	12.5	16.8	10.5	11.1
0– 15	37.1	17.3	13.4	17.3	8.8	6.1
15– 30	38.9	17.7	13.0	16.1	8.6	5.7
30– 55	34.8	15.1	11.6	15.4	9.2	14.0
55– 70	26.0	9.4	7.2	10.8	10.5	36.2
P. spiniger						
interior mound	16.4	13.2	17.8	32.2	17.8	2.6
outer wall	8.2	13.0	15.4	32.0	26.6	4.7
5– 10	12.7	9.0	11.3	25.3	20.0	21.7
20– 30	13.5	8.6	10.1	23.0	20.2	24.6
40– 50	14.1	9.8	9.4	18.8	22.4	25.5
60– 70	20.3	12.3	7.8	14.6	19.1	25.9
80– 90	19.1	13.7	9.7	16.6	17.0	23.9
100–110	17.9	14.2	11.8	16.9	18.2	21.0
120–130	20.4	12.3	9.2	10.7	14.4	33.0
140–150	26.4	15.7	12.8	13.0	7.5	24.6
C. testaceus	19.4	7.8	7.8	14.6	14.6	35.9
O. fulleri	20.3	14.2	15.4	14.2	21.0	14.8
5– 10	9.8	9.1	13.1	28.7	23.2	16.2
20– 30	9.7	8.5	13.4	28.9	20.7	18.8
40– 50	9.3	8.9	12.5	23.6	25.0	20.7
60– 70	11.5	8.5	12.3	23.8	23.0	20.8
100–110	9.5	8.7	10.6	19.0	18.6	33.5
120–130	9.9	6.7	9.2	18.3	17.3	38.7
140–150	11.4	7.3	7.8	16.7	18.8	38.0

terranean *O.fulleri* nest had similar contents of C and N as the adjacent subsoil. Total P is invariably higher in termite structures than in unmodified soil; organic phosphate compounds probably account for most of the difference.

Incorporated organic matter and clay explain the slightly increased cation exchange capacity of mound soil. The base saturation is markedly higher in termite structures than in the adjacent soil. This increase is largely caused by higher levels of exchangeable calcium and magnesium. Consequently, the mounds have a slightly higher pH than the soil from which they were built.

Funguscombs

The composition of funguscombs from *P.spiniger* and *O.fulleri* is given in Table 7.3., together with data from Boyer (1956b) and Wood and Sands (1978).

Table 7.3. Chemical composition of funguscomb material.

Species	Food	pH	weight %						
			C	N	C/N	Ca	Mg	K	Na
O. fulleri	litter	4.6	23.9	0.91	26	0.42	0.46	0.15	0.01
P. spiniger	litter	4.3	10.2	0.93	11	0.26	0.16	0.27	<0.01
Macrotermes bellicosus[1]	wood					0.81	0.15	0.09	0.30
Macrotermes bellicosus[2]	wood		29	0.80	36	0.85		0.10	

[1] After Boyer (1956b)
[2] After Wood and Sands (1978)

Funguscombs are largely composed of organic-rich excreta and have a low pH. Combs of *P.spiniger* contain less organic carbon than those of *O.fulleri* because of the incorporation of sand (nearly 50 % by weight). Comb material often has a high C/N ratio, although we obtained lower values than those reported by other workers (Lee and Wood, 1971). The difference may be caused by differences in feeding behaviour. The food of *O.fulleri* and *P.spiniger* contains a high proportion of non-woody litter, and C/N values of wood (50-80) are generally higher than those of leaf tissue (grass 25-40). The low C/N ratio recorded for *P.spiniger* is in fact equal to that of soil humus, and suggests advanced decomposition of funguscomb material.

Funguscombs are rich in mineral nutrients. Calcium contents appear to be higher in combs of *Macrotermes bellicosus* than the material analysed by us would suggest (Table 7.3). This may be explained by different feeding habits, since excrements of wood feeding species contain more Ca and less K than those of litter feeding termites (Lee and Wood, 1971).

7.1.4 Discussion

Most termite mounds and subterranean nests contain more clay and less sand than adjacent (top) soil material because of the enrichment with fine material by termites (Lee and Wood, 1971). As mounds continuously erode, redistributed mound material enriches the topsoil with finely textured soil. We found that this is also true for most mound types in the Kisii area with the exception of the *M.michaelseni* mound, which contained more sand than adjacent topsoil.

Chemical changes of soil material caused by termite activity are associated with incorporation of organic matter (faeces, saliva). Nevertheless, mounds of *M.michaelseni* and *P.spiniger* are predominantly built from subsoil material, that, even when enriched by termites, has an organic matter content below that of adjacent topsoils. Enrichment with carbon, nitrogen, phosphorus and exchangeable bases is reported in most studies on this subject (Lee and Wood, 1971) and is confirmed by our findings. Erosion of the mounds and redistribution of termite-modified soil enriches the topsoil with organic matter and mineral

nutrients, but this addition of nutrients seems to have a negligible effect on the overall fertility of the surrounding soils (Pomeroy, 1976; Wood and Sands, 1978).

The composition of faecal material of termites depends for a great deal on the kind of food (wood, grass, humus). Wood (1976) found that faecal structures of Australian termite species had C/N ratios of 32-92 (wood-feeders) and 21-23 (grass-feeders). Matsumoto (1976) mentions a C/N ratio of 25.5-28.3 for fungus-combs of *Macrotermes* spp. in Malaysia. The results reported by other workers are shown in Table 7.3. We obtained comparable results for the comb material of *O.fulleri*, but the composition of *P.spiniger* funguscombs seems to be different. Organic carbon content and C/N ratio are relatively low, suggesting advanced degradation of organic matter. Comb material contains many sand sized particles that are too large to have passed the termites' guts. They are probably carried in the mandibles and added during construction of the combs.

In spite of the generally high C/N ratio of faeces, the values for mound soil are equal to or even slightly lower than those of adjacent soil in all of the investigated termite structures. Similar results were obtained by Hesse (1955), Boyer (1956b), Maldague (1959) and others. This can probably be attributed to enhanced decomposition of organic matter in mounds, associated with increased levels of microbial activity in comparison with surrounding soils (Meiklejohn, 1965). Increased C/N values were recorded for various Australian species (Lee and Wood, 1971). These contrasting findings might be explained by differences in building behaviour of the examined species, especially regarding the use of faeces. In mounds of fungus-growing termites, there appears to be very little return of organic matter from funguscombs to the soil, unless the mound is abandoned (Wood, 1976). It is therefore likely that the enrichment of soil with organic matter (and nutrients) by Macrotermitinae results principally from the addition of saliva. Soil sheetings of *P.spiniger* and *O.kibarensis* in which saliva is the sole cementing agent, also have lower C/N ratios than adjacent soils (Section 7.2.). However, the mound of *C.testaceus*, although largely constructed from excrements, also had a slightly lower C/N ratio than the surrounding topsoil. Similar results were recorded for West African *Cubitermes* mounds, and attributed to the more advanced decomposition of organic matter in the mounds (Wood et al., 1983; Anderson and Wood, 1984).

7.2 SHEETINGS

7.2.1 Introduction

The construction of mounds and tunnels by termites involves the translocation of large quantities of soil. Part of the translocated soil is deposited at the surface. These so-called sheetings are composed of excreta or of soil particles cemented together with excreta or saliva (Lee and Wood, 1971). They cover the foraging trails that lead to concentrated sources of food (plant litter, logs, grass, dung pads). Sheetings probably serve to protect the foraging termites

Fig.7.1 Sheetings of *Pseudacanthotermes spiniger* on maize stalks

Fig.7.2 Longitudinal section of maize stalk partly filled with clay by *Microtermes sp.*

against desiccation, predators (notably ants) and competitors.

Sheetings of the *Odontotermes* workers were found on dry grass, plant litter, dry wood and occasionally on cow dung pads. In some cases, they extended over several square meters, but they were generally less abundant than *P.spiniger* sheetings. *P.spiniger* principally feeds on plant litter (Fig. 7.1) but also attacks timber work and thatched grass roofs of local houses. *Microtermes* makes no soil sheetings in the strict sense but feeds on the soft inner parts of maize stalks and leaves small amounts of clay on the inside of the attacked stems (Fig. 7.2).

The pedological significance of sheetings depends on their composition and the rate at which they are built. There are few data on the amount of soil moved to the surface in this way, but there is evidence that it may exceed that in mounds (Lee and Wood, 1971). Systematic measurements of the rate of sheetings construction by *Odontotermes* spp. indicated a significant effect on soil structure and texture in North Kenya (Bagine, 1984).

In this chapter, the composition and estimated amounts of translocated soil in sheetings of *P.spiniger* and *O.kibarensis* are discussed, and some attention is paid to their effect on the Kisii soils.

7.2.2 Methods

In Wanjare and at the NARS, square sample plots of 5×5 m were marked out in fields with various crops: maize, bananas, tea and coffee. Ten trays of small-mesh wire netting (30×30 cm), each with 35 g of dry chopped maize stalks, were randomly distributed in each plot. Once established, the trays were used for weekly collections of soil sheetings. The sheetings were carefully removed from the tray, or scraped off from the maize stalks, and weighed. Attacked maize stalks were replaced every week. The experiment was run for 11 weeks, of which 5 weeks in the dry season (November-December) and 6 weeks in the rainy season (March-April).

7.2.3 Results

The quantities of soil sheetings collected weekly from the trays varied considerably. The results are shown in Table 7.4., averaged separately for the dry

Tables 7.4. Averaged amounts of soil sheetings by different termites on foraging trays in dry and rainy seasons in g per 25 m².

Crop	Dry season			Rainy season		
	Pseuda	Micro	Odonto*	Pseuda	Micro	Odonto*
maize	60.8	3.8	2.5	64.3	8.2	0
banana	0	0	0	32.8	0.3	0
tea	0	0	0	36.7	10.3	0
coffee	n.d.	0	0	n.d.	0	0

* Pseuda = *P. spiniger* Micro = *Microtermes* Odonto = *O. kibarensis*.
n.d. = no data

season and the rainy season. In the maize plot *P.spiniger* maintained a permanent building activity, although it increased somewhat towards the onset of the first rains and decreased after the swarming of the alates. In all other plots, sheetings were less abundant and only constructed in the rainy season. The experiment gave little insight in the foraging activity of *O.kibarensis*. Although soil sheetings of this species were regularly found in the fields, they occurred only once on the trays. It appeared that *Odontotermes* spp. forage mainly in dry weather and only where there is an abundant supply of litter. In some places, we could easily collect 200 g of fresh sheeting material from 1 m². The method used in the experiments therefore seriously underestimates the quantity of soil moved by this species.

The physical and chemical characteristics of sheetings and adjacent soil are shown in Tables 7.5. and 7.6. Matching the colours of the sheetings with those of soil from different depths indicated that the material was collected just below the topsoil. Comparison of the grain size distribution and the sand: clay ratio indicates that most sheeting material is collected at a depth between 20 and 50 cm. Indeed, most of the foraging tunnels were found at this dept and material from these tunnels appears to be used for building the sheetings.

The proportions of sand and clay in sheetings do not differ significantly from those in the original soil material, but the composition of the various sand fractions indicates that termites preferentially move soil particles < 850 μm to the surface. A relative accumulation of the size classes 150-420 μm (*P.spiniger*) and 50-150 μm (*O.kibarensis*) is evident.

The organic carbon content and the nitrogen content of sheeting material are similar to or slightly higher than those of the soil because of the admixture of organic matter during construction of the sheetings. The source of this organic matter is probably saliva, since Macrotermitinae use their excreta exclusively for the construction of funguscombs. This is probably the reason why sheetings have a similar or slightly lower C/N ratio than the original soil material (see Section 7.1.4.). Increased total phosphorus content was only found in *O.kibarensis* sheetings. The sheetings of both species have a slightly higher cation exchange capacity than the surrounding soil, probably due to enrichment with organic matter. The base saturation is also higher in the sheetings. Calcium accounts for most of the difference in cation composition and percentage base saturation.

7.2.4 Discussion

All Macrotermitinae in the study area bring subsoil material to the surface for the construction of foraging sheetings, but the quantities and properties of this material vary with the species, the soil type and the availability of litter. *P.spiniger* is probably the most important earth-moving species in the area, particularly where maize is grown. If the experimental results are assumed representative for the land use system, the annual construction of sheetings in maize fields by *P.spiniger* is estimated at 1300 kg ha⁻¹ yr⁻¹. Similarly, the amount of soil packed in maize stalks by *Microtermes* is estimated at 80-180 kg ha⁻¹ yr⁻¹. The annual rate of soil translocation by termites is considerably less in fields

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Table 7.5. Physical and chemical analyses of material from sheetings and adjacent soil profiles.

Material/ Sample depth (cm)	Size fractions			sand /clay ratio	pH (H₂O)	C%	N%	C/N ratio	P-total g/kg	Exchange characteristics (mmol/kg soil)				
	Sand	Silt	Clay%							CEC	Ca²⁺	Mg²⁺	Na⁺	K⁺
P. spiniger sheeting	35.8	14.2	50.0	0.72	5.5	2.4	0.22	11	0.52	156	50	20	<1	6
5– 10	30.0	21.8	48.2	0.62	5.6	2.6	0.21	12	0.65	162	37	12	<1	1
20– 30	32.6	20.0	47.4	0.69	5.4	2.3	0.17	13	0.57	143	31	12	<1	1
40– 50	25.4	15.0	59.6	0.43	5.3	1.5	0.11	13	0.61	140	59	12	12	7
80– 90	27.7	17.0	55.3	0.50	5.5	0.8	0.08	10	0.48	126	17	7	<1	<1
100–110	29.6	9.4	61.0	0.49	5.5	0.7	0.07	10	0.48	121	11	7	<1	<1
140–150	70.2	12.6	17.2	4.08	5.1	0.3	0.02	15	0.65	94	<1	3	<1	<1
O. kibarensis sheeting	5.8	22.8	71.4	0.08	6.3	3.5	0.31	11	1.09	220	140	31	1	6
5– 10	7.4	22.5	70.1	0.11	6.1	3.3	0.26	13	0.79	194	104	29	3	6
20– 30	6.4	22.1	71.5	0.09	6.1	1.5	0.12	13	0.48	160	72	33	<1	1
40– 50	4.3	24.0	71.7	0.06	6.0	1.1	0.10	11	0.44	158	61	34	<1	<1
80– 90	5.0	19.0	76.0	0.07	6.1	0.6	0.07	9	0.44	141	42	41	7	3
120–130	4.9	21.2	73.9	0.07	5.7	0.7	0.06	11	0.52	141	30	38	<1	<1

Table 7.6. Granulometric composition of the sand fractions of sheetings and adjacent soil material (weight %).

Sample depth/ Material	Grain size (μm)					
	50–105	105–150	150–210	210–420	420–850	850–2000
P. spiniger sheeting	8.7	10.3	15.4	33.0	20.9	11.7
5–10	12.7	9.0	11.3	25.3	20.0	21.7
20–30	13.5	8.6	10.1	23.0	20.2	24.6
40–50	14.1	9.8	9.4	18.8	22.4	25.5
60–70	20.3	12.3	7.8	14.6	19.1	25.9
80–90	19.1	13.7	9.7	16.6	17.0	23.9
O. kibarensis sheeting	31.0	17.2	13.8	15.5	13.8	8.6
5–10	28.3	14.9	12.2	16.2	12.2	16.2
20–30	26.6	12.5	12.5	12.5	10.9	25.0
40–50	31.8	18.2	13.6	15.9	9.1	11.4
60–70	29.7	16.2	13.5	16.2	10.8	13.5
80–90	29.4	15.7	13.7	13.7	7.8	19.6

with other crops. This is attributed to a smaller supply or a lower palatability of crop residues under coffee, tea and bananas as compared with maize. The amount of soil moved by *O.kibarensis* could not be estimated because its activity is highly variable within each field.

There are few quantitative data on the rate of sheeting formation by termites. Lepage (1974) mentions a figure of about 800 kg ha^{-1} yr^{-1} sheeting material accumulated by *Macrotermes subhyalinus* in Senegal. The annual accumulation of sheetings by Macrotermitinae in savanna woodland in Nigeria was estimated at 300 kg ha^{-1} and the soil packed in maize stems by *Microtermes* at 250 kg ha^{-1} (Wood and Sands, 1978). Bagine (1984) found that *Odontotermes boranicus* translocated soil material at a rate of 1059 kg ha^{-1} yr^{-1} in an arid shrubland area in Kenya.

Our experiment shows that the soil material used for the construction of sheetings is excavated at depths between 20 and 50 cm, and gives evidence for a preferential transport of particles in the size classes 150-420 μm by *P.spiniger* and 50-150 μm by *O.kibarensis*, which corresponds with the size of their oral pellets (Chapter 4). There does not appear to be a consistent selection of clay particles for the construction of sheetings such as in mounds, possibly because sheetings have only a temporary function.

The chemical properties of the sheetings are mainly those of the original soil material, but sheeting material appeared to be enriched with organic matter and exchangeable bases, particularly calcium and magnesium. Increased nutrient levels in termite-modified soil are often attributed to the addition of saliva (Robinson, 1958; Lee and Wood, 1971; Pomeroy, 1983; Bagine, 1984).

Table 7.7. Estimated quantities of organic carbon, nitrogen, total phosphorus and available cations in soil sheetings and topsoil (0–10 cm), and the annual uptake by a maize crop (low production level).

Source	Quantity of nutrients (kg ha^{-1} yr^{-1})					
	C	N	P	Ca	Mg	K
Soil sheetings	31.3	2.9	0.7	1.3	0.3	0.3
Topsoil	31300	2520	786	888	175	47
Crop removal*		50	5	3	4	60

* After Wielemaker and Boxem (1982)

The practical significance of such chemical enrichment depends on the rate at which nutrients are returned to the surface soil. In the case of termite mounds, a large quantity of all nutrients that are normally available for plant growth, are temporarily taken out of circulation until the mounds are abandoned and erode. For example, Watson (1977) found that mounds of *Macrotermes falciger* in arable land contain 70-95 % of the total amount of nutrients in both mounds and Ap horizons. Soil sheetings, on the other hand, disintegrate within a few weeks, so that the nutrients contained in them return more quickly in the soil system.

Table 7.7. presents the estimated quantities of organic carbon, total phosphorus and available cations added to the surface soil in the case of a production of 1300 kg *P.spiniger* sheetings per hectare per year. For comparison, the quantities present in the upper 10 cm of soil (bulk density 1.2 g cm^3) and the estimated annual removal of some nutrients by a maize crop (yield 1100 kg ha^{-1}) are also given. It appears that the quantities of most nutrients in soil sheetings are only 0.1-0.2 % of the amounts in the upper 10 cm of the soil (potassium 0.6 %). With the possible exception of calcium, these quantities are insignificant when compared with the removal by crop growth. Similar conclusions were reached by Pomeroy (1976) and Wood and Sands (1978) in studies on nutrient cycling by erosion of termite mounds. It is nevertheless conceivable that the release of nutrients from soil sheetings creates scattered spots with enhanced fertility and plant growth, but no evidence for this was found in the study area.

7.3 LOCATION OF FOOD BY TERMITES

7.3.1 Methods

Three experiments were carried out to estimate the discovery time and the daily consumption of litter by *O.kibarensis* and *Microtermes* sp. These two species were chosen, because they were both very common in the study area and occurred close to the laboratory where removal of litter and disturbance by cattle could easily be kept at a minimum. The site was at 3 km to the west of Kisii Town at an altitude of 1610 m.

The first experiment was started towards the end of the dry period in February 1985. Twenty litterbags with maize stalks were placed in a semicircle near a nest of *O.kibarensis*. Ten bags were on the surface, ten at 0.1 m below. Also ten pegs of pine-wood were pushed into the soil between the bags. Every day in the afternoon bags and pegs were examined to check whether consumption had started or continued. All were removed after 55 days, washed, dried and weighed.

This experiment was repeated after the peak of the long rains (end of May) using bundles of maize stalks. Each bundle contained five stalks of ca. 40 cm, total dry weights being 200-400 g. At ca. 2 m from each of two nests of *O.kibarensis*, five bundles were placed on the surface and left for 54 days.

The last experiment was started a month later near a nest of *O.kibarensis* under some shrub at the border of a maize-field. Three rows of 3 maize bundles were placed at distances of 5, 10 and 20 m from the nest and were left for 26 days.

Some bundles in the process of being consumed were regularly examined during the course of one day and during special weather conditions to check for variations in activity.

7.3.2 Results

The results of the first two experiments are represented in Tables 7.8., 7.9. and 7.10. When *O.kibarensis* started consuming from a litterbag, usually *Microtermes* disappeared. Therefore, it was assumed that *Microtermes* only contributed appreciably to the total consumption before the other species moved in. In the second experiment, *O.kibarensis* stopped consumption before the experiment was terminated, so some consumption by other organisms may have taken place afterwards.

In the first experiment, the average consumption by *Microtermes* was calculated from the bags that were touched only by this species. This figure was used to calculate, separately for each other bag, the consumption by *Microtermes* before *O.kibarensis* had moved in, which was then subtracted from the total consumption. The remaining consumption was assumed to be almost completely attributable to *O.kibarensis*.

In the second experiment, consumption not attributable to *O.kibarensis* was estimated from the three bundles that were not touched by this species, which was appr. 0.2 % of the initial weight of a bundle per day. So for each day on which no consumption by *O.kibarensis* took place, 0.2 % of the initial weight was subtracted from the total consumption. Consumption from the bundles was higher than from the litterbags, but there is a relation between the two. If the daily consumption is expressed as a percentage of the initial dry weight, in both cases the same amount is consumed (1.4 % for litterbags and 1.3 % for bundles).

The results of the last experiment are not represented in a table. Only one bundle, at 5 m from the nest, was attacked after 9 days and termites were active for only 7 days.

Both termite species entered the maize stalks at points of contact with the

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Table 7.8. Consumption and time of discovery of litterbags placed in a lawn near a nest of *Odontotermes kibarensis* for 55 days.

a		b		c	d	
Start of comsumption (days)		Duration of consumption (days)		Consumption (g d.w.)	Consumption per day (g d.w.)	
Mic	Odo	Mic	Odo		Mic	Odo
On surface						
9.5	47.5	38	7.5	9.07		0.40
27.5	29.5	2	25.5	10.04		0.38
12.5		42.5		6.89	0.16	
37.5		17.5		2.62	0.15	
19.5		35.5		3.48	0.10	
18.5	49.5		bag destroyed			
2.5		52.5		9.90	0.19	
15.5		39.5		5.54	0.14	
16.5	49.5	33	5.5	7.25		0.36
19.5		35.5		8.22	0.23	
18.0 ± 3.0	44.0 ± 5.0				0.16 ± 0.02	0.38 ± 0.01
Below surface						
11.5	51.5	40	3.5	9.42		0.18
19.5		35.5		10.63	0.30	
4.5		50.5		13.66	0.27	
15.5		39.5		8.33	0.21	
2.5		52.5		9.98	0.19	
21.5		33.5		6.71	0.20	
4.5		25.5		4.62	0.18	
11.5		43.5		11.13	0.26	
6.5		48.5		7.44	0.15	
	2.5		52.5	21.19		0.40
11.0 ± 2.5	27.0 ± 24.5				0.22 ± 0.02	0.29 ± 0.11

Mic = *Microtermes*, Odo = *O. kibarensis*. Consumption/day in case of *Microtermes* calculated as consumption/duration (c/b) and in case of *O. kibarensis* as [consumption − (mean cons. of Mic)* (duration of Mic)]/(duration of Odo) or $(c - m_M * b_M)/b_O$.

ground. *O.kibarensis* rarely constructed soil sheetings and *Microtermes* never did. Both species appeared to prefer the soft inner tissues of the stalks: even vascular bundles were often left untouched, esp. by *Microtermes*.

7.3.3 Discussion

The experiments revealed differences in foraging strategy between *Microtermes sp.* and *O.kibarensis*. After locating a food source the former species continued consumption throughout the duration of the experiments. During some days it collected food from 18 litterbags in an area of 12 m², which amounts to a maximum daily consumption of ca. 0.29 g/m². The rate of consumption

Table 7.9. Consumption and time of discovery by *Microtermes* of pine-wood sticks in a lawn near a nest of *Odontotermes kibarensis*.

Start of consumption (days)	Duration of consumption (days)	Consumption (g d.w.)	Consumption per day (g d.w.)
7.5	47.5	3.83	0.08
19.5	35.5	13.84	0.39
27.5	27.5	4.22	0.15
2.5	52.5	3.62	0.07
2.5	52.5	12.60	0.24
24.5	30.5	9.97	0.33
4.5	7.5	0.66	0.09
38.5	16.5	3.53	0.21
2.5	52.5	3.14	0.06
33.5	21.5	4.19	0.19
16.5 ± 4.5 (mean start cons. $\pm$ s.e.)			0.18 ± 0.04 (mean cons. $\pm$ s.e.)

Table 7.10. Consumption and time of discovery by *Odontotermes kibarensis* of bundles of maize-stalks placed near nests of this species for 54 days.

a Bundle number	b Start of consumption Odontotermes (days)	c Duration of consumption Odontotermes (days)	d Total con-sumption (g d.w.)	e Cons./day by non-Odontotermes	f Corrected consumption Odontotermes	g Corr. cons. per day Odontotermes
Nest I						
1	n.c.		33.38	0.62 (0.2% of initial weight)		
2	n.c.		23.73	0.44 (0.2% of initial weight)		
3	n.c.		19.60	0.36 (0.2% of initial weight)		
4	12.5	bundle destroyed				
5	4.5	30	96.96	0.84	76.82	2.56
Nest II						
6	33.5	10	57.84	0.46	37.41	3.74
7	38.5	5	31.14	0.41	10.97	2.19
8	45.5	6	44.47	0.47	21.92	3.65
9	41.5	10.5	54.14	0.51	31.87	3.19
10	0.5	16	71.47	0.41	56.00	3.50

4–10 For *O. kibarensis:* average discovery time: 25.0 ± 7.0 days; average consumption/litterbag $\cdot$ day: 3.10 ± 0.26 g.

Consumption/day by 'non-Odontotermes' estimated from the first three bundles as 0.2% of initial weight. Corrected consumption of *O. kibarensis:* d–(54-c)e.
n.c. = no consumption by *O. kibarensis*.

seems to have remained more or less constant, because there was no relation between duration of consumption and average daily consumption rate. *Microtermes* appears to prefer foraging underground, because consumption from the litterbags below the surface was significantly higher than from those on the surface. In the pegs, tunnelling was extensive in the underground parts, but only a few tunnels extended above ground level and never for more than 1 cm.

Also *O.kibarensis* continued consumption from the litterbags until the end of the experiments, although in half of the cases that was only a few days. In the maize bundles, however, consumption ceased after a variable number of days (mean: 13 days). Since the daily examination of the bundles was not different from that of the litterbags, it is unlikely that this was the cause. Moreover, the same phenomenon might have been observed, if the litterbags had been left for a longer period. Maybe this species has the habit of regularly shifting its activity to another place.

The daily rate of consumption was higher in the bundles than in the litterbags, even in such a way that the amount collected in a day was always about the same proportion of the total initial weight of the maize stalks. This suggests that the number of *O.kibarensis* workers recruted for food collection may be more or less proportional to the size of the food source.

The average discovery time was much shorter for the maize bundles than for the litterbags. This may partly be explained by the larger bulk of the bundles and partly by the fact that there had been a period of heavy rain during experiment 1, which may have reduced searching activity.

Few quantitative data are available on consumption by Macrotermitinae. Wood (1978) mentions a figure of ca. 85 mg/g of termite/day for *Microtermes*. If the species in the present experiments consumes the same amount, it would mean that, with a mean fresh weight of 0.6 mg/termite, the amount collected daily from the litterbags and the pegs was equivalent to between 3165 and 4333 termite.days. The figures mentioned by Wood (1978) for *Odontotermes* species are in the order of 50 mg/g/day, but he thinks that these are probably underestimates. Using this figure and a mean fresh weight for *O.kibarensis* of 1.8 g/termite, the amount collected daily from the litterbags would be equivalent to about 3800 termite.days and from the maize bundles about 35000 termite.days.

Termite activity, esp. searching activity, fluctuated in response to rain. During periods with regular heavy showers little above-ground activity was observed and consequently few litterbags or maize bundles were discovered. At some days following moderate rain, columns of *O.kibarensis* and *P.spiniger* were observed marching through the vegetation without constructing protective soil sheetings. Most litterbags and maize bundles were discovered during dry periods and then also many soil sheetings were made.

Once a maize bundle had been discovered by *O.kibarensis*, collecting activity continued for 24 h per day without much variation as long as there was no heavy rain. During heavy showers, activity ceased but was usually resumed within an hour after the rain had stopped. Within the temperature range during the experiments (17-32°C) no effect of temperature on the activity was observed.

7.4.1   Methods

Three experiments were carried out in an unshaded lawn at the same site as the food-location experiments (7.3.1.) to determine the preference of *Microtermes* for certain types of litter. Again litterbags were used with ca. 25 g of litter.

In experiment 1, 8 bags with maize stalks and 8 bags with banana leaves were buried at 10 cm below the surface and left for 27 days. In experiment 2, 3 bags with maize stalks, 3 with tea branches and 3 with coffee branches were buried at the same depth for 25 days. Experiment 3 was done with maize stalks, coffee branches, tea branches, banana leaves and tea leaves, 5 bags of each, again at 10 cm below the surface. These were left for 34 days. In all three experiments, the bags were laid out in a random pattern. After each experiment, the contents of the bags were cleaned, dried at 105 °C for 24 h and weighed.

7.4.2   Results

In experiment 1, the difference between the consumption of maize stalks and banana leaves (Table 7.11.) is significant at the 5 % level (t-test). In experiment 2, *O.kibarensis* unexpectedly attacked some bags. The two species each invaded too few bags to be able to draw meaningful conclusions, though *O.kibarensis* seems to be attracted to tea branches.

In experiment 3, again both *Microtermes* and *O.kibarensis* invaded the bags. Signs of *Microtermes* activity were only found in bags with tea and coffee branches. The difference in consumption is not significant. Of course, in bags invaded by *O.kibarensis*, the signs of *Microtermes* may have been obliterated. *O.kibarensis* invaded every type of litter except coffee branches. There are no significant differences in consumption, but only one bag of tea branches and two bags of tea leaves were invaded, while all five bags of both maize stalks and banana leaves were invaded. Maybe this species prefers maize stalks and

Table 7.11. Average consumption of *Microtermes sp.* and *Odontotermes kibarensis* in bags with signs of termite activity (number attacked between brackets).

	Maize stalks	Banana leaves	Tea leaves	Tea branches	Coffee branches
	Experiment 1: 8 bags per litter type, 27 days				
Microtermes	7.61 ± 0.61 (7)	5.38 ± 0.45 (6)	–	–	–
	Experiment 2: 3 bags per litter type, 25 days				
Microtermes	4.78 ± 1.45 (2)	–	–	1.40 (1)	3.41 ± 1.57 (2)
O. kibarensis	5.06 (1)	--	–	14.26 ± 0.56 (2)	2.81 (1)
	Experiment 3: 5 bags per litter type, 34 days				
Microtermes	(0)	(0)	(0)	8.36 ± 0.66 (3)	6.82 ± 1.74 (4)
O. kibarensis	7.49 ± 2.09 (5)	6.41 ± 0.37 (5)	9.57 ± 5.25 (2)	7.18 (1)	(0)

banana leaves to the other litter types presented, though experiment 2 suggests a preference for tea branches.

From these preliminary experiments no hard conclusions can be drawn. On the other hand the results are largely in accordance with our field observations. The overall impression is that *Microtermes* has a preference for maize litter, which may partly explain the high population densities found in maize fields. The low population densities in tea fields may be explained by the fact that litter on these fields contains mainly tea leaves, which seem to be quite unpalatable. Also *O.kibarensis* does not seem to like tea leaves very much, but it is often observed eating the bark off the stem. Both species can periodically be present in large numbers, when the tea shrubs have been pruned. Apart from tea leaves, *O.kibarensis* appears to forage equally readily on all litter types present in the area, so food preference can not be used to explain the species' distribution.

7.5 SOIL PREFERENCE OF HUMUS-FEEDING TERMITES

7.5.1 Methods

Some experiments were done with humus-feeding termites (Apicotermitinae) to study the survival in and the preference for soils with different amounts of organic matter. Two types of soil were used: red soil with 0.9 % organic matter collected from a lawn near the laboratory and dark soil with 3.0 % organic matter from a banana field near Keumbu. Apart from the organic matter content, the textural composition of the two types of soil was almost the same. The termites were collected from the same lawn as the red soil.

First attempts were made to keep small colonies of *Astalotermes sp.* in containers with the two types of soil. Coarse organic particles were removed from the soil, which was then slightly moistened and put in transparent plastic containers of 15×15 cm, 25.5 cm high and open at the top. At least 100 termites, incl. a queen if possible, were introduced in every container. The containers were stored in a dark room with an average temperature of 21 °C (range 19-24°), which is close to the soil temperature in the field. They were loosely covered with hard-plastic sheets. Termite activity could be observed through the walls of the containers.

The preference of this species for one or the other type of soil was tested in two experiments. In the first experiment, four containers were prepared with both soil types. In two containers the two types were placed on top of each other in two layers of 10 cm: in one container red on top, in the other dark on top. Ca. 50 workers were introduced on the top layer. Two other containers were filled with the two types of soil side by side. In one container ca. 50 workers were put on the red soil, in the other one on the dark soil. All containers were examined daily and dead termites were removed until all termites had died.

The aforementioned method was not satisfactory because of high mortality, so in a second experiment preference was tested in another way. Twenty times,

forty workers were introduced in a container with the two types of soil side by side. They were not scattered evenly over dark and red soil, because that would have caused a very high mortality. These termites tend to stay close together, as was found in the course of the experimental work. Alone or in small groups they do not survive for long. For that reason they were put close together on one side of the boundary: 10 times on the red soil and 10 times on the dark soil. A Petri-dish (diam. 90 mm) was then placed over them, so that equal areas of both soil types were available to the termites. After three days the number of termites (dead or alive) in both soil types were recorded.

7.5.2 Results

Attempts to keep *Astalotermes sp.* in plastic containers were only partly successful. Colonies with a queen could easily be kept in dark soil, but without a queen all termites died within a few weeks. In red soil no colonies could be kept, even if a queen was present.

In the first experiment, all termites placed on red soil died within 6 days. They had hardly entered the soil. On the dark soil, the last termite survived 10 days in one container and 14 days in the other. They had tunnelled in the dark soil but had not entered the red soil.

If, in the second experiment, the soil type on which the termites were placed, were suitable, one would expect them to start tunnelling immediately. Else one would expect them to start wandering, at least after some time. The experiment showed (Table 7.12.), that termites placed on the red soil wandered much more than those placed on the dark soil. After three days on average about half of the former termites had crossed the boundary, while less than 10 % of the latter had done so. This difference is highly significant (t-test: $P < 0.01$), so the red soil appears to be less suitable for this termite species. The fact that some termites crossed from the dark soil to the red soil, could be an indication that they do

Table 7.12. Choice of *Astalotermes sp.* between red and dark soil. Each time 40 workers were introduced and after 3 days those alive were counted.

Introduced on red soil			Introduced on dark soil		
Total	Red soil	Dark soil	Total	Red soil	Dark soil
5	0	5	2	0	2
11	1	10	19	3	16
14	14	0	22	1	21
18	0	18	24	0	24
22	8	14	28	3	25
24	16	8	31	12	19
25	9	16	32	0	32
30	18	12	33	2	31
31	7	24	37	0	37
20.0 ± 2.9	8.1 ± 2.3	11.8 ± 2.4	25.3 ± 3.5	2.3 ± 1.3	23.0 ± 3.4

not immediately sense the unsuitability of the red soil.

Now the question arises why *Astalotermes sp.* can still be found in red soil. At the site where the red soil for the experiment was collected, they were even quite numerous. It is possible, that these termites do not only consume humus, but at least also decaying parts of roots, which were removed from the soil in the experiments.

7.6 DIGGING ACTIVITY IN UNDISTURBED SOIL

7.6.1 Methods

To study the origin of the material used for lining the tunnels and the fate of the excavated earth, two experiments were carried out. The first experiment was started in July 1984. A concrete container of 1×2 m (inner dimensions), open at the top, was filled with two layers of soil of 0.3 m thick. The bottom layer consisted of red Kisii soil and the top layer of black soil (Vertisol).

The central part of a *P.spiniger* nest, measuring approx. 0.5 m in all directions, was placed in one corner of the container. This species was chosen, because it builds compact nests, which can easily be transferred. In the remaining part of the nest no queen was found and it was assumed that she was present in the transferred part. A number of funguscombs was crumbled and scattered around the nest to serve as initial food source.

Part of a nest of *Basidentitermes amicus*, which was situated on top of the *P.spiniger* nest, was also transferred and placed near the other nest. At three places in the container, 4 intact funguscombs of *Microtermes* were placed close together with 100-200 workers and soldiers and these were covered with loose soil. Dry chopped maize stalks were scattered on the soil surface. The soil was examined after 5 months.

Another experiment was started in December 1984. A circular trench was dug around a nest of *P.spiniger* in a pasture on red soil near the laboratory. The trench was 0.5 m wide and 0.7 m deep with an inner diam. of 1.6 m. It was filled with black soil up to 10 cm below ground level. The upper 10 cm was filled with the original top soil. After 7 months the black soil and surrounding red soil were examined.

7.6.2 Results

When the soil in the concrete container was dug up, an extensive network of tunnels was found near the *P.spiniger* nest. Most belonged to *P.spiniger*, some to *B.amicus*. Both species had built new chambers. Some large tunnels (ca. 2.5 cm wide) of the former species extended away from the nest. Smaller tunnels of ca. 2 mm branched off at many places. No *Microtermes* were found nor signs of their activity.

Where a tunnel of *P.spiniger* crossed the boundary between the red and the black soil, the coating of the tunnel often contained both types of soil. At some distance from the nest (>0.3 m) this mixing never extended for more than 5

cm beyond the boundary. The amount of red soil at the black side (max. ca. 50 %) was always greater than the amount of black soil at the red side (max. ca. 30 %). The rate of mixing decreased with the distance from the boundary. Nearer to the nest many tunnels running through black soil had a thick (2-10 mm) coating of mainly red soil (ca. 90 %), but those penetrating red soil never contained more than ca. 50 % black soil and usually much less. Small tunnels (2-4 mm) did not often have coatings with mixed soil.

The newly built chambers of *P.spiniger* were mainly coated with red soil, except for one which was situated in the upper (black) layer and contained ca. 80 % black soil. The other chambers contained 5-40 % black soil: in the upper layer more than in the lower layer. Because of the mixing of two colours it could be seen that the coatings were deposited in thin layers of ca. 0.2 mm.

B.amicus had taken over two chambers of *P.spiniger*, in one of which a queen was found. Some black soil was deposited in these chambers. The rest of their activity had taken place in the upper layer where no mixing of soil was found.

The soil in the trench of the second experiment showed considerable termite activity. The rate of mixing of the two soil types was different for the various termite species:

P.spiniger: The situation was very much like that in the first experiment. No chambers had been built in the black soil and major outgoing tunnels passed underneath. Smaller tunnels occasionally entered the black soil and were always coated with red or mixed soil up to at least 15 cm from the red soil. The proportion of red soil in the coatings decreased gradually with distance. Tunnels in red soil never contained black, but in the coatings of two chambers black soil was found.

O.fulleri: Many large tunnels ran through the black soil. Where they passed the boundary, there was usually a thick (2-3 mm) coating of red soil, which decreased gradually until at 20-30 cm no red soil was present anymore. A little black soil was usually present at the red side of the boundary. Small tunnels were not often coated with red soil.

Microtermes sp.: Numerous tunnels were found in the black soil up to the bottom of the trench. The first 10-15 cm was always coated with red or mixed soil. Red coatings could be ca. 2 mm thick. No black soil occurred at the red side of the boundary.

B.amicus: This species had entered the black soil from above to a depth of ca. 10 cm. All tunnels contained varying amounts of red soil. Some black soil occurred at the red side.

Pr.gracilipes: Same as *B.amicus*.

Apicotermitinae: Though present in the red soil, signs of their activity were not found in the black soil.

It is apparent from these experiments that termites can create an extensive system of tunnels in a relatively short time. Because soil types of different colour were used, it could be seen that part of the soil material removed from the tunnels was packed in unused cavities. The fact that tunnel coatings near the boundary between the two types of soil were often made up of the two types mixed together,

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suggests that these coatings are usually put in place after a certain tunnel segment has been excavated. Red soil was more often displaced to the other side of the boundary than black soil. It may be that the termites had a slight preference for red soil as a coating. Whether conditioning is involved in this, can not be inferred from these experiments alone.

8 GENERAL DISCUSSION AND CONCLUSIONS

The most important factors influencing the distribution of termites in Kisii District are altitude, thickness of the soil, groundwater level, intensity of tillage and type of crop grown.

From west to east, the altitude of the area rises from 1400 to 2100 m. At lower altitudes, all species recorded for the area can be found, except *Odontotermes tanganicus*. *Macrotermes michaelseni* is common in South Nyanza District but disappears almost immediately beyond the border with Kisii District. The reason for this need not be the higher altitude, but more likely the fact that the Kisii farmers have removed all mounds of *M.michaelseni* from their area of occurrence. Destruction of the mounds of *Pseudacanthotermes spiniger* does not affect this species in the same way, because the nest proper (the hive) is almost entirely subterranean. The mounds are usually rebuilt within a few months.

P.spiniger quite abruptly disappears above an altitude of ca. 1700 m. No indications could be found for other factors than altitude, or more accurately temperature, which might cause this phenomenon. The same holds for some other species, though the boundary of their distribution does not appear as sharp. Above 1700 m, only *Microtermes* spp., *O.kibarensis*, *O.amanicus*, *O.tanganicus*, *Cubitermes testaceus* and some Apicotermitinae are common. At still higher altitudes, *Microtermes* disappears and *O.kibarensis* becomes less common.

Within its general area of distribution, as determined by altitude, other factors determine whether a species is actually present or not. In well-drained places with shallow soils, the most common species are *C.testaceus* and *Microcerotermes parvus* (the latter species only in the presence of woody litter). In places with regularly high groundwater levels, *Odontotermes* spp., *M.michaelseni* and *P.spiniger* build large mounds, thereby in effect raising the ground level. Other species, like *Microtermes* and Apicotermitinae species, take advantage of this.

As soon as a site is cultivated, a number of species disappears: *Cubitermes* spp., *O.fulleri*, *O.nolaenis*, *M.parvus*, *B.amicus*, *P.gracilipes* and often *Adaiphotermes*. Intensity of tillage partly depends on the type of crop grown. Fields with bananas, coffee, tea or trees are not tilled as frequently as fields with annual crops like maize, beans, sorghum etc. Therefore, fields under permanent crops harbour more species. Only *Microtermes* spp. thrive in intensely tilled fields, while *Astalotermes* and *Astratotermes* may be present in low numbers, mainly along the edges of the fields. *M.michaelseni* and *P.spiniger* may also maintain nests in such fields, though their nests usually disappear after many years of continuous cultivation. Some species that do not nest in these fields, do forage there, e.g. *M.michaelseni*, *P.spiniger* and *O.kibarensis*. Crops influence the density of termite populations through their annual litter production and the palata-

bility of this litter. Tea leaves, for instance, are not attacked by any of the species in Kisii District. The number of wood-eating species may increase after pruning of the tea shrubs. We have the impression that bananas, too, have a depressing effect on *Microtermes* spp. and *P.spiniger*.

8.2 EFFECTS OF TERMITES ON THE SOIL

8.2.1 *Modification of the soil structure*

8.2.1.1 Formation of subterranean nest and tunnel systems

In the study area, we found extensive systems of underground passages and nest chambers, mostly excavated by fungus-growing Macrotermitinae. Small fungus chambers (diam. < 5cm) of *Microtermes* spp. show a random, though somewhat aggregated, distribution in the upper 2 m of most soil profiles. Since this species has a widespread occurrence and excavates diffuse nest systems, fungus chambers and foraging tunnels were found in almost every soil pit. *Odontotermes* spp. and *P.spiniger*, on the other hand, have more or less centralized nest systems, composed of clusters of oval fungus chambers with a diameter of 5-20 cm. On well drained sites, fungus chambers of *P.spiniger* were found at depths between 10 and 100 cm and those of *Odontotermes* spp. between 50 and 200 cm. In poorly drained plains and valley bottoms, they were situated above the groundwater zone, either in mounds or just beneath the soil surface.

All examined species construct underground foraging tunnels. The larger tunnels, with a diameter of 0.5-4 cm, are excavated by *M.michaelseni*, *Odontotermes* spp. and *P.spiniger*. They ascend more or less radially from the nests and are plastered with clay particles, which suggests that they are permanent features. Smaller, presumably temporary passages connect this main system with sources of food at the soil surface. Both species construct soil sheetings and covered runways at the surface. *Microtermes* excavate only narrow tunnels (diam. < 1.5 mm), which usually occur in a dense network because of the disperse nest systems and subterranean feeding habits of this species. Some species construct tunnels for other purposes than foraging. Deeply situated *Odontotermes* nests may have one or more ventilation shafts, with a diameter up to 20 cm, which allow the release of metabolic heat and the exchange of gases.

Since many foraging tunnels seemed to be used only temporarily, we became interested in the dynamics of foraging systems. In an experiment with soil columns, we found that the rate at which new tunnels are made depends largely on species and feeding habits. *Microtermes* appeared to be the most active species, which may be attributed to its habit of foraging underground and the consequent necessity to exploit a large part of the soil system. However, their digging activity involves only a slight translocation of soil materials in comparison with the other Macrotermitinae. Very little disturbance was detected in soil columns in areas above 1700 m, which is caused by the gradual disappearance of some

litter feeding species (e.g. *M.michaelseni, P.spiniger, Microtermes* spp.) towards higher altitudes.

Little is known about the extension of underground foraging tunnels. Darlington (1982) estimated the volume of foraging tunnels of *M.michaelseni* at 366 ml/m² of area in the main foraging zone. As far as we know, no attempts have been made to measure the rate at which foraging systems are renewed.

The occurrence of large underground tunnels is supposed to have important consequences for the permeability and porosity of the soil, but these effects have hardly been measured (Lee and Wood, 1971). In most studies, conclusions are drawn from a comparison of termitaria and surrounding soils, whereby the presence of tunnels in the foraging area is neglected. Only few measurements were made on the importance of tunnel systems in soils with termite populations (Maldague, 1964; Spears, 1975).

We followed three approaches to investigate the effects of termite tunnels on physical soil properties. The first one was based on regional (natural) variations in termite activity, the second one on local variations associated with differences in land use and the third one based on field experiments.

In an attempt to relate the decrease of termite activity towards higher altitudes with differences in physical soil properties, we found that total pore space and capillary pore space gradually increased with altitude. However, we found no clear differences in the number of termite tunnels at various altitudes, and concluded that the increase of soil porosity is caused by higher humus contents. Neither could we detect differences in non-capillary porosity and hydraulic conductivity associated with lower termite activity. We concluded that the presence and properties of the deep humic topsoil are more important for the soil structure than the occurrence of termite-made tunnels. The high organic carbon content of soils in the eastern highlands is the result of a combination of circumstances. Mineralization of organic matter proceeds relatively slowly at higher elevations because of lower average soil temperatures. The presence of volcanic ash in these soils has probably promoted the formation of stable clay-humus complexes, so that the breakdown of organic matter is retarded. Finally, we suppose that the low population densities of litter-feeding termites may have contributed to a further accumulation of organic matter in the soil. In our column experiments we found that mulch, applied to attract the termites, was still untouched after 30 weeks.

In the Wanjare area, we examined the relation between farming practices and the effects that termites have on physical soil properties (Chapter 6). Population studies showed that cultivation practices and the type of crop grown affect the population density of termites. The highest foraging activity was recorded in maize fields and the highest species diversity in grassland. We attributed this to the abundance of litter in the first case, and the lack of cultivation in the latter. Micromorphological studies on impregnated soil samples nevertheless showed that the visible effects of termite activity were about equal among all examined fields. A comparison of various physical soil properties confirmed the structural uniformity of the examined soils. We concluded, therefore, that

changes in termite populations do not necessarily have measurable effects on the soil structure. This is particularly true when the soil has a porous and stable structure such as the clayey and iron-rich Oxisols of Wanjare. We supposed that this structure offers excellent habitat conditions for termites, as it reduces the amount of work they have to direct to construction and maintenance of nest and tunnel systems. Consequently, changes in termite populations have only marginal effects on these soils.

By means of an experimental set-up, in which various cultivation practices were considered (tractor ploughing, traditional hoeing, mechanical compaction), we attempted to manipulate the activity of termite populations, hoping to find evidence for subsequent changes in physical soil properties (Chapter 5). Ploughing appeared to decrease the number of tunnels made by *Odontotermes* and Apicotermitinae species. Application of aldrin resulted in a reduction of all termite tunnels, while mulching had the opposite effect. We noticed that similar differences occurred in the number of other biopores and suggested that many of them were in fact made by termites but had lost their specific shape in the course of time.

Considerable time was spent on the examination of physical soil properties associated with changes in the activity of termites. Unfortunately, the direct effects of tillage and compaction could not be distinguished from some of the effects caused by termites. Moreover, measurements of total pore space and saturated hydraulic conductivity appeared to be of little value. By means of moisture retention characteristics a distinction was made between various classes of equivalent pore sizes in order to find out how termites affect soil porosity. Similarly, measurements of hydraulic conductivity were made at various soil moisture tensions. Nevertheless, most measurements failed to produce statistically significant differences among the considered treatments.

Contrary to our expectations, the volume of large pores ($> 500 \mu m$) was hardly affected by the stimulation or obstruction of termite activity. However, we generally noted increased volumes of smaller pores (particularly those < 200 μm) under circumstances that were supposed to depress termite activity. The abundance of these pores decreased from aldrin-treated plots through plough plots, hoe plots, compacted plots and mulched plots. Although the differences were not statistically significant, these findings may be explained as follows. If termite activity is suppressed, their tunnels are no longer maintained and eventually collapse. This results in a reduction of the number of large pores and an increase in finer pores. The stimulation of termites has the opposite effect. Soil particles are then repacked to make room for tunnels and chambers. The notion that this may reduce capillary pore space is recognized by several authors (Lee and Wood, 1971; Spears et al., 1975).

Associated with the differences in capillary pore space, we recorded increased levels of hydraulic conductivity in plots in which termite activity was obstructed. It follows that termite-made tunnels have a negligible effect on hydraulic conductivity of the studied soils. This conclusion was supported by the results of staining tests with a methylene-blue tracer. We found that water flowed princi-

pally through the fine porous matrix of the soil mass and hardly through termite tunnels. Also on theoretical grounds we inferred the limited importance of termite tunnels for water flow. The soils have a very high capillary storage capacity, so that the tunnels remain air-filled after rainfall. Spears et al. (1975) found that the surfaces of termite tunnels were significantly more water repellant than the surfaces of adjacent peds and concluded that these structures may in fact decrease infiltration.

The effects of underground nest and tunnel systems on physical soil properties have been the subject of much dispute. Maldague (1964) reported a porosity of 58 % in forest soils with a high termite population compared with 48 % in adjacent fallow land, and attributed the difference to termites. However, this is probably not entirely correct, since cultivation of tropical forest soils often leads to structure decline and hence lower porosity of the soil. Spears et. al. (1975) found that chemical control of termites (*Gnathamitermes tubiformans*) in western Texas resulted in a higher capillary pore space and a lower non-capillary pore space, which is in accordance with our findings. They concluded that termites increase non-capillary pore space by construction of tunnels, and decrease capillary pore space by the repacking of soil particles. Termite control had no effect on hydraulic conductivity tests, which was however attributed to sealing of termite pores by the metal rings enclosing the core samples.

8.2.1.2   Sorting and homogenization of soil components.

In the study area, we found that termites transport large quantities of fine-textured soil material to the surface, where it is used for the construction of mounds, sheetings and covered runways. The removal of fine-grained material from deeper soil horizons and weathered rock results in the formation of a gravel or stone layer beneath a deep mantle of fine-textured soil. Wielemaker (1984) demonstrated that the activity of termites offers a plausible explanation for the existence of gravel layers beneath a gravel-free topsoil in the Kisii area.

Texture analysis pointed out that termites obtain their building materials from various depths in the soil. Collection depths range from less than 25 cm (humivorous termites) to about 150 cm or deeper (Macrotermitinae). In mounds, there is a tendency towards higher proportions of clay and lower proportions of sand. Selection of fine-grained material was less apparent in sheetings and covered runways. A comparison of the various sand fractions showed that termites prefer medium and fine sand to coarse sand. *M.michaelseni* and *P.spiniger* demonstrated a clear preference for particles of 150-420 μm, while the smaller workers of *O.fulleri* and *O.kibarensis* preferred particles of 50-210 μm. *Cubitermes* mounds appeared to contain lower amounts of particles of 105-850 μm than the soil material from which they were built. Mostly, the differences between mound soil and surrounding soil appeared to be much smaller than is often reported in the literature (Kemp, 1955; Maldague, 1959; Stoops, 1964). The reason for this discrepancy is undoubtedly the very high clay content of the soils under study. Termite mounds built on soils with a high clay content may in fact contain a greater proportion of sand than surrounding topsoils (Pomeroy, 1976).

The quantities of soil material accumulated in sheetings by *P.spiniger* was estimated at about 1300 kg ha⁻¹ yr⁻¹. Similarly, the soil packed in maize stalks by *Microtermes* amounts to 80-180 kg ha⁻¹ yr⁻¹. No measurements were made of the weight of soil present in termite mounds. Assuming a density of 5-10 *P.spiniger* mounds per hectare, each with a volume of 0.3 m^3 and a bulk density of 1 g cm^3, a total weight of 1500-3000 kg ha⁻¹ is obtained.

Soil particles are also translocated in horizontal and even downward directions. In our column experiments (Chapter 6), we found that particularly *M.michaelseni* and *Odontotermes* spp. had translocated small amounts of clay into the columns. The clay was used for the lining of foraging tunnels and occasionally it was deposited in abandoned cavities. Similar results were obtained in the experiments with red- and dark-coloured soils (Chapter 7). The red soil may of course have some favourable properties compared to the soil materials introduced in the experiments, so that the rate of translocation could be less under natural conditions. Evidence for downward transport was found in abandoned tunnels and nest chambers in the subsoil, which were occasionally backfilled with dark-coloured topsoil material. It is therefore conceivable that termites have had an important contribution to the homogeneous nature of the soils in the study area.

However, there is no evidence that the gradual decrease of termite activity towards higher altitudes has led to the development of more pronounced soil horizons. Also in Wanjare, no differences could be detected among the various farmer's fields. Again, the soil fabric is apparently sufficiently stable to prevent the appearance of soil profile differentiation. Soils in which 2:1 lattice clay minerals are dominant may benefit from the activity of termites. Wielemaker (1984) examined the importance of bioturbation in unstable Planosols and found marked differences in horizon differentiation between mounds and adjacent soils. Horizon differentiation away from mounds was caused by illuviation of clay, which is of no importance in the soils of the present study.

8.2.1.3 Formation of pellet structures

Micromorphological studies were conducted to examine the effects of termites on the soil structure. Apart from numerous tunnels and cavities excavated by termites, we observed large amounts of clay pellets of similar shape and arrangement, which were apparently formed by the mandibles of termites. From a comparison of pellets with the size and shape of cavities in which they occurred, we were able to trace the species responsible for their formation. The size of the oral pellets ranged from 20-50 μm for *Microtermes* to 80-120 μm for *P.spiniger* (pellets made by *M.michaelseni* were not studied). These pellets appeared to be cemented together with saliva and did not seem to contain faecal material. Other pellets, with a welded shape and a laminar arrangement, seemed to be composed of a mixture of clay and faecal material. Pellets occurred as backfill material in tunnels and cavities, but most of all as matrix material in the soil. In areas with large termite populations, such as Wanjare, the area fraction of termite pellets was about 20 % of the soil matrix. In the subsoil the pellets were

subject to degradation due to compaction, swelling and dispersion. Features indicative of degradation were common in soils containing 2:1 lattice clays developed on basic parent material. The most stable and well-developed pellet structures were observed in the Oxisols of Wanjare.

Associated with an increase in organic matter content of the soil at higher altitudes, we noticed a shift in the relative importance of oral pellets towards faecal pellets. This is attributed to the growing importance of humus-feeding termites and the small numbers of wood-and-litter-feeding species.

Pellet structures affect the entire range of soil properties discussed in the preceeding sections. They are the origin of the very high microporosity of the soil, the high moisture storage capacity and the high infiltration rate. Thus they illustrate the importance of biological homogenization of the soil profile, which is even more pronounced when the soils have less desirable physical properties than those studied by us.

8.2.2 Decomposition of organic material

Most species of termites consume dead organic matter, such as wood, leaves, dry grass, dung, 'humus' etc. Only a few species, which do not occur in the study area, attack living parts of plants, notably grass. Only one species in the area, *M.parvus*, is strictly a wood-feeder. Digestion of cellulose and lignin is aided by microorganisms in its gut. This species is only locally of some importance for the breakdown of woody litter.

Most species in the area are wood-and-litter-feeders and use fungi (*Termitomyces*) to help digesting the cellulose and lignin. For that purpose, special structures are built from pellets of masticated organic material that has passed the gut but has hardly been digested. On these funguscombs grows the fungus mycelium. After a certain period, the oldest part of a comb is eaten by the termites.

These species have to collect large amounts of organic material for the construction of funguscombs. We estimate that 30-90 % of the litter on farmer's fields is removed by termites, the highest percentages on maize fields and other fields with annual crops. When these crops are harvested, the plants are almost completely removed by the farmers, so termites can only collect what is left behind. Our field experiment showed that mulching increased the foraging of termites, but we did not measure which proportion of the mulch was actually removed. Collins (1981a) found that in central Nigeria, only 24 % of the annual litter production of primary woodland was removed by termites. However, another 31 % was removed by bush fires, which do not occur in Kisii District.

The removal of such a large proportion of the litter from the farmer's fields must have consequences for the fertility and the structure of the soil. Unfortunately, the project did not last long enough to study this for a sufficient period of time. We were not able to detect differences in fertility between farmer's fields which differed with respect to termite activity. Another point is that reference fields in which termites had never occurred, did not exist. As mentioned earlier, differences in soil structure between the farmer's fields were also insignificant. In our opinion, more research should be carried out on the removal and redistri-

bution of organic matter by litter-feeding termites, since it may have consequences for the agricultural practice.

The effect of humivorous termites on the organic matter content of the soil is even less studied. We were not able to spend much time on these species. In cultivated fields, they did not reach high population densities, so their effect on the soil of those fields is probably negligible compared to other species. In pastures it may be different. According to Okwalol (1980), depletion of organic matter by humivorous termites in pasture soils may eventually lead to denudation and erosion. In our study area, we did not find any evidence of this.

8.2.3 Chemical enrichment of soil materials

The chemical composition of samples from termite mounds and soil sheetings was examined and compared with that of surrounding soils. All the investigated termite structures appeared to be chemically enriched in comparison with the soil material from which they were made. Although subterranean species, like *Odontotermes* spp., do not normally build mounds, their effect on the soil material appeared to be the same. We noticed a general increase in organic carbon and nitrogen, exchangeable calcium and magnesium, cation exchange capacity (CEC) and total phosphorus. Except for mounds of humivorous species, in which faecal material is incorporated, the chemical enrichment was attributed to the addition of saliva to the soil particles.

The significance of termites in ecosystems is closely connected with their ability to consume a large part of the primary biomass production and to concentrate nutrients in mounds or subterranean nests. In the case of Macrotermitinae, most of the collected litter is used to maintain fungus gardens. Termite mounds and fungus gardens may thus contain a disproportionately large portion of all nutrients in the soil system. According to some authors, this has a negative effect on soil fertility. For instance, Parker et al. (1982) noticed an increase in soil nitrogen following the elimination of subterranean termites in a desert ecosystem.

The return of nutrients proceeds mainly through the erosion of termite structures. As mounds continuously erode, redistributed mound material enriches the topsoil, so that nutrients become available for plant growth. However, mounds of *M.michaelseni* and *P.spiniger* are predominantly built of subsoil material that, even when enriched by termites, has mineral and organic matter contents lower than those of adjacent topsoils. Soil sheetings, on the other hand, appeared to contain more nutrients than the topsoil, and besides, they desintegrate in a short time. Nevertheless, we found that nutrient turnover through erosion of sheetings was of little importance compared to uptake by crops. Similar conclusions were reached by Pomeroy (1976) and Wood and Sands (1978).

8.3 CONCLUSIONS

1. Highest species diversity of termites is found in uncultivated, deep, well-drained soils at lower altitudes.
2. The more intensive the tillage of the soil, the lower the species diversity of a locality.
3. Most species have lower population densities where tillage is more intensive, but *Microtermes* spp. attain higher densities.
4. The type of crop grown in a field affects termite populations through the required cultivation measures (tillage, weeding etc.) and through the amount and palatability of the litter produced.
5. Between 30 % and 90 % of the litter on the fields is removed by termites, the higher values on fields with annual crops. Most of it is used for the construction of funguscombs, so that return of nutrients to the soil is obstructed.
6. A small part of these nutrients is added to the soil in the form of saliva and faeces during the construction of mounds and sheetings. Erosion of these structures enriches the topsoil, but this enrichment is small in comparison with the average uptake of nutrients by annual crops.
7. Whereas the excavation of tunnels by termites mainly enhances the aeration and rootability of the soil, the formation of a soil matrix composed of pellets appears to determine its moisture characteristics and aggregate structure.
8. The balance between the formation and decay of pellet structures is primarily controlled by the physico-chemical properties of the mineral and organic fractions. To a large extent, this balance determines the suitability of the soil as a habitat for termites, since it determines the amount of work they have to invest in the maintenance of subterranean nests and tunnel systems.
9. Cultivation practices that depress the activity of termites, lead to a shift towards smaller pore size classes. In the long term, this may lead to soil compaction and eventually erosion.
10. However, soils with varying degrees of termite activity, either caused by land use or by climatic factors, appeared to be remarkably similar in most physical and chemical aspects.

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APPENDIX 1. SOIL PROFILE DESCRIPTIONS

Site characteristics

Profile: 1
Elevation: 1530 m
Agroclimatic zone: I 3
Geological formation: Post-Kavirondian intrusive
 in Nyanzian system (Precambrium)
Physiography: flat-topped ridge (Kisii surface)
Slope: almost flat, 2%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Igonga, Wanjare, Kisii District, 34° 42' E; 0° 37' S
Mapping index[1]: U3Ihn
Soil classification: Soil Taxonomy: Typic Haplohumox
  FAO/Unesco: Humic Ferralsol
Local petrography: quartz-diorite and granite
Surrounding landform: rolling
Land use: traditional, smallholder arable farming (maize, beans)
Human influence: slight, ox-plough
Soil fauna: Microtermes, Pseudacanthotermes
Date: 14-9-1984

Profile Description

Ap1	0– 10 cm	Dark reddish brown (5YR 3/2) moist, and dark reddish brown (5YR 3/3) dry, clay, moderate fine crumb; slightly sticky, slightly plastic (wet), firm (moist) and soft (dry) consistency; few fine and many very fine pores; clear smooth transition to.
Ap2	10– 25 cm	Dark reddish brown (5YR 32) moist, and dark reddish brown (5YR 3/3) dry, clay; moderate fine subangular blocky; slightly sticky, slightly plastic (wet), friable (moist) and slightly hard (dry) consistency; few fine and many very fine pores; clear wavy transition to.
B1	25– 70 cm	Dark reddish brown (2.5YR 2.5/4) moist, and dark reddish brown (2.5YR 3/4) dry, clay; moderate medium angular blocky; slightly sticky, non plastic (wet), friable (moist) and slightly hard (dry) consistency; thin patchy cutans as linings in few vertical pores; few medium, few fine and common very fine pores, few fine termite passages and few fungus chambers (Microtermes); gradual smooth transition to.
B21	70–100 cm	Dark reddish brown (2.5YR 3/4) moist, and dark red (2.5YR 3/6) dry, clay; very weak, medium subangular blocky structure, breaking easily into weak, very fine crumbs; slightly sticky, non plastic, very firm (moist) and soft (dry) consistency; thin patchy cutans as linings in few vertical pores; common fine and many very fine pores, few fine termite passages and few fungus chambers (Microtermes); gradual smooth transition to.
B22	100–140 cm	Dark red (2.5YR 3/6) moist, and red (2.5YR 4/6) dry, clay; very weak, medium subangular blocky structure, breaking easily into weak, very fine crumb; slightly sticky, non plastic (wet), very firm (moist) and soft (dry) consistency; thin patchy cutans as linings in few vertical pores; few coarse and medium, common fine and very fine pores, few termite passages and fungus chambers (Microtermes); clear wavy transition to
C1	140–180 + cm	Dark red (2.5YR 3/6) moist, and red (2.5YR 4/6) dry, gravelly sandy clay loam; moderate, medium to coarse subangular blocky; non sticky, non plastic (wet), loose (moist) and hard (dry) consistency; no cutans; very frequent (> 50%) angular, strongly weathered gravel (20–30 mm); frequent, small hard iron concretions; few fine pores.

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description no.: 1   Soil classification: Typic Haplohumox

Depth cm	5–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150	160–170	180–190
pH H_2O	5.6	5.4	5.3	5.5	5.5	5.5	5.3	5.1		5.0
pH KCl										
C%	2.61	2.26	1.48	0.92	0.81	0.73	0.81	0.31		0.31
N%	0.21	0.17	0.11	0.09	0.08	0.07	0.07	0.02		0.02
P_2O_5 % (total)	0.15	0.13	0.14	0.11	0.11	0.11	0.13	0.15		0.18
CEC (pH 7.8) mmol/kg	162	143	140	128	126	121	115	94		100
$\frac{1}{2}$ Ca^{2+} mmol/kg	37	31	59	21	17	11	1	<1		<1
$\frac{1}{2}$ Mg^{2+} mmol/kg	12	12	12	10	7	7	3	3		3
Na^+ mmol/kg	<1	<1	12	<1	<1	<1	2	<1		<1
K^+ mmol/kg	1	1	7	<1	<1	<1	3	<1		<1
$\frac{1}{3}$ Al^{3+} mmol/kg	11	12	15	5	5	5	13	5		5
H^+ mmol/kg	4	3	6	2	4	5	7	2		4
% B.S. (sum of cations)	31	31	64	24	19	15	8	3		3
Texture										
Sand 2.0 –0.85 mm	6.5	8.0	6.5	8.0	6.6	6.2	12.6	17.3	16.3	
Sand 0.85–0.42 mm	6.0	6.6	5.7	5.9	4.7	5.4	5.5	5.3	4.4	
Sand 0.42–0.21 mm	7.6	7.5	4.8	4.5	4.6	5.0	4.1	9.1	9.7	
Sand 0.21–0.10 mm	6.1	6.1	4.8	6.2	6.5	7.7	8.3	20.0	19.3	
Sand 0.10–0.05 mm	3.8	4.4	3.6	6.3	5.3	5.3	7.8	18.5	13.2	
Total sand %	30.0	32.6	25.4	30.9	27.7	29.6	38.3	70.2	62.9	
Silt %	21.8	20.0	15.0	12.4	17.0	9.4	13.0	12.6	11.7	
Clay %	48.2	47.4	59.6	56.7	55.3	61.0	48.7	17.2	25.4	
Texture class	C	C	C	C	C	C	C	S.L.	S.C.L.	
Bulk density (g/cm³)	1.17	1.21	1.29	1.04	1.04	1.08	1.20	1.49		

Site characteristics

Profile: 2
Elevation: 1530 m
Agroclimatic zone: I 3
Geological formation: Post-Kavirondian intrusive
  in Nyanzian system (Precambrium)
Physiography: flat-topped ridge (Kisii surface)
Slope: almost flat, 2%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Igona, Wanjare, Kisii District, 34° 42′ E; 0° 37′ S
Mapping index[1]: U3Ihn
Soil classification: Soil Taxonomy: Typic Umbriorthox
                    FAO/Unesco: Humic Ferralsol
Local petrography: quartz-diorite and granite
Surrounding landform: rolling
Land use: traditional, smallholder arable farming (bananas, pure stand)
Human influence: moderate, ploughing with oxen
Soil fauna: Microtermes, Pseudacanthotermes
Date: 14-9-1984

Profile description

Ap 0– 25 cm Dark reddish brown (5YR 2.5/2) moist, and dark reddish brown (5YR 3/2) dry, clay; weak fine crumb; slightly sticky, non plastic (wet), very friable (moist) and soft (dry) consistency; common fine and many very fine pores, few termite passages; clear smooth transition to.

B1 25– 45 cm Dark reddish brown (2.5YR 3/4) moist, and dark red (2.5YR 3/5) dry, clay; weak fine subangular blocky; non sticky, non plastic (wet), very friable (moist) and soft (dry) consistency; few fine and many very fine pores, few termite passages, gradual smooth transition to.

B21 45–105 cm Dark red (2.5YR 3/5) moist, and dark red (2.5YR 3/6) dry, clay; weak very fine angular to subangular blocky; non sticky, non plastic (wet), very friable (moist) and soft (dry) consistency; thin patchy cutans as linings in few vertical pores; few fine and very fine pores; gradual smooth transition to.

B22 105–150 cm Dark red (2.5YR 3/6) moist, and red (2.5YR 4/7) dry, clay; weak very fine angular blocky; non sticky, non plastic (wet), very friable (moist) and soft (dry) consistency; thin patchy cutans as linings in few vertical pores; few fine and very fine pores, few fine termite passages, abrupt smooth transition to.

BC 150 + cm Red (2.5YR 4/6) moist, and red (2.5YR 4/6) dry, strongly gravelly clay; weak, fine angular blocky; non sticky, non plastic (wet), very friable (moist) and soft (dry) consistency; very frequent gravel, mainly quartz and felspars, very frequent hard iron- and manganese concretions; few very fine pores, few termite passages

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description no.: 2 Soil classification: Typic Umbriorthox.

Depth cm	5–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150	150–160
pH H_2O	5.6	5.4	5.3	5.1		5.0		4.9	
pH KCl									
C%	3.07	1.61	1.00	0.91		0.77		0.59	
N%	0.23	0.13	0.09	0.08		0.07		0.05	
P_2O_5 % (total)	0.14	0.12	0.10	0.12		0.10		0.10	
CEC (pH 7.8) mmol/kg	179	139	158	138		121		116	
$1/2$ Ca^{2+} mmol/kg	66	35	14	8		5		7	
$1/2$ Mg^{2+} mmol/kg	20	13	5	2		2		2	
Na^+ mmol/kg	<1	<1	<1	<1		<1		<1	
K^+ mmol/kg	3	1	2	1		<1		<1	
$1/3$ Al^{3+} mmol/kg	2	7	13	14		19		13	
H^+ mmol/kg	<1	5	6	7		10		6	
% B.S. (sum of cations)	50	35	13	8		6		8	
Texture									
Sand 2.0 –0.85 mm	1.8	5.2	5.4	2.9	2.2	5.0	2.5	7.0	6.4
Sand 0.85–0.42 mm	4.6	5.2	4.1	3.7	3.5	3.5	2.8	3.2	3.5
Sand 0.42–0.21 mm	8.4	4.3	4.2	3.7	3.7	3.4	3.1	3.3	3.8
Sand 0.21–0.10 mm	8.1	3.8	4.5	5.5	6.3	4.6	6.7	4.8	5.0
Sand 0.10–0.05 mm	4.3	2.0	3.3	4.6	4.4	2.3	5.0	3.1	3.2
Total sand %	27.2	20.5	21.5	20.4	20.1	18.8	20.1	21.4	21.9
Silt %	18.9	16.0	15.8	12.2	13.8	15.8	9.5	15.3	16.2
Clay %	53.9	63.5	62.7	67.4	66.1	65.4	70.4	63.3	61.9
Texture class	C	C	C	C	C	C	C	C	C
Bulk density (g/cm³)	0.99	1.11	1.08	1.12	1.01	1.08	1.22	1.27	

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Site characteristics

Profile 3:
Elevation: 1530 m
Agroclimatic zone: I 3
Geological formation: Post-Kavirondian intrusive
  in Nyanzian system (Precambrium)
Physiography: flat-topped ridge (Kisii surface)
Slope: almost flat, 2%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Igonga, Wanjare, Kisii District, 34° 42' E; 0° 37' S
Mapping index[1]: U3Ihn
Soil classification: Soil Taxonomy: Typic Umbriorthox
             FAO/Unesco: Humic Ferralsol
Local petrography: quartz-diorite and granite
Surrounding landform: rolling
Land use: low-input, smallholder coffee-growing
Human influence: slight, manual weeding
Soil fauna: Microtermes, Pseudacanthotermes, Apicotermitinae
Date: 8-5-1984

Profile description

Ap   0– 20 cm   Dark reddish brown (5YR 3/2) moist, clay; weak very fine subangular blocky, crushes easily into fine crumb; slight plastic (et), very friable (moist) consistency; few medium, few fine and common very fine pores, few termite passages, gradual smooth transition to.

A3   20– 40 cm   Dark reddish brown (5YR 3/3) moist, clay; weak fine subangular blocky; slightly sticky, slightly plastic (wet, and very friable (moist) consistency; few fine and common very fine pores, few termite passages; clear wavy transition to.

B1   40– 75 cm   Dark reddish brown (2.5Yr 3/4) moist, clay; moderate fine subangular blocky; slightly sticky, slightly plastic (wet) and friable (moist) consistency; few fine and common very fine pores, few termite passages and fungus chambers (Microtermes); diffuse smooth transition to

B21   75–110 cm   Dark red (2.5YR 3/6) moist, clay; moderate fine angular blocky; slightly sticky, slightly plastic (wet) and friable (moist) consistency; few fine and common very fine pores, few fine termite passages and fungus chambers (Microtermes); diffuse smooth transition to.

B22   110–150 cm   Red (2.5YR 4/8) moist, clay; moderate fine angular blocky; slightly sticky, slightly plastic (wet) and friable (moist) consistency; thin patchy cutans as linings in few vertical pores; few fine and common very fine pores; diffuse smooth transition to.

B23   150 + cm   Red (2.5YR 4/8) moist, clay; moderate fine angular blocky; slightly sticky, slightly plastic (wet) and friable (moist) consistency; thin patchy cutans as linings in few vertical pores; few fine and common very fine pores.

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description no.: 3   Soil classification: Typic Umbriorthox

Depth cm	5–10	20–30	40–50	60–70	80–90	100–110	120–130	140–150	180–190	200–210
pH H_2O	5.4	5.4	5.3		5.5		5.6	5.7		5.4
pH KCl										
C%	2.76	1.85	1.03		0.66		0.63	0.61		0.47
N%	0.25	0.18	0.12		0.07		0.06	0.05		0.04
P_2O_5 % (total)	0.13	0.12	0.11		0.09		0.12	0.10		0.10
CEC (pH 7.8) mmol/kg	144	161	139		141		129	129		93
$^1/_2$ Ca^{2+} mmol/kg	47	70	46		37		35	33		21
$^1/_2$ Mg^{2+} mmol/kg	20	17	13		10		14	15		7
Na^+ mmol/kg	<1	<1	<1		<1		<1	<1		<1
K^+ mmol/kg	2	<1	<1		<1		<1	<1		<1
$^1/_3$ Al^{3+} mmol/kg	1	3	9		1		1	1		1
H^+ mmol/kg	3	2	1		2		2	1		2
% B.S. (sum of cations)	48	54	42		33		38	37		30
Texture										
Sand 2.0 –0.85 mm	1.7	4.1	4.2	7.0	3.9	4.3	4.5	7.2	9.0	4.8
Sand 0.85–0.42 mm	5.8	5.9	5.0	5.7	4.6	4.5	3.7	3.7	3.7	3.4
Sand 0.42–0.21 mm	10.2	8.3	5.9	5.6	4.6	4.4	4.5	3.2	3.1	3.3
Sand 0.21–0.10 mm	7.2	6.2	4.5	4.3	3.6	4.3	3.5	3.0	3.8	3.9
Sand 0.10–0.05 mm	3.3	2.7	2.5	2.7	2.3	3.3	1.9	1.5	3.6	3.4
Total sand %	28.2	27.2	22.1	25.3	19.0	20.8	18.1	18.6	22.9	18.8
Silt %	17.9	16.9	20.4	13.1	18.0	11.8	19.8	20.3	16.2	16.5
Clay %	53.9	55.9	57.5	61.6	63.0	67.4	62.1	61.1	60.9	64.7
Texture class	C	C	C	C	C	C	C	C	C	C
Bulk density (g/cm³)	1.08	1.08	1.23	1.14	1.10	1.17	1.15	1.23	1.28	1.29

Site characteristics

Profile: 4
Elevation: 1530 m
Agroclimate zone: I 3
Geological formation: Post-Kavirondian intrusive
   in Nyanzian system (Precambrium)
Physiography: flat-topped ridge (Kisii surface)
Slope: almost flat, 2%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Igonga, Wanjare, Kisii District, 34° 42' E; 0° 37' S
Mapping index[1]: U3Ihn
Soil classification: Soil Taxonomy: Typic Haplohumox
                    FAO/Unesco: Humic Ferralsol
Local petrography: quartz-diorite and granite
Surrounding landform: rolling
Land use: grassland, sportsground
Human influence: none
Soil fauna: Odontotermes, Microtermes, Pseudacanthotermes, soilfeeders
Date: 7-6-1984

Profile description

A1   0– 25 cm   Dark reddish brown (5YR 3/4) moist, and dark reddish brown (5YR 3/3) dry, clay; weak fine subangular blocky; slightly sticky, slightly plastic (wet), friable (moist) and soft (dry) consistency; few medium and fine, common very fine pores, few termite passages; gradual smooth transition to.

A3   25– 45 cm   Dark reddish brown (5YR 3/4) moist, and dark reddish brownd (5YR 3/3) dry clay; weak fine subangular blocky; non sticky, non plastic (wet), friable (moist) and soft (dry) consistency; few fine and common very fine pores, few termite passages; clear smooth transition to.

B1   45– 75 cm   Reddish brown (2.5YR 3.5/4) moist, and dark red (2.5YR 3/6) dry, clay; weak fine subangular blocky; non sticky, non plastic (wet), friable (moist) and soft (dry) consistency; fewfine and common very fine pores; common termite channels; gradual smooth transition to.

B21 75–100 cm   Dark reddish brown (2.5YR 3/4) moist, and dark red (2.5YR 3/6) dry, clay; weak fine subangular to angular blocky; slightly sticky, non plastic (wet), friable (moist) and soft (dry) consistency; few fine and common very fine pores, few fine termite passages; gradual smooth transition to.

B23 110–145 cm   Dark red (2.5YR 3/6) moist, and red (2.5YR 4/6) dry, gravelly clay; moderate medium angular blocky; non sticky, non plastic (wet), firm (moist) and slightly hard (dry) consistency; thin patchy cutans as linings in few vertical pores; few very fine pores, gradual smooth transition to.

BC   145–235 cm   Dark red (2.5YR 3/6) moist, and red (2.5YR 4/6) dry, gravelly clay loam; moderate medium angular blocky; non sticky, non plastic (wet), firm (moist) and slightly hard (dry) consistency; thin patchy cutans as linings in pores; few very fine pores

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982)'

Laboratory data of profile description No.: 4 Soil Classification: Typic Haplohumox.

Depth cm	20–30	40–50	60–70	80–90	100–110	120–130	140–150	200–210	250–260	350–360	L
pH H$_2$O	5.4	4.9	5.0	5.0		5.1	4.8	5.0	5.2	5.4	5.5
pH KCl	4.8	4.4	4.5	4.4		4.5	4.4	4.6	4.6	4.4	4.4
C %	3.20	2.45	1.50	1.09		0.71	0.69	0.60	0.21	0.12	0.07
N %	0.25	0.18	0.10	0.09		0.07	0.07	0.05	0.03	0.01	<0.01
P$_2$O$_5$ % (totaal)	0.11	0.08	0.07	0.07		0.08	0.09	0.07	0.09	0.01	0.01
CEC (pH 7.8) mmol/kg	174	126	132	136		112	129	105	86	71	49
$^1/_2$ Ca^{2+} mmol/kg	56	20	22	13		12	16	11	17	15	31
$^1/_2$ Mg^{2+} mmol/kg	19	7	3	2		<1	3	<1	2	2	2
Na$^+$ mmol/kg	3	3	<1	<1		2	<1	<1	1	<1	<1
K$^+$ mmol/kg	4	4	4	2		1	<1	<1	<1	<1	<1
$^1/_3$ Al^{3+} mmol/kg	6	26	22	24		18	15	13	14	21	15
H$^+$ mmol/kg	1	3	3	2		2	6	2	1	4	2
% B.S. (sum of cations)	47	27	22	13		13	15	10	23	24	67
Texture											
Sand 2.0 –0.85 mm	5.3	6.2	5.8	5.4	6.8	8.8	11.0	9.3	10.4	13.6	18.8
Sand 0.85–0.42 mm	7.6	6.8	7.0	6.0	5.6	4.9	4.9	4.6	4.5	7.3	8.4
Sand 0.42–0.21 mm	9.4	9.5	6.6	6.2	5.5	5.0	5.2	4.1	2.7	3.2	7.1
Sand 0.21–0.10 mm	7.3	7.2	6.0	5.4	5.2	5.1	4.5	3.7	3.4	4.5	8.8
Sand 0.10–0.05 mm	3.2	3.2	2.6	3.0	3.1	2.5	2.8	2.8	2.9	4.4	6.2
Total sand %	32.8	32.9	28.0	26.0	26.2	26.3	28.4	24.5	23.9	33.0	49.3
Silt %	11.3	9.6	10.0	10.9	9.4	7.3	7.8	9.4	11.4	28.7	34.4
Clay %	55.9	57.5	62.0	63.1	64.4	66.4	63.8	66.1	64.7	38.3	16.3
Texture	C	C	C	C	C	C	C	C	C	CL.	L
Bulk density (g/cm^3)	1.06	1.16	1.06	1.07	1.11	1.13	1.20	1.28	1.44	1.49	1.46

Site characteristics

Profile: 5
Elevation: 1710 m
Agroclimatic zone: I 4
Geological formation: Bukoban system (Precambrium)
Physiography: upper footslope facing a
  quartzite escarpment
Slope: gently sloping, 3%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck, M. Oostrom

Location: Nyanza Agric. Res. Station, Kisii District, 34° 47 Eij 0° 41' S
Mapping index[1]: U3Bhn
Soil classification: Soil Taxonomy: Orthoxic Palehumult
                    FAO/Unesco: Humic Nitosol
Local petrography: basalt
Surrounding landform: rolling to hilly
Land use: cultivated, hybrid maize, modern technology
Human influence: strong, terracing, mechanical ploughing, fertilizer
Soil fauna: Odontotermes, Microtermes, Apicotermitinae
Date: 19-6-1984

Profile description

Ap1   0– 20 cm   Dark reddish brown (5YR 3/4) moist, and dark reddish brown (5YR 3/3) dry, clay; weak fine crumb to weak fine subangular blocky; sticky, plastic (wet), firm (moist) and soft (dry) consistency; common fine faint reddish brown mottles; few fine and many very fine pores; clear, wavy transition to.

Ap2   20– 40 cm   Dark reddish brown (5YR 3/4) moist, clay; moderate fine subangular to angular blocky, in some places weak fine crumb (krotovinas); sticky, plastic (wet) and firm (moist) consistency; patchy, moderately thick humus coatings; few fine and many very fine pores, few termite passages; clear wavy transition to

B21t   40– 80 cm   Dark red (2.5YR 3/6) moist, clay; moderate medium angular blocky to fine prismatic; sticky, plastic (wet) and very firm (moist) consistency; thin broken clay skins and patchy humus coatings; shiny ped faces; few fine and common very fine inped and exped tubular pores, few coarse and medium exped pores, few termite passages and fungus chambers (Microtermes); gradual smooth transition to.

B22t   80–170 cm   Dark red (2.5YR 3.5/6) moist, clay; moderate medium prismatic breaking to fine angular blocky; sticky, plastic (wet) and very firm (moist) consistency; continuous thick clay skins, shiny ped faced; few fine and common very fine inped tubular pores, few medium and coarse exped pores, few termite passages and fungus chambers (Microtermes); clear wavy transition to.

B23   170–200 cm   Like B22t but with 10–20% irregulary shaped basalt stones (40 cm) and angular quartz gravel (5 cm)

B24   200–230 + cm   Red (2.5YR 4/6) moist, slightly gravelly clay; weak medium angular blocky to fine prismatic; sticky, plastic (wet) and firm (moist) consistency; broken thick clay skins, shiny ped faces; few fine and common very fine inped and exped pores; few termite passages.

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description no.: 5   Soil classification: Orthoxic Palehumult

Depth cm	5-10	20-30	40-50	60-70	80-90	100-110	120-130	140-150	160-170	200-210
pH H_2O	6.1	6.1	6.0		6.1		5.7	5.5		5.3
pH KCl										
C%	3.30	1.53	1.09		0.64		0.67	0.55		0.40
N%	0.26	0.12	0.10		0.07		0.06	0.06		0.03
P_2O_5 % (total)	0.18	0.11	0.10		0.10		0.12	0.13		0.13
CEC (pH 7.8) mmol/kg	194	160	158		141		141	138		132
$^1/_2$ Ca^{2+} mmol/kg	104	72	61		42		30	24		19
$^1/_2$ Mg^{2+} mmol/kg	29	33	34		41		38	31		24
Na^+ mmol/kg	3	<1	<1		7		<1	<1		<1
K^+ mmol/kg	6	1	<1		3		<1	<1		<1
$^1/_3$ Al^{3+} mmol/kg							1	2		8
H^+ mmol/kg							1	2		3
% B.S. (sum of cations)	73	66	60		66		48	40		33
Texture										
Sand 2.0 –0.85 mm	1.2	1.6	0.5	0.5	1.0	0.5	0.5	0.7	0.5	1.2
Sand 0.85–0.42 mm	0.9	0.7	0.4	0.4	0.4	0.5	0.5	0.5	0.5	1.3
Sand 0.42–0.21 mm	1.2	0.8	0.7	0.6	0.7	0.8	1.0	0.7	0.7	1.9
Sand 0.21–0.10 mm	2.0	1.6	1.3	1.1	1.4	1.4	1.4	1.6	1.5	3.6
Sand 0.10–0.05 mm	2.1	1.7	1.4	1.1	1.5	1.4	1.5	1.4	1.5	3.3
Total sand %	7.4	6.4	4.3	3.7	5.0	4.6	4.9	4.9	4.7	11.3
Silt %	22.5	22.1	24.0	20.9	19.0	23.2	21.2	21.2	18.6	29.6
Clay %	70.1	71.5	71.7	75.4	76.0	72.2	73.9	73.9	76.7	59.1
Texture class	C	C	C	C	C	C	C	C	C	C
Bulk density (g/cm³)	1.07	1.20	1.21	1.18	1.16	1.14	1.16	1.23	1.22	

Site characteristics

Profile: 6
Elevation: 1700 m
Agroclimatic zone: I 4
Geological formation: Bukoban system (Precambrium)
Physiography: upper footslope (Kisii surface)
  below a quartzite escarpment
Slope: sloping, 10%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Coffee Research Station, Kisii District, 34° 37′ E; 0° 41′ S
Mapping index[1]: U3Bhn
Soil classification: Soil Taxonomy: Typic Paleudoll
                FAO/Unesco: Luvic Phaeozem
Local petrography: basalt
Surrounding landform: rolling to hilly
Land use: high input coffee (pesticides, herbicides), research station
Human influence: strong, terracing, contour ditches, zero tillage
Soil fauna: Odontotermes, Microtermes, Apicotermitinae
Date: 17-9-1984

Profile Description

A1   0– 10 cm   Dark reddish brown (2.5YR 2.5/4) moist, and dark reddish brown (2.5YR 3/4) dry, clay; moderately strong, very fine subangular blocky; non sticky, non plastic (wet), very firm (moist) and hard (dry) consistency; few fine and very fine pores; gradual smooth transition to.

A3   10– 30 cm   Dark reddish brown (2.5YR 2.5/4) moist, and dark reddish brown (2.5YR 3/4) dry, clay; moderate fine subangular blocky, in some places weak very fine crumb (krotovinas); non sticky, non plastic (wet), very firm (moist) and slightly hard (dry) consistency; few medium and fine, common very fine pores, few termite passages; clear irregular transition to.

B21t   30– 60 cm   Dark reddish brown (2.5YR 2.5/4) both moist and dry, clay; strong medium angular blocky; sticky, plastic (wet), friable (moist), and hard (dry) consistency; thin broken clay skins on ped faces and as linings in pores; few medium, common fine and very fine pores, few termite passages; clear smooth transition to.

B22t   60– 90 cm   Dark reddish brown (2.5YR 3/4) both moist and dry, clay; moderately strong, fine to medium prismatic breaking to fine angular blocky; slightly sticky, slightly plastic (wet), very firm (moist), and hard (dry) consistency; continuous, moderately thick clay skins, shiny ped faces; few fine and very fine pores; gradual smooth transition to.

B23t   90–170 cm   Dark reddish brown (2.5YR 3/4) moist, and dark red (2.5Yr 3/6) dry, clay; moderate, fine to medium angular blocky; slightly sticky, slightly plastic (wet), very firm (moist), and hard (dry) consistency; continuous, moderately thick clay skins, shiny ped faces; few fine and very fine pores.

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description no.: 6 Soil classification: Typic Paleudoll

Depth cm	5-10	20-30	40-50	60-70	80-90	100-110	120-130	140-150	160-170	180-190
pH H$_2$O	4.6	5.2	5.4		5.6	5.5		5.6		
pH KCl										
C%	3.24	1.90	1.61		0.94	0.78		0.61		
N%	0.28	0.21	0.15		0.11	0.10		0.08		
P$_2$O$_5$% (total)	0.21	0.13	0.13		0.11	0.11		0.12		
CEC (pH 7.8) mmol/kg	178	172	165		153	156		150		
$^1/_2$ Ca^{2+} mmol/kg	15	64	76		63	55		40		
$^1/_2$ Mg^{2+} mmol/kg	3	21	27		25	29		39		
Na$^+$ mmol/kg	<1	<1	<1		<1	<1		<1		
K$^+$ mmol/kg	2	<1	<1		<1	<1		<1		
$^1/_3$ Al^{3+} mmol/kg	42	6	2		1	1		1		
H$^+$ mmol/kg	10	3	<1		1	1		<1		
% B.S. (sum of cations)	11	49	62		58	54		53		
Texture										
Sand 2.0 –0.85 mm	0.5	0.3	0.3	0.5	0.6	1.0	0.8	0.6	0.8	0.1
Sand 0.85–0.42 mm	0.7	0.4	0.7	0.8	0.8	1.0	1.1	0.7	0.9	0.9
Sand 0.42–0.21 mm	1.1	0.6	0.8	1.2	0.9	1.0	0.9	0.5	0.8	1.0
Sand 0.21–0.10 mm	1.6	1.0	1.6	3.5	1.8	2.1	1.6	0.6	3.2	2.1
Sand 0.10–0.05 mm	1.4	0.8	1.7	4.1	1.7	1.7	1.0	0.5	2.4	1.5
Total sand %	5.3	3.1	5.1	10.1	5.8	6.8	5.4	2.9	8.1	5.9
Silt %	31.7	32.4	28.0	31.0	28.9	20.8	17.4	24.4	21.7	24.6
Clay %	63.0	64.5	66.9	58.9	65.3	72.4	77.2	72.7	70.2	69.5
Texture class	C	C	C	C	C	C	C	C	C	C
Bulk density (g/cm^3)	0.97	1.05	1.04	1.08	1.14	1.18	1.19	1.14	1.18	1.10

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Site characteristics

Profile: 7
Elevation: 1845 m
Agroclimatic zone: I 5
Geological formation: Bukoban system (Precambrium)
Physiography: convex upper slope (Keroka surface)

Slope: sloping, 12%–14%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Keumbu, Kisii District, 34° 50′ E; 0° 45′ S
Mapping index[1]: U1Xh
Soil classification: Soil Taxonomy: Typic Palehumult
                    FAO/Unesco: Luvic Phaeozem
Local petrography: rhyolite and Tertiary volcanic ash
Surrounding landform: hilly
Land use: traditional smallholder arable farming (maize, beans, bananas)
Human influence: moderate, manual cultivation (hoe), contour terracing
Soil fauna: Microtermes, Apicotermitinae
Date: 18-3-1985

Profile Description

Ap   0– 20 cm   Dark reddish brown (5YR 2.5/4) moist, and dark reddish brown (5YR 3/2) dry, clay; moderate fine subangular blocky; non sticky, non plastic (wet), friable (moist) slightly hard (dry) consistency; few medium and fine, common very fine pores; clear, wavy transition to.

A3   20– 60 cm   Dark reddish brown (5YR 2.3/2) moist, and very dark gray (5YR 3:1.5) dry, clay; moderate medium subangular blocky breaking into fine subangular blocky; slightly sticky, slightly plastic (wet), friable (moist) and moderately hard (dry) consistency; few fine and common very fine pores, few termite passages; clear broken transition to.

B1   60– 95 cm   Dark reddish brown (5YR 3/3) moist, clay; moderate medium prismatic to angular blocky, breaking to fine subangular blocky; slightly sticky, slightly plastic (wet) and firm (moist) consistency; thin patchy clay skins and humus coatings as linings in few vertical pores; few fine and common ver fine pores, few termite passages; gradual smooth transition to.

B22t   95–150 cm   Dark reddish brown (2.5YR 3/4) moist, clay; moderate medium prismatic breaking to very fine angular blocky; slightly sticky, slightly plastic (wet) and firm (moist) consistency; broken, moderately thick clay skins, shiny ped faces; few fine and very fine pores; diffuse smooth transition to.

B23t   150–190 + cm   Dark reddish brown (2.5YR 3/4) moist, clay; moderate medium to fine prismatic breaking to very fine angular blocky; slightly sticky, slightly plastic (wet) and firm (moist) consistency; broken, moderately thick clay skins, shiny ped faces; few fine and very fine pores

[1] After 'Soils of the Kissii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description No.: 7 Soil Classification: Typic Palehumult.

Depth cm	5–10	20–30	40–50	70–80	100–110	140–150	180–190
Texture							
Sand 2.0 –0.85 mm	1.9	1.1	0.7	0.3	0.3	0.3	0.4
Sand 0.85–0.42 mm	1.6	1.5	0.9	0.6	0.5	0.6	0.7
Sand 0.42–0.21 mm	2.1	2.2	1.5	1.4	1.3	1.4	1.2
Sand 0.21–0.10 mm	3.4	3.7	2.5	4.0	2.4	3.1	2.0
Sand 0.10–0.05 mm	4.3	4.9	3.0	4.6	3.1	3.3	2.1
Total sand %	13.3	13.4	8.6	10.9	7.6	8.7	6.4
Silt %	34.7	33.8	37.9	18.0	21.0	31.1	26.3
Clay %	52.0	52.8	53.5	71.1	71.4	60.2	67.3
Texture class	C	C	C	C	C	C	C
Bulk density (g/cm³)	1.03	0.99	1.07	1.09	1.14	1.06	1.19

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Site characteristics

Profile: 8
Elevation: 2025 m
Agroclimatic zone: I 5
Geological formation: Bukoban system (Precambrium)
Physiography: convex ridge (Keroka surface)
   upper slope
Slope: sloping, 10%
Drainage: well drained, class 4
Surface stones, rock outcrops: none
Described by: R. F. M. Onck

Location: Tombe, Kisii District, 34° 52' E; 0° 39' S
Mapping index[1]: U1Xh
Soil classification: Soil Taxonomy: Typic Palehumult
              FAO/Unesco: Luvic Phaeozem
Local petrography: rhyolite and Tertairy volcanic ash
Surrounding landform: hilly
Land use: traditional smallholder arable farming (maize, beans
Human influence: moderate, manual cultivation, occasionally ploughing
Soil fauna: Apicotermitinae
Date: 21-3-1985

Profile Description

Ap   0– 20 cm   Dark reddish brown (5YR 2.5/4) moist, clay; moderately weak fine and very fine crumb; non sticky, non plastic (wet) and very friable (moist) consistency; few fine and very fine pores; clear, broken transition to.

A3   20– 40 cm   Dark reddish brown (5YR 5/2) moist, clay; moderate medium subangular blocky crushing to fine crumb; slightly plastic (wet) and very friable (moist) consistency; few fine and common very fine pores; gradual smooth transition to.

B1   40– 60 cm   Dark reddish brown (5YR 2.5/2) moist, clay; moderate medium angular to subangular blocky, breaking to very fine subangular blocky; slightly sticky, slightly plastic (wet) and friable (moist) consistency; no cutans; few fine and very fine pores; gradual smooth transition to

B21t   60– 80 cm   Dark reddish brown (5YR 3/3) moist, clay; moderate medium angular to subangular blocky breaking to fine subangular blocky; sticky and plastic (wet) and friable (moist) consistency; broken thin clay skins and humus coatings on few peds and as linings in vertical pores; few fine and common very fine pores; gradual smoot transition to.

B22t   8o–160 cm   Dark reddish brown (5YR 4/4) moist, clay; moderately strong, medium angular blocky to prismatic, breaking to fine angular blocky; sticky and plastic (wet) and firm (moist) consistency; broken, moderately thick clay skins, shiny ped skins; few fine and very fine pores; gradual smooth transition to.

B23t   160–180 + cm   Dark reddish brown (5YR 4/4) moist, clay; moderately strong medium angular blocky to fine prismatic; sticky and plastic (wet) and firm (moist) consistency; broken, moderately thick clay skins, shiny ped faces; few fine and very fine pores

[1] After 'Soils of the Kisii area, Kenya, (Wielemaker and Boxem, 1982')

Laboratory data of profile description No.: 8 Soil Classification: Typic Palehumult.

Depth cm	5–10	20–30	40–50	70–80	90–100	120–130	150–160	180–190
pH H_2O	4.8	5.2	4.9	4.9	4.9	4.8	4.8	4.8
pH KCl								
C %	4.19	3.76	3.20	1.68	1.02	0.67	0.65	0.54
N %	0.48	0.35	0.25	0.16	0.12	0.09	0.08	0.07
P_2O_5 % (total)	0.21	0.17	0.14	0.16	0.19	0.15	0.18	0.15
CEC (pH 7.8) mmol/kg	193	191	203	183	156	144	159	164
$1/2\,Ca^{2+}$ mmol/kg	37	56	41	21	37	19	10	7
$1/2\,Mg^{2+}$ mmol/kg	12	19	14	16	15	17	18	14
Na^+ mmol/kg	<1	<1	<1	<1	<1	<1	<1	<1
K^+ mmol/kg	4	2	<1	<1	<1	<1	<1	<1
$1/3\,Al^{3+}$ mmol/kg	33	16	36	21	17	17	17	21
H^+ mmol/kg	3	3	2	1	4	4	4	6
% B.S. (sum of cations)	27	40	27	20	33	25	18	13
Texture								
Sand 2.0 –0.85 mm	0.5	0.5	0.8	0.7	0.3	0.9	0.8	0.7
Sand 0.85–0.42 mm	0.9	0.9	0.8	0.6	0.6	0.8	0.8	0.6
Sand 0.42–0.21 mm	1.6	1.5	1.3	1.0	1.0	1.2	0.9	1.1
Sand 0.21–0.10 mm	2.9	2.2	1.7	1.6	1.8	3.3	2.1	3.7
Sand 0.10–0.05 mm	3.1	2.6	1.8	1.5	1.7	3.0	1.9	2.9
Total sand %	9.0	7.7	6.4	5.4	5.4	9.2	6.5	9.0
Silt %	33.9	32.4	30.1	17.7	34.9	19.6	10.9	11.3
Clay %	57.1	59.9	63.5	76.9	59.7	71.2	82.6	79.7
Texture class	C	C	C	C	C	C	C	C
Bulk density (g/cm³)	0.87	0.89	1.08	1.02	1.05	0.99	1.05	1.08

APPENDIX 2. ANALYTICAL METHODS

Most physical measurements were done at the field laboratory at Kisii. Bulk density, porosity and soil moisture retention were determined on soil core samples of 100 cc. Soil moisture retention was determined gravimetrically after equilibration of the core sample at pF values between 0.4 (saturation) and 2.0 (matric head of –100 cm) on a sandbox (Stakman et al., 1974). Hydraulic conductivity was measured at various matric potentials on 100 cc soil core samples. A special laboratory stand was used which enabled continual registration of flow rate under the application of variable suctions (see Figure). A matric head (h) between 0 and –15 cm, which was the air-entry value of the ceramic plates, could be applied to top and bottom of the sample by adjusting the air-inlet level and the discharge level. Flow rate was measured against a scale on a Mariott burette.

Texture analyses were done at the Soils and Crops Laboratory Oosterbeek, the Netherlands. The fraction < 2 mm (fine earth) was separated and pretreated with hydrogen peroxide to destroy organic mattter. Clay contents were determined by the pipette method after dispersion with sodium pyrophosphate. After drying, the sand was sieved into fractions of 2000-850 μm, 850-420 μm, 420-210 μm, 210-150 μm and 150-105 μm, according to the fraction limits used by the Soil Survey Institute, Wageningen, the Netherlands.

Chemical analyses of the fine earth fraction were done at the laboratories
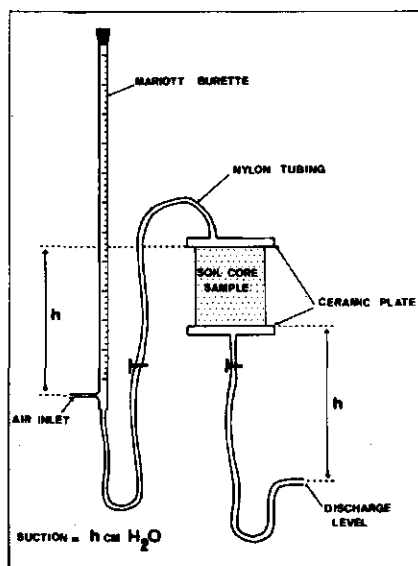

Fig. Laboratory arrangement for measuring hydraulic conductivity at various suctions.

of the Dept. of Soil Science and Geology, Agricultural University, Wageningen, the Netherlands. pH-values were measured with a combined glass calomel electrode in a 1:2.5 (water) suspension. Total carbon content was determined by potentiometry, after wet combustion of carbon (Allison, 1960), according to Begheijn (1980). Total nitrogen was measured by semi-micro Kjelldahl. Total phosphorus was determined by colorimetry in an ammonium-molybdenic acid extract after destruction with HF (Begheijn, 1980). Exchangeable characteristics were investigated with a LiEDTA single extraction method (Begheijn, 1980). Exchangeable Na and K were determined by flame emission, exchangeable Ca and Mg by atomic absorption spectrometry. Cation exhange capacity was determined by measuring excess Li in the extract, at a pH of about 7.5. Exchangeable acidity was measured by extraction with 1.0 N KCl and titration with NaOH; exchangeable Al was determined by colorimetry.

Chemical analyses of funguscomb material were done at the National Agricultural Laboratories, Nairobi. Organic carbon content was determined by the Walkley-Black wet oxidation method, and organic nitrogen by the Kjelldahl distillation. Phosphorus was measured by colorimetry in an ammonium-molybdenic acid extract after destruction with a mixture of HCl and H_2SO_4. CEC and exchangeable cations were determined by neutral ammonium acetate extraction.

Undisturbed soil samples for the preparation of thin sections were collected in tins of $15 \times 8 \times 5$ cm and $5 \times 5 \times 5$ cm, and impregnated with a polyester resin (Synolite Type 544). The hardened block was sawed, mounted on an object glass, and grinded to a thickness of 20 μm. The thin sections were covered with a thin cover glass and studied with a polarization microscope.