

The Biological Management of Tropical Soil Fertility
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CHAPTER 6

The relationship between soil macrofauna and tropical soil fertility

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Invertebrates are major determinants of soil processes in tropical ecosystems. Whereas pest management is an integral part of crop production, the potential for the beneficial manipulation of soil animals has rarely been considered in the design of management practices. Recent research, however, demonstrates that practices which eliminate beneficial soil faunal communities are unlikely to be sustainable in the long term, especially in low-input systems based on organic fertilisation. Key groups such as earthworms, termites, ants and litter-feeding arthropods have been shown to affect the physical structure of the soil and influence nutrient dynamics through their effects on immobilisation and humification (Anderson and Flanagan, 1989; Lavelle et al., 1992).

The presence of soil invertebrates can be conspicuous (for example, the large nest structures of the fungus-growing termites which may be 10 m high), but more often it is less obvious. Although rarely seen on the surface, in some hydromorphic soils earthworms may deposit up to 200 t/ha of casts at the soil surface (Kollmansperger, 1956). The habitat structure, vegetation architecture and litter cover is utilised by a wide range of litter-feeding arthropods and their predators within natural ecosystems, resulting in complex food webs and habitat structures. The combination of soil- and litter-dwelling species results in a diverse faunal community, which may be severely reduced by certain agricultural practices (Critchley et al., 1979; Lavelle and Pashanasi, 1989; Dangerfield, 1990). Degraded soils also have reduced faunal complexities and biomass (Barois et al., 1988; Betsch et al., 1990). These changes in community organisation may favour species that are potential pests of food and cash crops.

The economic costs of pests and pest control have overshadowed the potential beneficial effects of soil invertebrate activity on soil properties and plant production. The diversity and role of soil fauna have been largely ignored by traditional and conventional agriculturalists. Termites and leaf-cutting ants are often considered as serious pests and destroyed in high-input farming systems. The beneficial effects of soil invertebrates on plant production, when they are acknowledged, are considered negligible in comparison with the spectacular effects obtained in the short term by energy-intensive pest control measures. Consequently, little attention has been paid to the conservation of these fauna



by using pesticides with less widespread effects or by adopting appropriate cultural practices. Soil degradation is seldom attributed to the decline of soil fauna and the reduction of their activities. Nonetheless, it is likely that accelerated losses of organic matter and soil disaggregation derive, in part, from the destruction of those fauna which regulate soil organic matter dynamics. In studies in which the soil fauna have been sampled in highly degraded soils, a severe depletion of population has been observed (for example, Barois et al., 1988; Betsch et al., 1990).

Despite a wide range of opinions among soil zoologists as to the exact role of the various groups of soil animals in soil fertility processes (Anderson, 1987; Persson, 1988; Anderson and Flanagan, 1989; Lavelle et al., 1992), it has been hypothesised that the activities of many soil animals could be better managed in order to promote sustainable production in tropical agroecosystems (Swift, 1987).

This chapter discusses why and how soil fauna communities must be taken into consideration in soil fertility issues. After explaining the general ecological functions observed in soil invertebrates, data from the faunal communities of sites in the Tropical Soil Biology and Fertility Programme (TSBF) are examined in detail. The response of native communities to different types of land use practices is assessed in order to identify those practices which maintain or enhance soil fauna activities or indicate which practices have destructive effects. The major part of the chapter then analyses the effect of major components of soil fauna on relevant processes of soil fertility, including soil organic matter dynamics and soil physical structure. Earthworms and termites are treated in greatest detail because these key groups have a major impact on soil processes and a high potential for manipulation at the community level. Finally, the results of manipulative experiments are presented in order to draw attention to the potential that earthworms and termites represent for the improvement of agroecosystem function.

In the TSBF programme two key features of tropical soil invertebrates are recognised. First, in many tropical soils the direct effects (respiration and mineralisation) and indirect effects (interaction with microorganisms and modification of soil structure) of soil and litter invertebrates influence microbial activity, thereby determining the immobilisation, storage and release of nutrients, the dynamics of soil organic matter and water relations within the soil. Second, soil faunal communities are themselves sensitive to the climatic and edaphic factors which determine the availability of food resources and microclimate conditions and thus there is a risk that disturbances will alter their communities; however, this responsiveness represents the potential to manipulate these communities in order to improve plant production, either through careful control of habitat components or direct introduction/exclusion of particular species.

This general hypothesis is reflected in the TSBF 'soil fauna' theme, which states that 'soil fauna can be manipulated to improve the physical properties of soil and regulate decomposition processes' (see Appendix 1). Although intrinsically sound, the implementation of this theme was constrained by a shortage of information on the activity, behaviour and environmental tolerances of many tropical species of soil fauna, and by the limited understanding of the structural and functional stability of soil fauna communities. Three major research objectives were thus identified within the soil fauna theme:

- to quantify the structure of soil faunal communities in terms of the abundance and biomass of taxonomic and functional groups, with emphasis on the effects of land use patterns on this structure
- to describe and quantify the role of soil fauna in the major soil processes
- to manipulate soil faunal communities to improve soil fertility

Consistent with the overall rationale of TSBF, a standardised and readily applicable method was developed to achieve these objectives. Hand sorting of 25 x 25 x 30 cm soil monoliths and the collection

of all macrofauna (loosely defined as individuals with a body length > 2 mm) was used to quantify the major taxa as part of site characterisation (Anderson and Ingram, 1989, 1993). Implicit in the choice of the sampling method was the assumption that, initially, species with individuals of large body mass (macrofauna) would present the best opportunity for conservation or manipulation within agroecosystems. These groups have a significant effect on soil fertility parameters because of their ability to modify their environment through nest building or through burrowing (Lavelle, 1988; Wood, 1988).

FUNCTIONAL CLASSIFICATION OF SOIL FAUNA

Soil fauna comprise thousands of species with a wide range of ecological strategies. Attempts have been made to construct functional classifications that allow a comprehensive understanding of the respective roles of such diverse organisms and identify situations where defined components may be manipulated. This represents a means of handling the high biological diversity at a functional or process level.

Ecological strategies of soil organisms

Soil organisms face three major constraints within the soil environment: they feed on relatively low-quality resources; they move in a compact and dark environment; and they face intermittently unfavourable microclimatic conditions (Lavelle et al., 1992).

A series of strategies associated with a continuum of increasing body sizes can be recognised. At one end of this continuum are the microorganisms that have an apparently unlimited ability to digest any natural substrate. The main constraints to their activity are their dependence upon soil water films and their limited ability to migrate towards new substrates. Although fungi have some ability to reach new substrates through mycelial growth and translocation of cytoplasm, it has been demonstrated that the dispersion of their propagules is better performed with the assistance of invertebrates (Swift and Boddy, 1984). At the other end of the continuum, macroinvertebrates, such as earthworms or termites, are rarely able to digest the complex carbohydrates, lignins, humic and phenolic compounds which comprise most of the resources available in litter and soil. Nonetheless, they have a considerable ability to modify their immediate environment and greatly influence microbial activity through burrowing and nest building.

During the course of evolution, mutualistic relationships have developed between microorganisms and macroorganisms for a common exploitation of organic resources. Microorganisms perform most of the chemical transformations of decomposition, whereas the larger organisms tend to stimulate and take advantage of that activity through their ability to operate at relatively large scales of time and space. Associations of micro- and macroorganisms may take different forms, depending upon the size of the associated invertebrate. The larger the invertebrate, the closer and more effective (in terms of completeness of decomposition and extension in space) the association.

The microfauna (invertebrates < 0.2 mm diameter) are only slightly more mobile than microflora. Many are predators of microorganisms and form food webs of great functional importance in specific microhabitats, such as the rhizosphere system (Trofymow and Coleman, 1982; Clarholm, 1985; Ingham et al., 1987). The mesofauna (0.2-2.0 mm diameter) are mobile throughout the pores, cracks and interfaces of litter and soil. Some of them are predators of microorganisms but others have

developed an 'external rumen' type of digestion (Swift et al., 1979). This consists mainly of stimulating microbial activities in their faecal pellets and re-ingesting this material once microorganisms have released assimilable elements.

The macrofauna (> 2mm diameter) dig burrows and galleries that transport and mix mineral and organic elements. Their larger size allows them to host a significant variety of microorganisms and develop internal, mutualistic digestive systems. These systems have diverse forms, ranging from transient and facultative mutualisms with the ingested free soil microflora in endogeic earthworms (Barois and Lavelle, 1986) to the obligate symbiosis of termites with bacteria or protozoa (Breznak, 1984). In these interactions, macroinvertebrates often produce assimilable organic matter in the anterior gut which exerts a priming effect (*sensu* Jenkinson, 1966) on the ingested microflora to accelerate their digestion of organic substrates during transit through the gut. These products are the functional equivalent of the exudates produced by roots (Lavelle, 1987; Martin et al., 1987). Nonetheless, a significant proportion of macrofauna, such as larger arthropods (Myriapoda, Diplopoda, Blattoidea and Isopoda) and litter-feeding earthworms, rely on an external rumen type of digestion. Exploitation of woody material by fungi-growing termites is but a sophisticated version of the latter strategy.

Ecological categories of soil macroinvertebrates

The macrofauna can be further divided into three groups which play different roles in the ecosystem (Bouché, 1977): the epigeics, the anecics and the endogeics.

The epigeics live and feed in surface litter. They include saprophagous arthropods and small pigmented earthworms, as well as predators of these species (chilopods, ants and some coleopterans). They progressively fragment litter and participate in decomposition *in situ*.

Anecics feed on surface litter but build subterranean burrows and nests that provide shelter. This group consists of some large pigmented earthworms and the vast majority of termite species. The main effect of these invertebrates is to remove litter from the litter system and transport it to different environments, such as the subsoil or a termite nest, thus changing dramatically the kinetics of decomposition and the spatial distribution of its products.

The endogeics live in the soil. Consisting mainly of termites and unpigmented earthworms, they are geophagous and feed on soil organic matter and live or dead roots. Endogeics produce casts and faecal pellets which are the component elements of macroaggregate soil structures. They dig galleries, nests and chambers and eventually egest soil at the surface as earthworm casts, termite sheetings or epigeic nests of ants or termites. These processes have an important influence on the physical organisation of the soil.

MACROFAUNA COMMUNITIES IN THE HUMID TROPICS

As a contribution to the first objective of the TSBF soil fauna theme, available data on macrofaunal communities from tropical rainforests, grasslands and cropland have been compiled and compared. The aims were to assess the overall and relative importance of the different biological systems of regulation based on invertebrate activities indicated by the abundance of arthropods other than termites (litter system), the abundance of earthworms (drilosphere) and the abundance of termites (termitosphere), and to assess the effect of different management options on these communities.

General patterns of macroinvertebrate communities

Seventy-three macroinvertebrate communities from 29 sites were subjected to principal component analysis (PCA) in order to identify the major trends of composition and the relative effect of vegetation type, biogeography and land use practices.

The first three factors in the PCA accounted for 54.7% of the variance. The first factor (26.1%) distinguished sites with reduced termite ($r = -0.36$), arachnid ($r = -0.35$) and ant ($r = -0.34$) populations and total population densities ($r = -0.42$). It also clearly separated sites with dominant termitosphere and ant effects, such as the forests in Kenya and Peruvian Amazonia, from low-input cropping systems derived from those forests, the dry savannas sites such as Marondera in Zimbabwe and low-external-input cropping systems in Mexico and Martinique. This factor integrates the effects of biogeographical features and types of land use on termite abundance (*see* Figure 6.1 *overleaf*).

The second factor (15.9%) related mainly to the abundance and biomass of earthworms ($r = 0.43$ and $r = 0.48$, respectively). It clearly separated pastures and natural humid African savannas with high populations of introduced earthworms from dry African savannas, annual cropping systems and South-Eastern Asian forests which have the lowest earthworm biomasses. This factor may be identified as the effects of vegetation type on earthworm abundance, with maximum values in savannas and pastures, intermediate values in fallows and tree plantations and minimum values in forests.

The third factor (12.7%) characterised sites with high arthropod abundance, indicating in particular the importance of isopods ($r = 0.47$), myriapods ($r = 0.38$) and arachnids ($r = 0.25$) in contrast with earthworms where correlations were negative ($r = -0.30$) with biomass. This factor isolated sites with high rates of litter accumulation, which have especially high populations of litter-dwelling arthropods, coleopterans and endogeic larvae.

A major outcome of this analysis has been the identification of three major groups, each containing termites, earthworms and litter arthropods. The groups tend to react independently within ecosystem types and land use practices. Termites and/or earthworms tend to be dominant in most cases, while termite communities vary considerably, depending upon biogeographical patterns. They are important components of many African and Australian soils. In America, termites often are of little or no importance. This is due, in part, to limitations of their functional diversity; in South America, for example, the fungus-growing termites do not occur. Another important characteristic of termites is that they have adapted to a wide range of semi-arid systems where earthworms are not found (Menaut et al., 1985). Earthworms are best represented in grasslands in humid areas; their abundance decreases towards both forested and dry areas. At a finer scale of resolution, they are sensitive to the nutrient status and organic contents of soil (Fragoso and Lavelle, 1992). Litter arthropods seem to be predominant in ecosystems where sufficient litter is available as a consequence of low termite and earthworm activities. They are represented mainly by millipedes or coleopterans which, in some areas, may account for the dominant proportion of the biomass, as is the case with millipedes in the miombo woodlands of southern Africa (Dangerfield, 1990) and coleopteran larvae in Mexican tropical pastures (Villalobos and Lavelle, 1990). In such ecosystems, mesofaunal communities may also have higher densities than in those systems dominated by earthworms and termites, where their abundance is very low (Adis, 1988).

Effects of land use practices

Annual crops on land recently cleared of natural vegetation always have highly depleted macroinvertebrate communities (*see* Figure 6.2 *overleaf*). They have the lowest mean biomass (5.1 g fresh

Figure 6.1 Position of communities of macro-invertebrates from soils in the humid tropics in relation to two principal component analyses

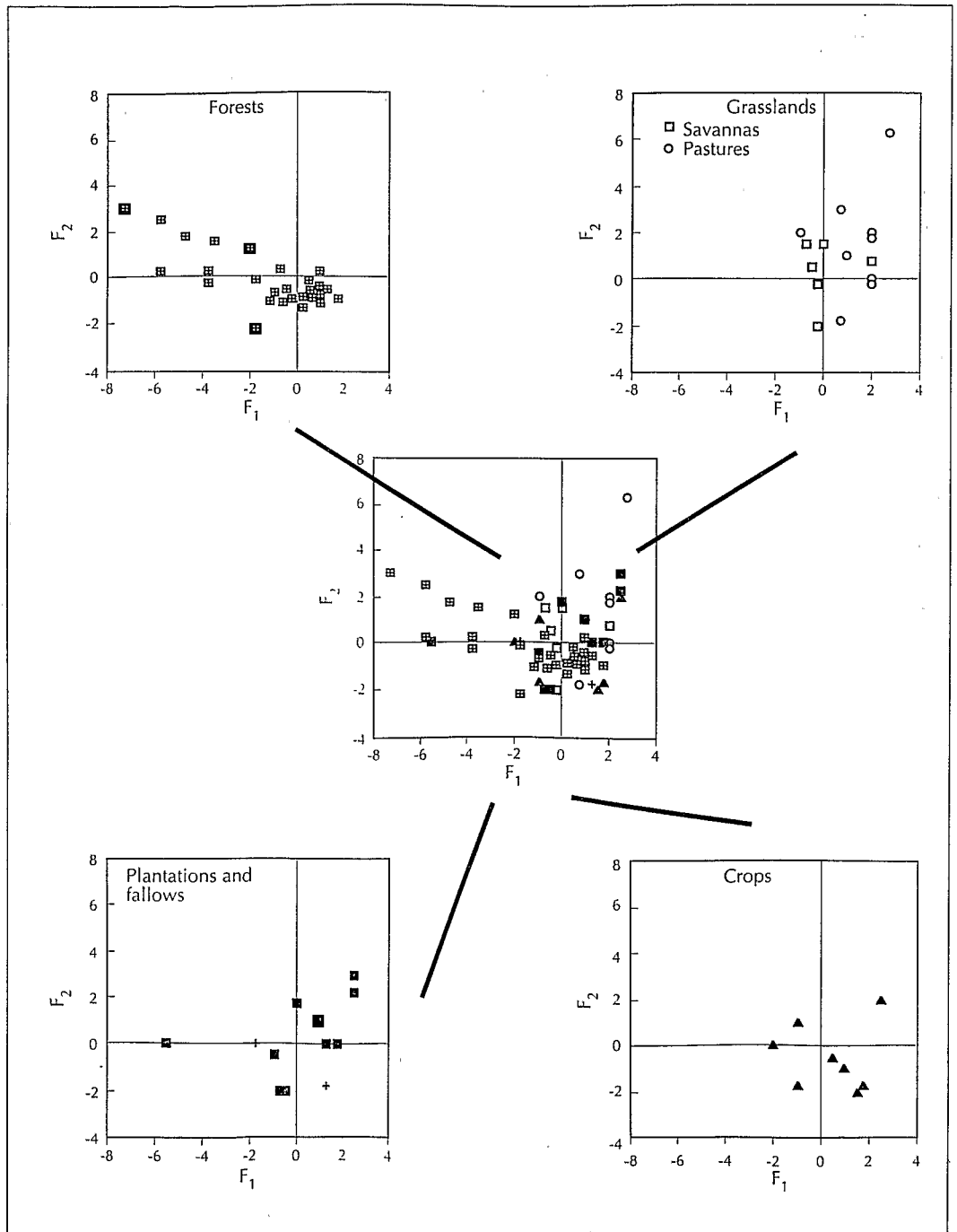
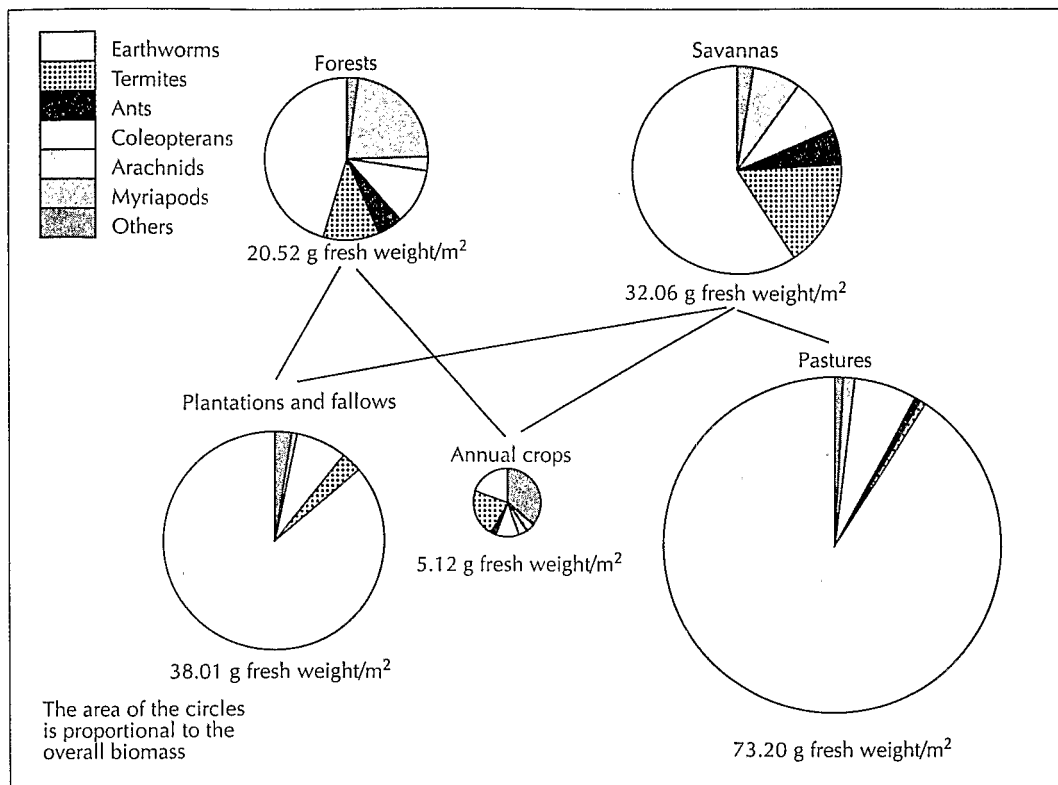


Figure 6.2 Composition of soil macrofaunal communities in tropical grasslands (savannas and pastures), fallows + tree plantations, and forests



weight/m²) and a highly depleted diversity. Earthworms and litter arthropod populations rapidly disappear following major disturbances and are often not replaced by adaptable exotic species. Some groups of termites (mainly humivorous) resist perturbation better and as a result their relative proportions increase.

Pastures are functionally similar to savannas. They are highly favourable to earthworm development when they are established in forest areas with high annual rainfall, provided adaptable species are present. This is the case in many sites where peregrine species with a pantropical distribution (mainly *Pontoscolex corethrurus* and *Polypheretima elongata*) establish a biomass of several hundreds to 4000 kg fresh weight/ha (Barois et al., 1988; Fraile, 1989; Lavelle and Pashanasi, 1989). Interestingly, sugarcane plantations show similar patterns, with earthworm biomasses of 33 and 53 g fresh weight/m² in two sites in tropical Mexico and Guadeloupe, respectively (Barois et al., 1988). In terms of soil faunal relations, this indicates that these plantations are essentially humid grasslands.

Tree plantations, such as palm plantations with herbaceous legume cover or cocoa with a litter layer at the soil surface and a stratum of high trees, usually have numerous and diverse communities. They retain components of the original fauna because the overall structure of the system is close to that of a degraded forest. Nonetheless, the disturbance and/or establishment of an herbaceous stratum

provides niches which allow some exotic species to colonise. This is particularly the case for earthworms, which may achieve sizeable populations. As a result, tree plantations have an average biomass of 38 g fresh weight/m² (*see* Figure 6.2), which is higher than that found in natural forests (20.5 g/m²) and savannas (32.1 g/m²).

Species richness and diversity

Disturbances linked to land use practices severely affect the species richness of soil invertebrate communities. The conversion of forests to annual crops eliminates the vast majority of species which rely on woody or leaf litter material or require specialised microclimatic conditions. Conversely, perennial systems maintain a multistrata structure and conserve species from the original ecosystem, as well as providing niches for exotic colonisers.

A preliminary compilation of data (*see* Table 6.1) on the species richness of earthworm communities documents a significant increase in the dominance of exotic species in disturbed ecosystems compared with undisturbed ecosystems. The data also show that there was an increase in the richness of native species with increasing organic matter content and that the greatest faunal diversity occurred in tree plantations (9.5 species on average) and savannas (8 species). Species inhabiting epiphytic communities were not taken into consideration, which probably accounts for the comparatively lower diversity observed in rainforests. Nonetheless, rainforest communities showed a greater balance between ecological categories than other environments included in this study.

Table 6.1 Species richness and abundance of earthworm communities in ecosystems in the humid tropics

Ecosystem	Density (D)	Biomass (B)	Number of spp.	Epigeics		Endogeics		Anecics (% D)
				(% D)	(% B)	(% D)	(% B)	
Pastures	310 (93-740)	59.7 (0.6-153)	6.5 (2-9)	0.75	1.75	99.25	98.25	0
Tree plantations	170 (84-341)	28.6 (2.9-87)	9.5 (7-12)	6.5	32.5	93.5	67.5	0
Crops	19 (10-42)	1.1 (0.6-1.5)	2.5 (2-3)	0	0	100.0	100.0	0
Savannas	236 (187-286)	44.1 (38-50.1)	8 (8)	3.5	6.5	96.5	93.5	0
Tropical deciduous forest	37 (8-78)	4.1 (0.6-10.1)	2.7 (2-4)	4.5	6.0	95.5	94.0	0
Tropical rainforest	77 (4-401)	13.9 (0.2-71.9)	6.6 (5-11)	32.4	32.8	67.2	60.5	0.4

Source: Fragoso (1992)

THE ROLE OF SOIL MACROFAUNA IN SOIL ORGANIC MATTER DYNAMICS

Soil invertebrates influence soil organic matter dynamics over a range of spatial and temporal scales. At the smallest scale, the digestion transit of substrate requires from a few minutes to hours. At an intermediate scale (hours to days), the production of fresh fecal pellets promotes microbial activities established during the gut transit and results in further modifications of soil organic matter and nutrient pools. Beyond this scale is the ageing process of faecal material in which the dynamics of organic matter may change, because of the composition of pellets, at a time scale of months to years and influence g to kg per square metre of soil and organic matter. These processes are important in maintaining the structure of the whole soil profile. Research on a few termite and earthworm species has demonstrated that distinct processes operate within each of these scales.

Short-term effects

Feeding and digestive activities have three main consequences for soil organic matter dynamics: the choice of feeding substrate to ingest, which depends upon feeding habits; the comminution of organic materials (that is, fragmentation and physical modification without chemical transformation); and the assimilation and excretion of metabolites (for example, nutrients and mucus).

Selection of food

Food selection patterns vary greatly, depending upon the ecological category of invertebrates. Epigeics ingest only organic matter such as leaf litter or wood. They bring about an *in situ* transformation of litter with concurrent fragmentation, comminution and chemical transformation of the substrate. For example, tropical millipedes are primarily epigeic during the rainy season when they are often observed on the surface in large numbers (Lewis, 1971; Banerjee, 1980; Dangerfield, 1990). They are generalist detritivores and feed on a variety of materials, including leaf litter, seeds and dead invertebrates. The consumption of litter occurs during periods of surface activity, which in southern Africa is strongly seasonal, coinciding with the summer rainy season (Dangerfield and Telford, 1991).

In contrast, anecics ingest surface leaf or woody material that they export beyond the litter zone and mix with substrate from underlying soil horizons. Most termites may be classified as anecics as they feed on surface plant material and bring it to their nests, where decomposition patterns differ from those of the surface litter system. The most extreme case is that of the fungus-growing termites. Clear differences exist in the feeding regimes of termites well beyond the broad classification into leaf litter and wood feeders (Wood, 1978). Anecic termites may ingest high proportions of the above-ground production, especially in semi-arid environments (Lepage, 1974). Nutrients contained in this material are not rapidly released for plant nutrition as they tend to be fixed on clay minerals incorporated into termite constructions or accumulated in undigested residues. The gut content of *Millsonia lamtoiana*, an anecic earthworm of West African savannas, contributed 9-13% surface litter to the ingested soil. The ingested litter consisted mainly of recognisable dead grass debris (67-72%, depending upon the density of shrub cover), together with seeds (2-8%) and tree leaf debris (1.4-7.2%). A large proportion (24-48%) of the debris had a surface area greater than 2 mm² (Kanyonyo, 1984).

Endogeic invertebrates are usually geophagous. They have been classified as meso-, poly- or oligohumics according to whether the soil they ingest has a soil organic matter content equal to, greater

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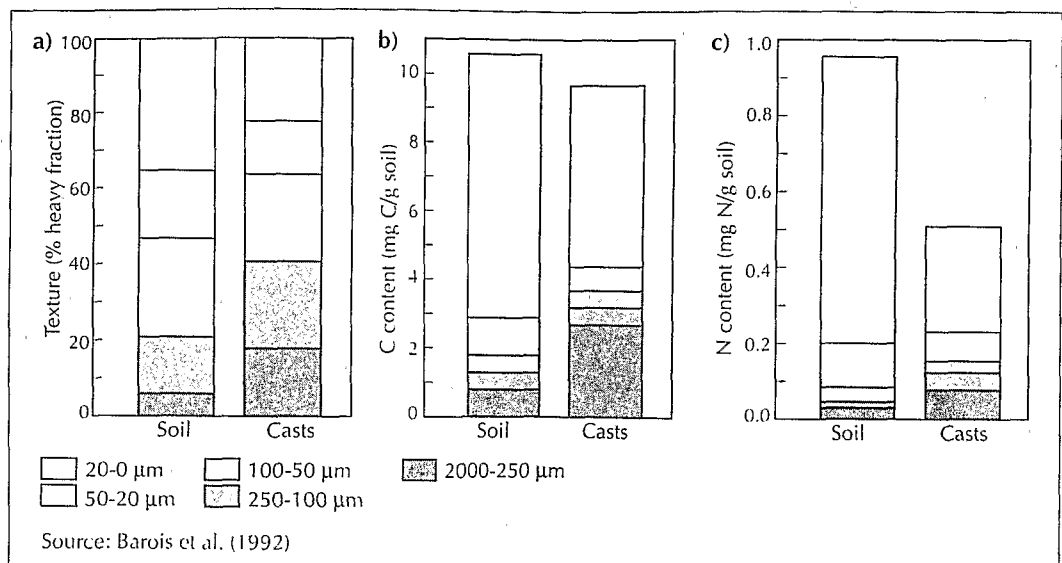
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than or inferior to that of the bulk soil of the upper 10-15 cm, respectively. Endogeics may or may not select the soil that they ingest by choosing particle size fractions or concentrations of organic matter, by ingesting root litter or exudates in the rhizosphere (Spain et al., 1992) or by feeding at the interface of the litter and soil. Evidence for selectivity comes from the observation that earthworm casts and termite nests often have finer textures and higher organic contents than the bulk soil (Barois et al., 1992) (see Figure 6.3).

Figure 6.3 Texture and particle size fractionation of soil organic matter in earthworm (*Zapataadrilus guapotus*) casts and the bulk soil (0-10 cm) at the TSBF Panuco site, Veracruz, Mexico



Immediate effects of digestion

One evident effect of digestion is the assimilation of part of the organic substrate by organisms. Assimilation rates vary from a few percent in geophagous earthworms feeding on low-quality organic matter to maximum values of 10-20% for litter-feeding invertebrates and 54-93% for termites (Wood, 1978; Lee and Wood, 1983). Undigested organic matter is also transformed during the intestinal transit. Martin (1991a) has demonstrated that assimilation accounted for only 6% of the 25% decrease in the coarse (> 50 μm) organic fraction after digestion by the endogeic earthworm *M. anomala*, while 21% was comminuted into smaller particle size fractions without being digested. When the same worms were provided with fresh organic matter, there was a different response. Assimilation was maximum for freshly cut leaves and 2-week-old leaf debris, the legume material with a high N content being particularly well assimilated. In contrast, fresh root material was a poor food. After 5-10 weeks, the quality of applied organic materials tended to become homogeneous, irrespective of the origin of the material (Lavelle et al., 1989).

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Millipedes and other macrosaprophages consume relatively poor food and have low assimilation efficiencies (7-24%) (M. Dangerfield and H. Milner, unpubl.). Specific energy and nutrient requirements are supplied partly by a wide selection of food items (Kheirallah, 1979) and high ingestion and throughput rates. The consumption of leaf litter by millipedes results in comminution, some hydrolysis of cellulose, hemicellulose and pectin (Beck and Friesse, 1981) and the activation of microorganisms in faecal pellets which can be reingested after days or weeks (Anderson et al., 1985). This feeding strategy, combined with abundances of up to 50 individuals/m², has a major impact on litter decomposition by millipedes. In miombo woodland at Marondera, Zimbabwe, the density of millipedes was 28.2/m² (Dangerfield, 1990) and their surface activities lasted for 100 days (Dangerfield and Telford, 1991). Seasonal production of faecal pellets by these animals was estimated to be 32.7 g/m², which is 6% of the total litter standing crop and 27.7% of the total fine litter.

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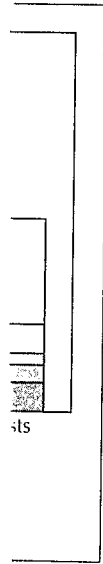
Nutrients in earthworm casts

A significant proportion of the ingested materials assimilated by earthworms is secreted as intestinal and cutaneous mucus with greater C/N ratios than those of the original resource (Lavelle et al., 1983; Cortez and Bouché, 1987; Martin et al., 1987). As a result, excesses of N must be excreted as ammonium. Another mechanism of mineral N excretion by soil fauna is the rapid turnover of N in earthworm biomass (Ferrière and Bouché, 1985; Barois et al., 1987). In those species that have endonephridia, the N is excreted mainly as ammonium in the urine. By this means it is mixed into the soil and incorporated within the casts (Laverack, 1963; Lee, 1985).

In the forest Ultisols of the TSBF Yurimaguas site in Peruvian Amazonia, the mineral N content in fresh casts of *Pontoscolex corethrurus* was 160 µg/g soil, equivalent to 9% of total soil N. This was present both as ammonium (120 µg/g) and nitrate (40 µg/g). In the control soil, total N, ammonium and nitrate were 27.3, 5.7 and 21.6 µg/g, respectively. In addition, 73.3 µg N/g soil was present as microbial biomass in fresh casts. Labile N in the casts rapidly decreased following deposition. After 12 hours, the mineral N concentration had fallen to 77.7 µg N/g soil (Lavelle et al., 1992) (see Figure 6.4 overleaf). By day 16.5, nitrate concentration had risen to 49.8 µg N/g soil. Microbial biomass decreased sharply to 25.2 µg N/g soil after 12 hours but by day 1.5 had increased to 30.5 µg N/g soil; it then declined until the termination of the experiment. At Yurimaguas, the annual accumulation of mineral N within casts of *P. corethrurus* in pastures was approximately 100 kg/ha.

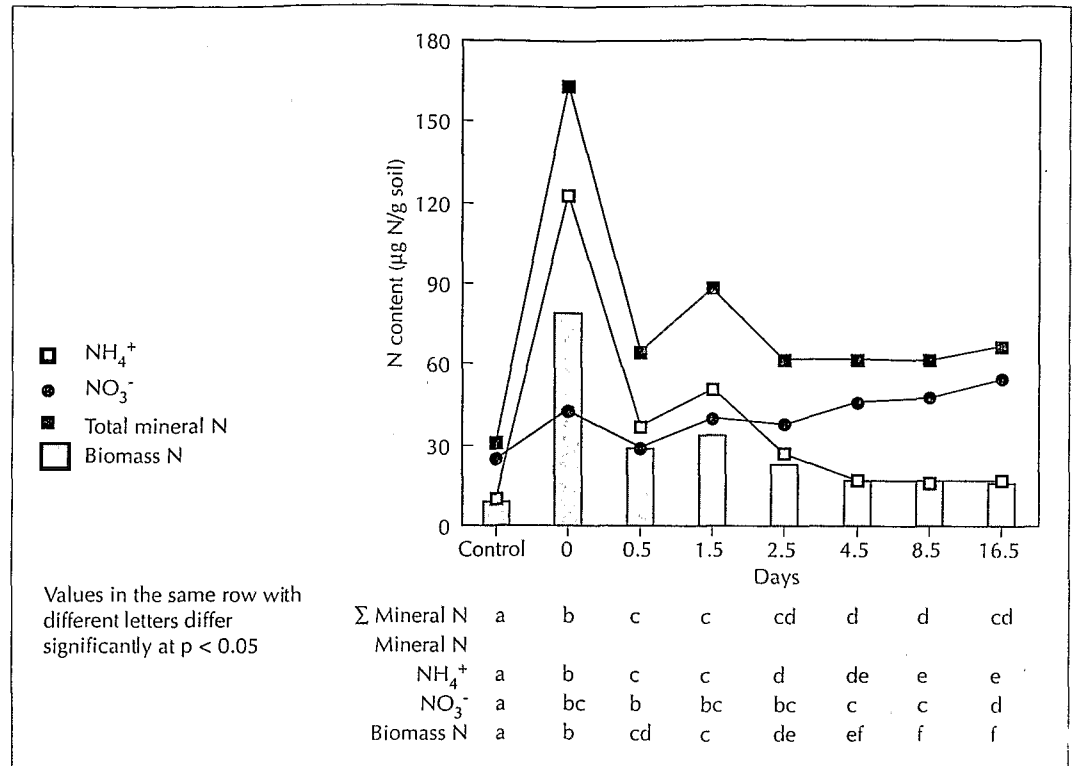
The proportion of ammonium released in earthworm casts and the evolution of this N towards nitrification and/or reorganisation vary according to species and soil types (Barois et al., 1992). Phosphorus availability also seems to be affected by endogeic earthworm activities. An experiment to assess the release of mineral P from a soil with a low P-retention value (Ferric Acrisol at Lamto, Côte d'Ivoire) and from another soil with a high P-retention value (Luvisol at Laguna Verde, Mexico), using the ³²P dilution technique described by Fardeau (1981), showed that exchangeable and water-extractable inorganic P in casts of *P. corethrurus* was more abundant than in non-ingested control soils (see Table 6.2 overleaf). Fresh (12 hour) and ageing (96 hour) casts obtained from the Lamto soil had a higher amount of inorganic exchangeable P than did the control soil. The exchangeable P value of the control soil was low (2.0 µg P/g soil). In fresh casts the concentration had significantly increased to 6.0 µg P/g soil; in ageing casts it had increased to 15.9 µg P/g soil after 4 days.

In the high phosphate-sorbing soil of Laguna Verde, water-soluble and exchangeable P in casts increased after 24 hours and then decreased after 4 days to values which did not differ greatly from control and fresh cast soils. A similar experiment was conducted with casts of the peregrine endogeic



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Figure 6.4 Variations in mineral nitrogen and nitrogen contained in the microbial biomass in casts of *Pontoscolex corethrus* of different ages and a control soil (Ultisol from Yurimaguas, Peru)



Polyphoretima elongata established in a Vertisol from Martinique. Three extraction techniques were used: extraction with resin to assess assimilable P immediately accessible to plants; extraction with NaHCO_3 of exchangeable P; and assessment of exchangeable P contained in microbial biomass.

There was a significant increase of resin P (50%) in casts compared with non-ingested soil. Fractions extracted with NaHCO_3 showed a further 30% increase in casts. Comparison between particle size distribution in casts and non-ingested soil showed that this species tends to ingest selectively the fine fractions of soil. Nonetheless, this selection results in limited differences (< 10%) in the proportion of fine particles ingested. It is inferred from these results that the increase of mineral P observed in casts is attributable mainly to digestion processes rather than to the simple selection of fractions richer in labile P (see Table 6.3).

Nutrients in fresh termite pellets and structures

The faecal pellets of termites have low contents of mineral elements, particularly N which is efficiently conserved during the gut transit. It has been demonstrated that during the gut transit of some termites,

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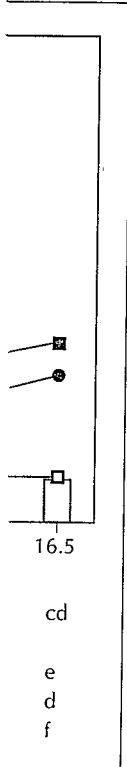


Table 6.2 Available forms of exchangeable and water-extractable inorganic phosphorus in casts of *Pontoscolex corethrus* of different ages from soils with a low (Lamto, Côte d'Ivoire) and high (Laguna Verde, Mexico) P retention capacity

	Water-extractable P ($\mu\text{g/g soil}$)	Exchangeable P ($\mu\text{g/g soil}$)
Lamto, Côte d'Ivoire (sandy Alfisol)		
control soil	0.060 +/- 0.005 a ^a	2.00 +/- 0.11 a
casts (12 hours)	0.158 +/- 0.005 b	6.00 +/- 1.78 b
casts (96 hours)	0.499 +/- 0.10 c	15.89 +/- 1.78 c
Laguna Verde, Mexico (Vertisol)		
control soil	0.026	15.00 +/- 0.78 b
casts (12 hours)	0.021	10.11 +/- 1.78 a
casts (24 hours)	0.053	43.33 +/- 1.11 c
casts (96 hours)	0.032	11.44 +/- 1.11 a

Note: a Values in the same column followed by the same letter do not differ significantly at $p < 0.05$
 Source: Lopez-Hernandez et al. (1993)

Table 6.3 Assimilable phosphorus (in $\mu\text{g P/g dry soil}$) in fresh casts of *Polypheretima elongata* as extracted by different methods

	Resin P (n = 6)	NaHCO ₃ (n = 3)	NaHCO ₃ after CHCl ₃ (n = 3)
Control soil			
mean	13.00	9.10	10.60
standard error	0.53	0.16	0.40
Fresh casts			
mean	19.50	12.10	12.10
standard error	0.49	0.10	0.10

mechanisms are available for the retention of waste N in symbiotic bacteria although it is not known how general these mechanisms may be (Lee and Wood, 1983). The major contribution of termites to nutrient cycling in the ecosystem therefore appears to be through mortality.

Some structures built by termites may constitute sources of nutrients that are readily available to plants. Soil from walls of fungus comb chambers of Macrotermitinae have a great ability to mineralise N in laboratory incubations. After 30 days, ammonium concentrations were 50 and 140 $\mu\text{g/g}$, respectively, in a control soil and the 0-2 mm surface layer of chambers (Abbadie and Lepage, 1989).

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Nitrogen fixation associated with termite guts has been shown by Sylvester-Bradley et al. (1982) in some *Nasutitermes* in central Amazonia. They studied the nitrogenase activity in 21 species of five genera and concluded that the highest activities (100 nmol C₂H₄ g dry weight/h) occurred in the genus *Nasutitermes*. Nonetheless, the technical difficulties of the acetylene reduction method make it difficult to extrapolate these results in terms of the contribution of termites to the N economy of these ecosystems.

A small amount of information is available on the role of termites in the P dynamics of tropical savannas on highly weathered soils. Phosphorus is a common limiting element in these environments. Early studies showed that the total P content of termite-modified soils differed only slightly from that of bulk soil (Lee and Wood, 1971). Wood et al. (1983) later reported that humus-eating termites probably increased the available P in the nest compared with adjacent sites. Comparable results have been obtained with *N. ephratae*, a common species of South American savannas. Phosphorus sorption, measured by phosphate radioactivity remaining in solution, was considerably lower in the mounds than in the nearby soil. This suggests that termites play an important role in P cycling by locally reducing fixation of P in soil. The lower values of P adsorption in the mounds was ascribed to organic matter complexation with potentially sorptive minerals. The organic content of the mounds was more than four times greater in the mounds than in the adjacent soil (see Table 6.4). Although the organic C content was significantly higher in the mounds than in the adjacent soils, there was no corresponding increase of phosphatase activity. This suggests that a factor other than soil organic matter controlled phosphatase activity in the mounds (Lopez-Hernandez et al., 1989a).

Table 6.4 Phosphorus accumulation in termite mounds in savannas^a

Sample	Total P		Inorganic P		Organic P		Available P		Water-soluble P	
	S	T	S	T	S	T	S	T	S	T
Mean	162.4	396.5	49.3	224.3	113.1	172.3	19.5	37.9	0.059	1.235
SD	39.2	91.6	28.3	104.6	39.6	82.6	7.3	8.2	0.033	0.702
P	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

Note: a S = bulk soil, T = termite mound soil
Source: Lopez-Hernandez et al. (1989b)

This study was extended to some other termite species of Côte d'Ivoire (D. Lopez-Hernandez and M.G. Lepage, unpubl.), and the general conclusion was that the effect of termites on P dynamics is strongly related to their feeding habits. Changes in forms of available P in termite-modified soil were not significant for species in the genus *Macrotermes* and of little importance in *Cubitermes* species, but they differed from the bulk soil in the royal chamber of *Trinervitermes geminatus* that was enriched through the transport of plant debris.

The effects of termites on macronutrients other than N and P have been studied for Australian species (Lee and Wood, 1971; Okello-Oloya et al., 1985), African species (Hesse, 1955; Boyer, 1971; Lopez-Hernandez and Febres, 1984) and South American species (Lopez-Hernandez et al., 1990). The higher concentrations of Ca, K and other exchangeable cations in mounds of soil feeders and other species are, in general, related to species' feeding habits and their use of saliva and faecal-derived

et al. (1982) species of five in the genus could make it any of these

s of tropical environments. ly from that ng termites results have us sorption, he mounds by locally l to organic s was more the organic responding controlled

organic materials to construct the nests. The exceptional amount of Ca found in concretionary form at the base of *Placotermes* mounds (Hesse, 1955) was a result of evaporative processes of a Ca-rich groundwater and impeded drainage. The high K level in *T. geminatus* mounds was due to the accumulation of K-enriched *Loudetia* debris within the nest.

Medium-term effects

The evolution of organic matter has been observed in medium-term (420 days) incubations of earthworm casts and a non-ingested control soil (2 mm sieved) in laboratory conditions (Martin, 1991a). The results showed a clear negative exponential pattern in casts, with a rapid decrease in soil organic matter in the first 16 days of the experiment followed by a rapid stabilisation of mineralisation in older casts. In the control soil, decomposition was initially reduced but it was later maintained at a greater rate than in the casts. As a result, after about 50 days the organic content in casts overtook that in control soils and was about 10% greater after 420 days (Martin, 1991a).

Detailed analysis of variations within each particle size fraction indicated that the decomposition of particles larger than 250 μm fell by 63% in casts. Thus, earthworm activities would have the effect of protecting soil organic matter, particularly large particle size fractions.

Accumulation of soil organic matter in termite structures

Termites consume a significant proportion of above-ground production in African and Australian ecosystems and exert contrasted effects on soil organic matter dynamics at intermediate time scales (months to years). They digest cellulose and lignin in an efficient manner (60-93%; Wood, 1988). Lignin degradation occurs through demethoxylation and depolymerisation (Butler and Buckerfield, 1979). Plant material is ingested by Macrotermitinae undergo transformation as a result of the successive synergistic degradative action of the enzymes of the exosymbiotic *Termitomyces* fungus, the termites themselves and their endosymbiotic microorganisms (Garnier-Sillam, 1989; Garnier-Sillam et al., 1989). Weak organo-mineral bounds are formed during passage through the gut of *Macrotermes nuelleri* which may be easily broken by soil microorganisms. However, considerable undigested organic matter is accumulated in termite mounds. There are several reports that termite species accumulate organic C and nutrients in their mounds within humus-clay complexes with low C/N ratios (Lee and Wood, 1971; Garnier-Sillam et al., 1985, 1987; Okwakol, 1987; Arshad et al., 1988). This phenomenon is not universal as some termites do not incorporate their organic residues into mounds, which in turn have lower organic contents than the surrounding soil. In addition, this mound type does not exert a long-term effect of protecting and conserving organic matter and nutrients.

Long-term effects

More work has been done on evaluating the long-term effects of earthworms on soil organic matter dynamics in temperate soils than in the humid tropics (O'Brien and Stout, 1978; Hoogerkamp et al., 1983). Comparison of two adjacent soils with and without introduced populations of *Pontoscolex corethrurus* in non-climax savannas systems showed that they had contrasting chemical compositions. In the soils without introduced earthworms, the soil was compact and humivorous termites were

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Australian yer, 1971; 990). The and other al-derived

dominant. Both C and N concentrations were greater but grass cover was reduced. In contrast, where *P. corethrurus* had been accidentally introduced, the soil had a well-aerated macroaggregate structure and was covered by a thick layer (1 cm) of casts. The C and N contents of the soil were lower but plant productivity was more prolific.

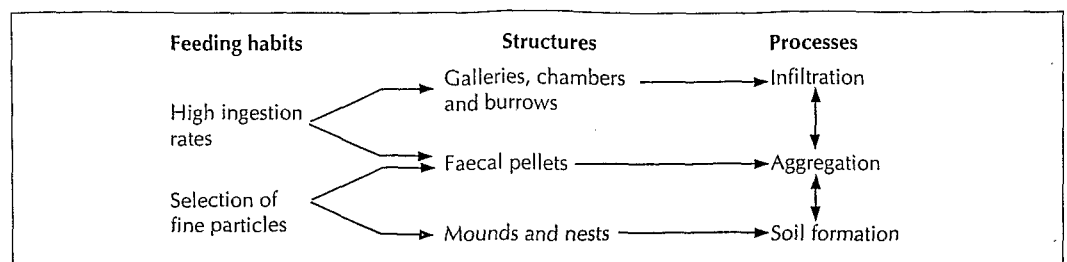
At Lamto in Côte d'Ivoire, the turnover of soil organic matter has been assessed in soils with high earthworm activity after the shift from savanna to forest vegetation, using the natural ^{13}C labelling of soil organic matter (Martin et al., 1990). In a savanna which had received only C_3 woody material for 16 years, the proportion of soil organic matter turned over during that time was estimated to be 65% in the upper 10 cm of soil. In addition, differences between particle size fractions were observed. The turnover time for 50% of the coarse fractions was less than 1.5 years, whereas that for the fine fraction ($< 50 \mu\text{m}$) was more than 18 years. The turnover of soil organic matter was much reduced with soil depth. Mineralisation rates of only 40% in 16 years were measured in the 10-25 cm layer. It is hypothesised that such a rapid turnover of soil organic matter, which is much greater than values reported earlier (Cerri et al., 1985; Balesdent et al., 1988), may be due to the intense earthworm activity observed at the site.

The long-term effect of termites varies tremendously because of different specific behavioural patterns and adaptive strategies. The absence of termites from semi-arid soils results in increased soil organic matter content and accumulation of litter at the soil surface (Moore et al., 1967; Parker et al., 1982; Elkins et al., 1986). This contradicts observations showing increased organic matter content in soil close to the termite mounds of some species (for example, Lee and Wood, 1971; Anderson and Wood, 1984; Garnier-Sillam et al., 1988).

EFFECTS OF SOIL FAUNA ON SOIL FABRIC AND PHYSICAL PROPERTIES

Soil fabric is the 'physical constitution of a soil material as expressed by the spatial arrangement of the solid particles (simple or compound) and associated voids' (Brewer, 1964). The soil invertebrates that have important direct effects on soil fabric are those that are able to dig and/or to ingest and transport mineral and/or organic soil material. The effects are often so prominent that the term 'biofabric' (biologically produced soil fabric) has been proposed (Johnson, 1990). The effects on soil fabric result primarily from high ingestion rates, the selection of fine particles and the building of specific structures. Several kinds of structures are constructed as a result of these activities, including galleries, chambers, burrows, faecal pellet accumulations, mounds and nests. Depending upon the spatial

Figure 6.5 Relationships between soil invertebrate behaviour and soil physical processes



distribution and density of these structures, the aggregation and infiltration rates of soil are greatly affected and the whole process of soil formation influenced (*see* Figure 6.5).

The diggers and/or geophagous invertebrates are represented mainly by earthworms, termites and ants. Since little information is available on the effects of ants, only termite and earthworm effects will be considered here.

Earthworms: Drilospheric effects

The drilosphere is composed of the galleries and the fresh or ageing casts produced by earthworms. Earthworms seldom make mounds (Nye, 1955; Bachelier, 1971). They affect the soil fabric mainly by mixing and aggregating the soil, which has positive influences on infiltration rates and erosion.

Soil mixing and cast deposition

Soil mixing, referred to as pedoturbation by Hole (1961), results from the upward and downward transportation of soil material by animals. Endogeic earthworm communities daily ingest 5-30 times their own weight on a dry soil basis in moist West African savannas. At Lamto in Côte d'Ivoire, the soil which annually passes through the guts of earthworms has been estimated to be 250-1250 t/ha dry weight, depending upon savanna types and annual rainfall (Lavelle, 1978). Communities with comparable compositions are found in Central America and in some pastures dominated by the exotic endogeic species *Pontoscolex corethrurus* and *Polypheretima elongata*.

Forming and back-filling voids

Anecic earthworms dig vertical galleries which are maintained for some time. Truly anecic earthworms are restricted to a few families (South American Glossoscolecidae and Australian Megascolecidae). In some tropical regions in West Africa and Central America, communities are dominated by endogeic species that open galleries by ingesting soil material. They eject their faeces into the soil, thus back-filling the galleries. In the Guinean savanna at Lamto, 1.7-3.5% of the total ingested material is deposited as casts at the soil surface. Between 25 and 30 t of dry soil material are thus translocated annually above the soil surface (Lavelle, 1978). Similar figures have been reported for wet savannas in Cameroon (Kollmansperger, 1956). The back-filling of the galleries is often incomplete and numerous macropores exist between the casts (Blanchart, 1990).

Forming and destroying peds

Earthworm casts are bio-aggregates (Eschenbrenner, 1986). Earthworms may selectively ingest finer particles, resulting in a finer granulometric composition and lower porosity in the casts than the adjacent soil (Bates, 1960; Lavelle, 1971; Mulongoy and Bedoret, 1989; Blanchart, 1990). Changes of pore abundance and distribution observed in casts of *Millsonia anomala* compared with the non-ingested soil are assumed to be responsible for modified dynamics of soil organic matter. Observations of thin sections of casts of *M. anomala* and non-ingested soil have confirmed this hypothesis

(Blanchart, 1990); the casts are more compact than the surrounding soil and have a thin cover of organic particles and clay minerals. Long-term (30 months) field experiments have shown that these structures may persist for several years (Blanchart, 1990).

Two types of casts were identified above and within the soil (Lavelle, 1978). Type 'a' was globular and was composed of rounded, coalescent sub-units ranging in size from 1 to 10 cm. These casts were produced by large earthworm species such as *M. anomala* and *Dichogaster terrae-nigrae* and had a bulk density of 1.8-2.0 g/cm³, whereas that in the control soil was 1.1-1.3 g/cm³. The total porosity of casts was also lower. Nonetheless, the increased number of micropores resulted in available water reserve increases from 10 to 14%. Type 'b' was granular, made of small millimetric sub-units that were weakly coalescent. These casts were produced by small filiform earthworms (*Chuniodrilus zielae* and *Stuhlmanina porifera*).

A spectacular effect of earthworms in savannas is in soil aggregate formation. Aggregates with a diameter larger than 2 mm represent 17-32% of the bulk soil in grass savannas and 25-54% in shrub savannas at Lamto. The highest values are observed at the end of the rainy season when earthworm activity has been at a maximum for several months. Such a level of aggregation is remarkable given the low clay (5-10% of kaolinitic clay minerals) and organic matter contents (1-2%). Laboratory and field experiments have demonstrated that these aggregates derive directly from earthworm activities (Blanchart, 1990; Blanchart et al., 1989, 1990). Field observations at Lamto indicated that the formation of aggregates coarser than 2 mm never affected more than 60% of the soil despite the annual ingestion of up to 60% of soil from the upper 10 cm (Blanchart, 1990). This observation may be due to either a limitation of the activity of large earthworms, because worms can only ingest aggregates of the size of their mouth, or the splitting of old casts into smaller ones (0.5-2 mm) by filiform earthworms of the family Eudrilidae.

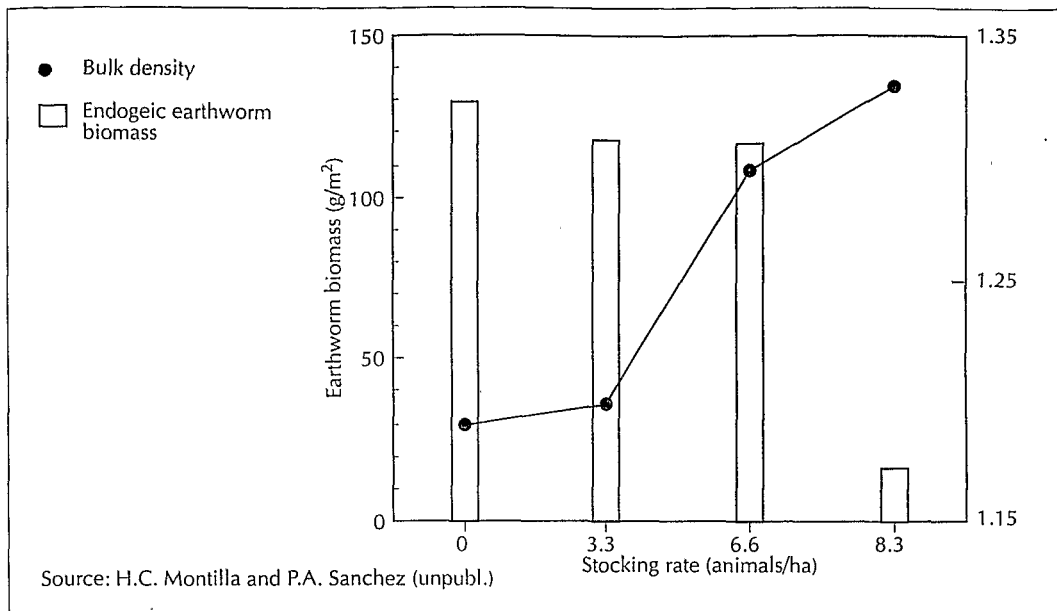
Significant evidence of the disintegration of old earthworm casts appeared after 30 months when earthworms were excluded from soil monoliths at Lamto. The disintegration of casts was more rapid when small filiform earthworms (Eudrilidae) which produce type 'b' casts were introduced after the exclusion of larger worms. Together, these two types of earthworms regulate the degree of macro-aggregation in many soils.

Effects on erosion and movements of fluids in the soil

Field studies have demonstrated that earthworm-worked soils have low bulk densities and high infiltration rates (Lal, 1974; Wilkinson, 1975; Aina, 1984; Lee, 1985).

In sub-humid West Africa, rainfall simulation experiments coupled with morphological determinations of soil surface status confirmed this statement. Infiltration rates of 40-75 mm/h were correlated with the presence of earthworm casts at the soil surface when less than 20% of the surface was covered with casts. When the casts covered over 20% of the surface, this rate was 70-85 mm/h (Casenave and Valentin, 1988). The consequences of cattle trampling on pasture degradation have been investigated at Yurimaguas in the Peruvian Amazonia. It has been demonstrated that earthworm activities help maintain low bulk densities and suitable infiltration rates as long as the stocking rate is at a reasonable level (H.C. Montilla and P. Sanchez, unpubl.; see Figure 6.6). At Lamto, type 'a' surface casts protect the soil from sheet erosion whereas type 'b' casts are disaggregated by rain splash and furnish material for runoff (Lavelle, 1971). Thus, the effects on soil erosion may vary depending upon the composition of the earthworm communities and the type of casts that are formed. In a few cases, however, an apedal sticky mass may form in the surface horizon when the activities of the

Figure 6.6 Variations of earthworm biomass and bulk density of soil as a function of stocking rates in pastures at the TSBF Yurimaguas site, Peru



earthworms is too intense; in these cases, infiltration is impeded and runoff increased (Rose and Wood, 1980).

Termites: Termitospheric effects

The termitosphere comprises nest mounds, galleries within the soil and dead wood, covered runways and sheetings covering the soil surface, twigs, fallen logs and the exterior of standing trees.

Mounding

Many species do not build mounds but, instead, construct nests within the soil, stumps or fallen logs or around living trees. Termite mounds vary greatly according to species in size and shape, number, percentage of area occupied and nature of the materials used for construction. They range in size from small structures, only a few tens of centimeters in height and diameter, to the huge domes built by some African Macrotermitinae which reach 9 m in height and 30 m in diameter (Lee and Wood, 1971; Wood and Sands, 1978; Grassé, 1984). The mound shapes may be domed, conical, columnar, turreted, fluted, mushroom-like or cathedral-like.

The number of termite mounds per hectare varies from less than one to more than a thousand (Lee and Wood, 1971; Spain et al., 1983; Aloni and Soyer, 1987). The dry weight per hectare ranges from less than 0.3 t/ha to 2400 t/ha. The latter value is the equivalent of a layer, 20 cm deep, over the entire surface area (Meyer, 1960; Lee and Wood, 1971). Occupied mounds, covered runways and sheetings

are continually eroded by rain splash and repaired by termites. This results in a continuous transfer of material from beneath the soil surface.

Behaviour studies of the building activities of various termite species (Grassé, 1984; Eschenbrenner, 1986) have shown that, in spite of the diversity of the materials used to build nests, mounds, covered runways, sheetings and galleries infillings, these insects make use of the same elementary building units. The units are ovoidal or cylindrical in shape, 0.2-2 mm in size, and mineral, organic or organo-mineral. They are called 'termite pellets'.

Soil (or organic material) which is to be used for construction purposes can be taken and carried in two different ways. The finer size fractions (< 100-300 μm) are ingested and subsequently they are either regurgitated (as oral pellets) or excreted (as faecal pellets). In contrast, the larger soil particles (0.4-3 mm) are carried between the mandibles and they are then incorporated into the construction, using saliva or excrement as cement. Thus, according to the nature, proportion and mode of assembly of the pellet, the same species is able to construct different fabrics within different parts of a single termitosphere.

Forming and back-filling voids

Voids associated with termite activities are composed mainly of interconnected networks of galleries (1-15 cm in diameter) and chambers (3-25 cm in diameter) in the subsoil. The galleries and chambers, whose length may reach 7.5 km/ha (Darlington, 1982; Wood, 1988), are often partially back-filled by mineral pellets transported and assembled by termites with different amounts of inter-pellet macroporosity (Eschenbrenner, 1988). These infillings by termites lead to the formation of pedotubules (Brewer, 1964).

Regulation of soil erosion and soil, air and water movement

The effects of termite activities vary between species with different feeding and structure-building behaviour, and within the same species between the mound and the 'trophic area'. Humus-feeding termites (*Thoracotermes macrothorax*) in the Congo improve the permeability as well as the structural stability of the soil of their trophic area (Garnier-Sillam et al., 1988). Conversely, fungus-growing termites (*Macrotermes muelleri*) reduce permeability and structural stability (Garnier-Sillam et al., 1988). Infiltration rates in sub-humid West African areas are very low (6-38 %) on and around the mounds of grass-feeding termites (*Trinervitermes* spp.) but away from the mounds, where termite sheetings and covered runways cover more than 30% of the soil surface, the rates are 85-100% (Janeau and Valentin, 1987; Casenave and Valentin, 1988).

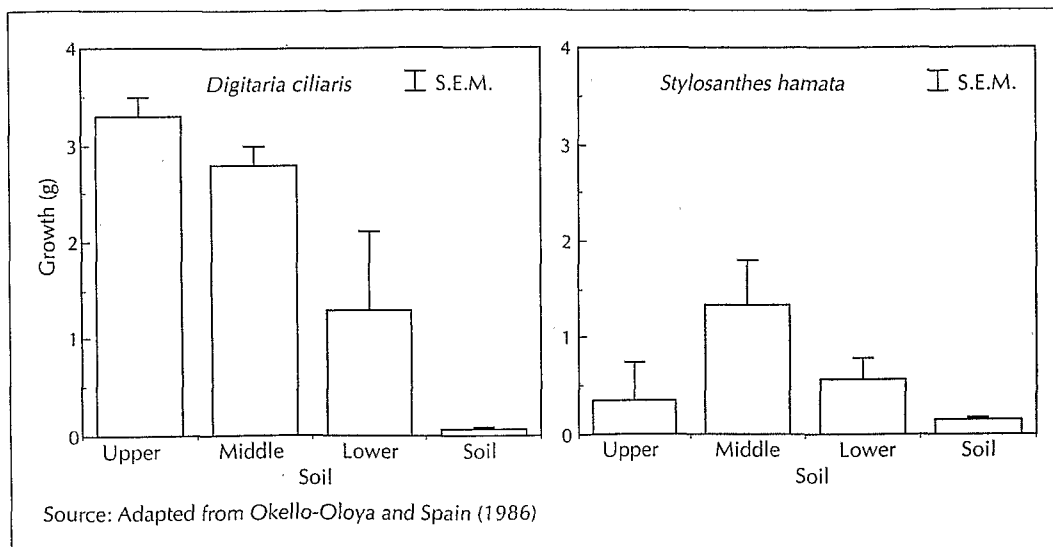
EFFECTS OF SOIL FAUNA ON SOIL FERTILITY

The previous two sections provided examples of the roles of earthworms, termites and other soil fauna in a variety of soil processes. The significance of these roles lies in the influence on soil properties that affect plant growth. Soil fauna activities may dramatically influence fertility processes in natural ecosystems to the extent that the physical and chemical properties of soils may be largely determined by the digestive activities of the animals and the modifications of the environment caused by them.

Influence of termites

Soil from termitaria is sometimes used as fertiliser in tropical cropping systems (Swift et al., 1989). Experiments have demonstrated that the growth of *Stylosanthes hamata* and *Digitaria ciliaris* is significantly increased when they are grown on soil from mounds of *Amitermes laurensis*, a common grass-feeding species in the semi-arid zones of north-eastern Australia (see Figure 6.7). Production was significantly increased using soil from the mound, with a better growth in soil from the upper part of the mound than the lower part and the control soil (Okello-Oloya and Spain, 1986).

Figure 6.7 Production of the legume fodder species *Digitaria ciliaris* and *Stylosanthes hamata* on soil taken at different distances from a termite mound of *Amitermes laurensis*



However, the information concerning the role of termite mounds as soil amendments is far from complete, and in some cases contradictory. Any effect of localised change on soil properties depends upon the amount of termite-modified soil available and the rate at which it is distributed by erosion (Wood, 1988). It also depends upon the nature of the subsoil particles which have been brought to the surface. If these particles have a lower fertility value than the surface particles, the overall effects may be negative. In soils of Africa and South America with a very low natural fertility, the addition of enriched fragments of termite mounds may produce an immediate response in crop production. Nonetheless, the possibility of using this material as a renewable resource depends upon their abundance within the environment and the rate of turnover of the nests. The potential role of mounds as soil amendments has been emphasised in Zimbabwe (Watson, 1977). The weight of mounds of *Macrotermes falciger* was estimated to be 620 t/ha. The application of 10 t/ha of this material produced a significant increase of pasture production. When termite activity produces an equal amount of termite mounds, the resource can be considered as renewable. It is important to mention that the nutrient levels

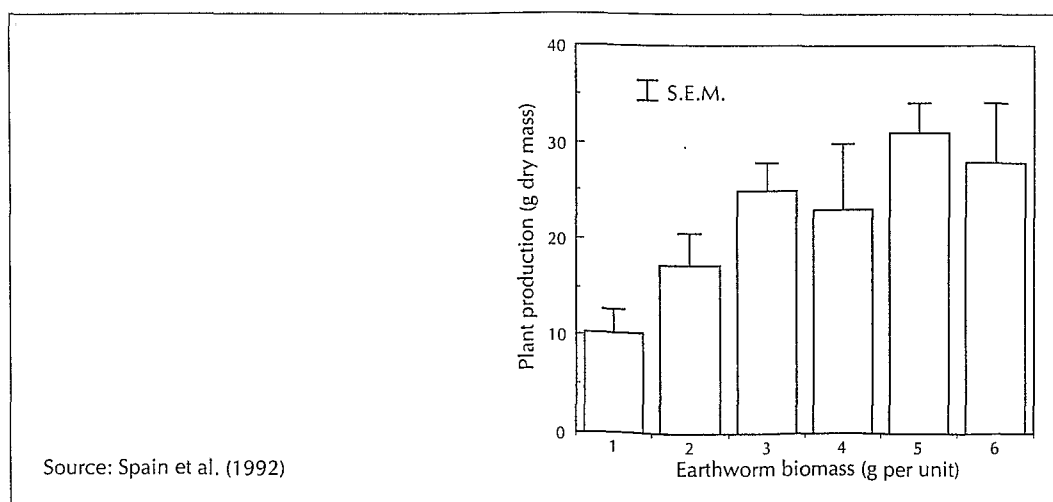
presented in this study were higher than values reported in the literature for other lignivorous species (Lee and Wood, 1971).

Influence of earthworms

Short-term container experiments

Plant production has been shown to be significantly improved by earthworm activities. In a 67-day pot experiment, the growth of *Panicum maximum* was significantly increased when geophagous earthworms were present (Spain et al., 1992). The soil was a sandy Acrisol (80% sand, 5-10% kaolinitic clay) with a low organic content (1-1.5%) and poor nutrient status (ECEC 1-2 cmol/kg). Total plant production increased with the introduced earthworm biomass. The maximum production was obtained with a biomass equivalent to 80-90 g fresh mass/m² (see Figure 6.8). Plant material, particularly roots, produced in the presence of earthworms had higher N and P concentrations. Using ¹⁵N labelling techniques, it was demonstrated that this increased accumulation of N was associated with a more efficient mobilisation of N recently incorporated into microbial biomass. A significant proportion of ¹⁵N lost by labelled earthworms was found in plants, indicating that earthworms may participate directly in the mineral nutrition of plants. When greater earthworm biomass is introduced, a slight decrease of production may result from the negative effect of excessive earthworm activity (Rose and Wood, 1980).

Figure 6.8 Effect of degraded biomass of endogeic earthworms (*Millsonia anomala*) on the production of *Panicum maximum* in a short-term (67 days) pot experiment



These results agree with observations by Pashanasi et al. (1992a) for tropical fruit tree seedlings and Stockdill (1959), Marshall (1971), Lee (1985) and Haimi and Huhta (1991) for diverse plants from temperate regions, which indicated that earthworms may improve plant growth in short-term pot

experiments. This demonstrates that earthworm inoculation can have dramatic effects on short-term plant growth. Under these experimental conditions, however, earthworm activities are not limited by environmental conditions and food resources.

Long-term experiments

TSBF field experiments have recently been conducted at Lamto in Côte d'Ivoire (Gilot, 1992) and Yurimaguas in Peru (Pashanasi et al., 1992b) to test whether the effects of earthworms on parameters of soil fertility observed in small experimental designs are also applicable to larger field units and whether these effects are sustainable over time.

Traditional shifting agricultural systems were duplicated for the purpose of the experiments. Small plots including a few plants were isolated with plastic fabric or nylon mesh to prevent undesired movements of earthworms. These units were separated from each other by border areas that served as a buffer and prevented interactions among treatments. A combination of two kinds of treatments was used. The incorporation of organic residues of different origins was compared with treatments lacking mulch, and the inoculation of adaptable endogeic earthworms was compared with treatments lacking earthworms. This design permitted the following hypotheses to be tested:

- that it is possible to maintain active earthworm populations within cropping systems provided that a suitable species is introduced
- that, over the long term, earthworm activities maintain or even improve soil fertility, soil structure, water infiltration, soil organic matter content and nutrient reserves
- that nutrients contained in surface mulch are better used by crops in the presence than in the absence of earthworms
- that the quantity and quality of crop production is significantly increased by earthworm activities

The cropping systems at Lamto consisted of maize and grass (*Panicum maximum*) in a cleared secondary forest soil and yam in a savanna soil. Grass mulch (2 t/ha) from the nearby savanna was applied to the first crop. Crop residues were applied to the second crop. The original populations of earthworms were eliminated with Carbofuradan. Populations of *Millsonia anomala*, the locally dominant endogeic species, were later reintroduced at a rate of 25g fresh weight/m², the population density observed in the nearby natural savanna.

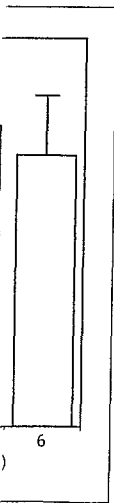
The cropping system at Yurimaguas was a rotation of maize, upland rice, cowpea, rice, rice and cowpea, as recommended by the experimental station to local farmers. Three organic treatments were applied: no mulch; crop residues alone (2.5 t dry weight/ha); and crop residues + legume green manure of *Centrosema macrocarpum* (2 t dry weight/ha at the first crop and 2.5 t dry weight/ha thereafter). Once the earthworm communities from the cleared secondary forest had been eliminated, adult individuals of the peregrine tropical species *Pontoscolex corethrurus* were reintroduced in the 'earthworm' treatments. The original biomass was equivalent to 36 g fresh weight/m². This is a lower biomass than that observed in pastures (80-150 g/m² at the end of the rainy season).

The inoculated earthworm populations colonised satisfactorily at both sites during the first two crops. The major difficulty was to obtain a satisfactory 'no earthworm' control. The *M. anomala* biomass at Lamto decreased in all the experimental plots but reproduction had occurred, demonstrating

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that the population would persist, albeit with a lower biomass than expected. No significant difference was noticed between treatments with earthworms and mulch. Surprisingly, however, treatments with no surface mulch had a larger biomass of *M. anomala* (41.4 g fresh weight/ha), four times as much as in treatments with mulch.

The elimination of earthworms from control plots at Yurimaguas was more complete. Unlike the situation at Lamto, the introduced species *P. corethrus* was almost absent from the controls and the remnant earthworm communities from the previous forest were not well adapted to the cultivated soil. Earthworm biomass decreased slightly during the first crop because the population was composed mainly of young earthworms and a large number of cocoons. The maximum value was observed in the bare soil treatment but the differences were not significant, as shown in Table 6.5. There was an increase in biomass in all the treatments during the second crop. The difference was significant only in the treatment which had received applications of both crop residues and legume green manure, where the earthworm biomass was 81.6 g fresh weight/ha; this was 2.3 times greater than the original introduced biomass.

Table 6.5 Density and biomass (g fresh weight/m²) of *Pontoscolex corethrus* in treatments

Treatment	Initial	First crop ^a	Second crop
Bare soil	36.0	35.3 a	47.2 a
Stubble	36.0	32.5 a	42.1 a
Stubble + legume green manure	36.0	27.5 a	81.6 b

Note: a Values in the same column followed by different letters differ significantly at $p = 0.05$

No difference was observed between the 'earthworm' and 'no earthworm' treatments in the production of maize and grass at Lamto. In the first crop of maize, the grain yield was 4 t/ha; this decreased significantly in the second crop (1.4 t/ha). The presence of earthworms and the application of mulch did not induce any significant difference between grain and shoot production. During the second crop, however, root production was much higher in treatments without mulch, irrespective of earthworm biomass. No significant differences were observed in soil physical and chemical parameters.

The experiment with yam on a savanna soil gave a different result. Although some earthworms were still present in the 'no earthworm' treatment, significant differences were observed in yam production as a result of the presence of larger populations of earthworms. Respective increases of 19.6%, 51.9% and 20.3% were observed in shoot, root and tuber production, respectively (Gilot, 1992).

The production of maize grain from the first crop varied from 1.2 to 2.5 t/ha at Yurimaguas. There was a significant effect of treatments as production increased with the amount of mulch incorporated into the soil. The effect of earthworm inoculation also appeared to be highly significant, resulting in increases of 23.4%, 43.7% and 59.7% in the stubble + legume green manure treatment, the stubble alone treatment and the bare soil control, respectively. The improvement in production was particularly marked in treatments with lower organic input (see Table 6.6 and, *overleaf*, Table 6.7). Similar trends were observed with shoot and root production. Unlike the experiments conducted at Lamto, no

difference was observed in the nutrient contents of plant material. During the second crop, rice grain production ranged from 0.83 to 1.63 t/ha. The effect of earthworm introduction was significant but the effect of mulching was not. Respective increases of 96.3%, 97.6% and 50.5% in grain production were observed in the control, the residue and the residue + earthworm treatments, respectively. Again, the effect of earthworms was more marked in treatments with low organic inputs. Production obtained with stubble + legume green manure in the presence of earthworms was higher than local yields, being close to that obtained with high inputs of fertilisers.

Table 6.6 Crop yield and production of stubble and roots (t/ha) from the first two crops at the TSBF Yurimaguas site, Peru, in response to various treatments^a

Crop	n	C	CL	CR	CRL	CRV	CRVL	LSD ^b
First crop — maize								
grain	36	1.19	1.90	1.42	2.04	2.01	2.48	0.62
stubble	36	2.19	3.37	2.53	3.22	3.52	3.86	0.42
roots	6	0.29	0.48	0.27	0.44	0.33	0.50	0.20
Second crop — rice								
grain	30	0.83	1.63	0.84	1.62	0.99	1.49	0.22
stubble	30	1.42	2.30	1.52	2.27	1.92	2.88	0.28
roots	6	0.30	0.29	0.22	0.58	0.39	0.50	0.16

Note: a C = bare soil; CL = bare soil + earthworms; CR = stubble; CRL = stubble + earthworms; CRV = stubble + green manure; CRVL = stubble + green manure + earthworms
b p 0.05

There is clear evidence of significant changes in soil fertility at the Yurimaguas site after the first crop. Bulk density of soil, N mineralisation rates and water regimes were the first three parameters that exhibited a significant effect of earthworm inoculation. There was a significant increase of 11% in bulk density in the 'earthworm' treatment compared with bulk density in the 'no earthworm' treatment. In the second crop, however, bulk density increased in the 'no earthworm' treatments such that the difference fell to 3.8% and was no longer significant. The infiltration rates also differed, with lower values in those plots where earthworms were present. Soil water tension as recorded by field tensiometers was greater in the 'earthworm' treatments at the end of the growing period of the second crop (rice). This difference, however, might have been produced by an increase in water demand by larger plants.

Although no detectable difference could be observed in most chemical and physicochemical parameters of the soil, N mineralisation was significantly affected by the presence of earthworms. The production of nitrate in standard laboratory incubations was 24% more active on average in those soils from the 'earthworm' treatments. Some interesting trends could be detected in soil chemical parameters. These included increased pH (an average of 0.2 units), decreased acidity (an average of 1.7 meq. in the 'earthworm' treatments and 2.2 in the 'no earthworm' treatments) and decreased Al saturation (an average of 40.1% in the 'earthworm' treatments and 47.2% in the 'no earthworm' treatments). No changes could be detected in the N, P, Ca, Mg and K contents of soils (Pashanasi et al., 1992b).

Table 6.7 Analysis of variance in agronomic treatments in the presence or absence of earthworms in experiments at the TSBF Yurimaguas site, Peru

Crop	Treatment	Biomass DMR ^a	Earthworms ^b	
First crop — maize	grain	Bare soil	a	+ 41.0%**
		Stubble	ab	
		Stubble + green manure	abc	
	shoots	Bare soil	a	+ 28.3%**
		Stubble	ab	
		Stubble + green manure	abc	
	roots	Bare soil	a	+ 57.0%*
		Stubble	a	
		Stubble + green manure	a	
Second crop — rice	grain	Bare soil	a	+ 78.0%**
		Stubble	a	
		Stubble + green manure	a	
	shoots	Bare soil	a	+ 52.1%**
		Stubble	a	
		Stubble + green manure	b	
	roots	Bare soil	a	+ 45.3%*
		Stubble	a	
		Stubble + green manure	a	

Note: a Values for crop and yield components followed by different letters differ significantly by Duncan's Multiple Range test ($p < 0.05$)

b Increase due to the introduction of earthworms, ** $p < 0.05$; * $p < 0.01$

CONCLUSION

Soil faunal communities show a variety of reactions to changes induced by land management. Their abundance and diversity are indicators of the quality of soils and influence soil organic matter dynamics, nutrient contents and physical parameters such as bulk density, porosity and water availability. Annual cropping has generally depleted soil faunal communities, especially in the case of earthworms, but termites have been less affected. Perennial cropping systems, pastures and plantations generally have less diverse communities than the original ecosystem but the biomass is often higher owing to the colonisation by peregrine earthworm species and the persistence of native species. Nonetheless, the degradation of these systems frequently results in a depletion of soil macrofauna communities.

Short-term experiments have demonstrated that earthworm activities may result in significant increases in production. Similar results have been obtained by growing plants in soil taken from termite mounds. In low-input shifting agriculture systems, it is possible to introduce and maintain adapted

of earthworms

worms^b

1.0%**

3.3%**

7.0%*

10.0%**

11.1%**

13.3%*

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earthworms within fields provided they are introduced immediately after land clearing. Such introductions resulted in increases of 23-98% in grain production in the first two crops at Yurimaguas in Peru. The highest increases were obtained in treatments with low organic inputs. At Lamto in Côte d'Ivoire the effect of introduced earthworms in the early phases of the culture did not result in such spectacular increases. It is too early to determine whether these effects are sustainable. Beyond the increase in production observed in the early stages, the main objective of these experiments was to demonstrate that production may be sustained for longer periods when soil fauna, especially earthworms, are promoted. To test this hypothesis, long-term field experiments are necessary to evaluate the effects of earthworm inoculation in a wide range of soil/crop/earthworm species combinations.

The next phase will be to design agricultural techniques derived from these experiments. Three successive steps will be involved in this phase: selecting non-harmful chemicals and cultivation techniques which prevent the destruction of soil macroinvertebrate communities whenever possible; providing beneficial invertebrates with food and, through the application of appropriate mulch in suitable quantities, favourable environmental conditions in order to facilitate the activities of these invertebrates; and manipulating communities by introducing selected species which have positive effects on plant production and the sustainability of the system. The interpretation of soil fertility effects and the development of management methods beyond the purely empirical depend upon yet further improvement in the understanding of the behaviour of soil fauna and its relation to specific processes of soil fertility.

Specific techniques need to be developed to identify species suitable for inoculation and methods designed to implement the colonisation of soils by their populations. Colonisation may be active (through a direct introduction of inocula) or passive (by facilitating the spread of populations from colonisation foci situated within or near the fields). The importance of the relative position of plots and history of land use are critical issues to consider. Colonisation will be more easily accomplished if a parcel with dense populations of the species selected for introduction is adjacent to the field or if the abundance of populations has been maintained in the field at a level that allows a rapid re-colonisation once suitable conditions have been re-established.

A better understanding is needed of the potential for the management of populations of ants (particularly the leaf-cutting ants of South America), termites (of critical importance in most tropical areas of Africa and Australia) and saprophagous myriapod and coleopteran larvae (abundant in Central American soils). Interactions between species also need attention in order to design manipulations of several species with complementary functions. The regulation of such complex processes as the dynamics of soil organic matter or soil fabric results from integrated activities of several species organised in complex foodwebs. Therefore, the introduction of a single species may well result in detrimental effects if other species with complementary effects are negatively influenced.

Finally, careful attention needs to be paid to the socioeconomic context of the manipulations being considered. Local knowledge of soil faunal activities and their relation to fertility must be evaluated in order to make better use of the potential of native species and design practices that are technically feasible, economically profitable and most likely to be adopted by local farmers.

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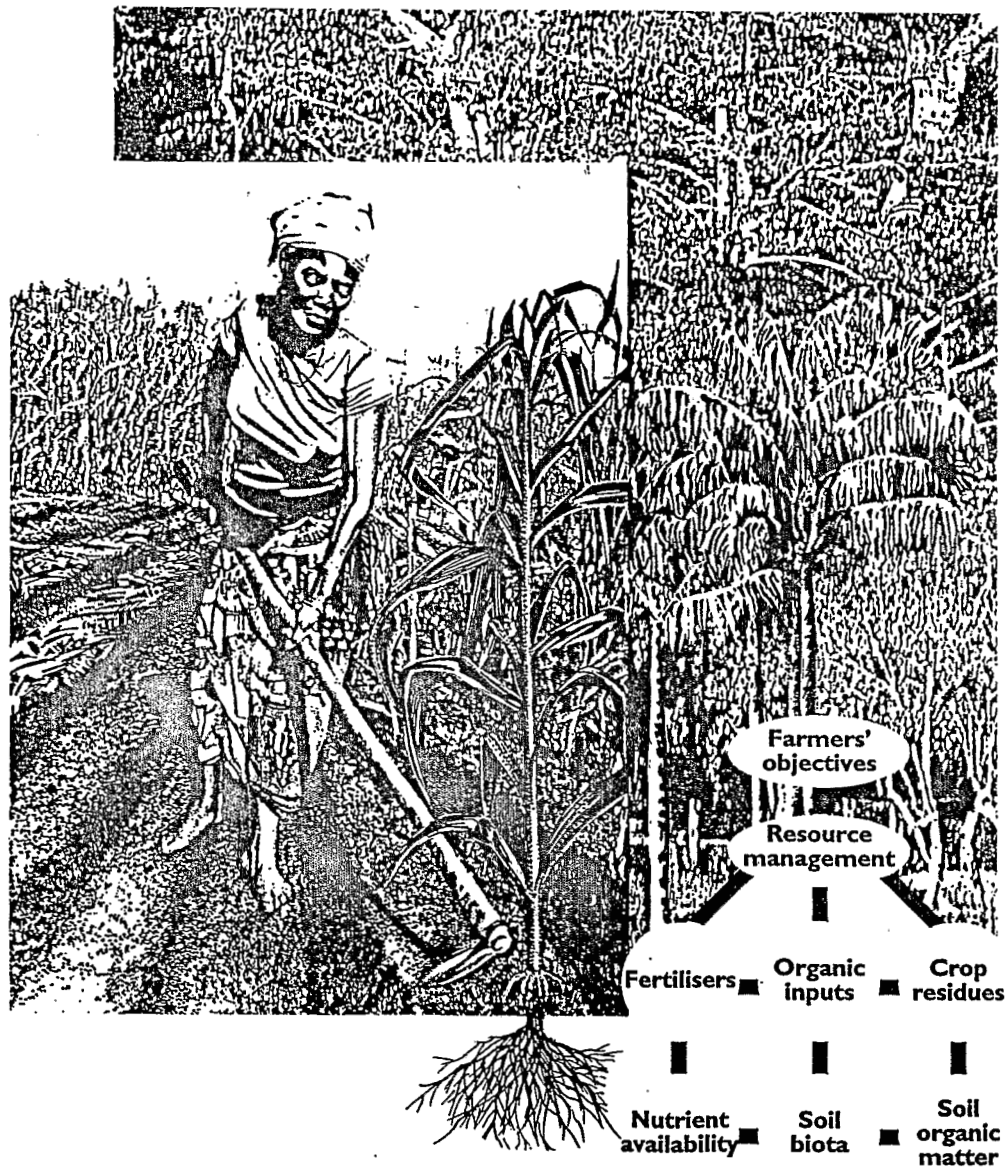
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THE BIOLOGICAL MANAGEMENT OF TROPICAL SOIL FERTILITY

Edited by P.L. Woomer and M.J. Swift



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Preface

The fertility status of many tropical soils, particularly those of smallholder farmers, is regulated by key biological processes and the organic resources available to farmers. Too often, these processes are not understood well enough by agriculturalists to be placed in the soil management context. Failure to understand the complexities of tropical soil fertility has resulted in the lack of well-integrated management strategies, and this has led to the recognition that agricultural systems must become more sustainable if the food requirements of future generations are to be met.

This book reports on the first five years of research by scientists of the Tropical Soil Biology and Fertility Programme (TSBF). TSBF is sponsored as a component project of the International Biological Sciences (IUBS) programme The Decade of the Tropics and of the Man and the Biosphere (MAB) programme of UNESCO, and is hosted by the UNESCO Regional Office for Science and Technology in Nairobi, Kenya. TSBF is a voluntary participatory international research programme whose members are committed to the concept that the fertility of tropical soils is controlled by biological processes and can be managed by the manipulation of these processes. Participating network scientists conduct field studies in Central and South America, sub-Saharan Africa, South Asia and Australia, and maintain close institutional links with researchers in Europe and North America. TSBF's main intention is to review the potential for the biological management of tropical soils, focusing on the programme's four main research themes: soil organic matter management; nutrient-use efficiencies; manipulation of the soil water regime; and the potential for the utilisation of soil fauna for soil fertility improvement. Each theme is discussed, together with accompanying chapters which set the context of the drive for sustainable agriculture, lay the foundations for an agroecological approach to soil and discuss the socio-economic implications of TSBF research.

The book contains nine multi-author chapters but it has been prepared as a continuous discursive text. The authors have all worked together at workshops and in the field and share a common philosophy of research and soil management. The book is thus intended as a basic text for research in sustainable soil management. It is aimed primarily at young, post-graduate scientists in the disciplines of soil science, agronomy, forestry or ecology, as well as senior scientists and decision-makers concerned with the sustainable development of agriculture and other land uses in the tropical regions.

The publication of this book would not have been possible without the generous financial support from several organisations. Direct funding for the initial meeting of the authors was received from the Rockefeller Foundation, ORSTOM and the United Nations Environment Programme (UNEP). The editors' salaries were provided by the Natural Environment Research Council (NREC, UK) through the Institute of Terrestrial Ecology (ITE), the Overseas Development Administration (ODA, UK) through the International Centre for Research in Agroforestry (ICRAF) and the International Institute of Tropical Agriculture (IITA). Financial support for TSBF Headquarters in Nairobi, Kenya was also provided by the United Nations Scientific, Cultural and Educational Organisation (UNESCO) through the Man and Biosphere Programme (MAB) and the Regional Office for Science and Technology for Africa (ROSTA). We gratefully acknowledge the involvement by, and the financial contributions from, all of the above organisations.

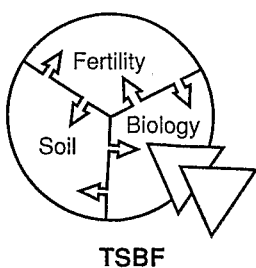
P.L. Wooster and M.J. Swift
Tropical Soil Biology and Fertility Programme (TSBF)

Tropical Soil Biology and Fertility Programme (TSBF)

TSBF was established in 1984 under the patronage of the Man and Biosphere programme of Unesco and the Decade of the Tropics initiative of the International Union of Biological Sciences (IUBS). The objective of the programme is to develop appropriate and innovative approaches for sustaining tropical soil fertility through the management of biological processes and organic resources. To achieve this objective, TSBF aspires to:

- make available to farmers and other land managers in the tropics methods for soil management which will improve agricultural productivity but conserve the soil resource
- contribute to increasing the carbon storage equilibrium in tropical soils in the face of global changes in land use and climate
- improve understanding of the role of biological resources in soil fertility and the sustainability of tropical land-use systems
- improve the research and training capacity of national institutions in the tropics in the fields of soil biology and management of tropical ecosystems

TSBF is a voluntary participatory international research programme whose members are committed to the concept that the fertility of tropical soils is controlled by biological processes and can be managed by the manipulation of these processes. Research is conducted at both the ecosystem level and the process level on the basis of two principles: that the capacity to manage soil fertility depends on a mechanistic understanding of the biological processes regulating nutrient flux, organic matter dynamics and soil physical structure maintenance, and that successful management for sustainable soil fertility must be implemented at the ecosystem level by integrating soil biological processes with those of human decision making in relation to all components of the ecosystem.



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