

Chapter 18

Soil Fauna and Sustainable Land Use in the Humid Tropics

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Introduction

It has been long claimed that soil fauna are key actors in sustainable land use. Long after Aristoteles called earthworms the 'intestine of the earth', Darwin (1881) said that '*It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures*'. Since that time, considerable efforts have been made to substantiate these statements and extend them to the whole soil fauna community. Their importance and role in energy cycling has been widely studied during the IBP Programme (Petersen and Luxton, 1982). These studies reinforced the feeling that they had significant impacts on major soil processes. During the last decade, considerable efforts have been made to describe and quantify these effects and assess the influence of land use on their communities (see e.g. Veeresh *et al.*, 1991; Andren *et al.*, 1988 and syntheses by Lee, 1985; Anderson and Flanagan, 1989; Lavelle *et al.*, 1992b).

Processes whereby soil fauna may affect the dynamics of soil fertility have been described and quantified, mostly at the 'micro' and 'meso' scales at which these organisms operate. These studies gave a clear understanding of the processes involved; none the less, the lack of experiments at the scale of a farmer's plot have not so far allowed the evaluation of the exact role of these processes, and the potential to manipulate them to improve soil fertility.

This chapter gives an overview of the effects of land management practices on soil fauna communities in tropical soils. The effects of soil fauna on processes relevant to sustainability are discussed, and finally, recent results of manipulative experiments are presented.

Soil Fauna Communities

Soil fauna comprise a large variety of organisms with contrasted sizes and adaptive strategies. The abundance and composition of their communities, and hence their impact on soil processes, vary greatly depending on vegetation and land use practices.

Invertebrates in the soil system

Adaptive strategies

Microfauna comprise hydrobiont invertebrates which live in free soil water and water films that cover soil particles; they are usually either micro-predators of microorganisms and other microinvertebrates, or plant parasites. Their average size is less than 0.2 mm. Protozoa and nematodes are the main representatives of this group. The spatial range of their activities is of micro- to millimetres. They usually form foodwebs of micropredators with a significant impact on nutrient cycling, e.g. in the rhizosphere (e.g. Trofymow and Coleman, 1982; Setälä *et al.*, 1991a);

Mesofauna comprise microarthropods and small Oligochaeta Enchytraeidae. Average length ranges from 0.2 to 2 mm. They are typical inhabitants of litter systems where they feed on litter and microorganisms. None the less, they may also colonize the whole profile of soil, although with reduced densities. They may have a significant impact on litter comminution and dispersal of fungal spores (Persson *et al.*, 1980; Swift and Body, 1985).

Macrofauna operate at much larger scales of time and space. They are large-sized invertebrates that may disrupt the soil and modify its structure through their movements and feeding behaviour. They are 'ecosystem engineers' (Stork and Eggleton, 1992) that may transport and mix soil and organic residues in the whole soil profile and create diverse and conspicuous structures, e.g. mounds, galleries and soil aggregates.

These groups adapt differently to the three main constraints that soil organisms face, i.e., feeding on relatively poor quality resources, resisting occasionally unfavourable microclimatic conditions and moving in the limited and discontinuous pore space of soil. Small invertebrates have a much higher resistance to environmental stress than larger ones. They are unable to develop mutualistic associations with microflora to easily digest organic resources. As a consequence, they rely mainly on predation or plant parasitism. On the other hand, large invertebrates have better abilities to develop external ('exhabitational' *sensu* Lewis, 1985) or internal ('inhabitational') mutualistic associations with microflora. These associations are efficient at using low-quality resources, e.g. woody or humified material.

Although these invertebrates may escape from unfavourable microclimatic conditions by building suitable structures for their shelter and movement, they are limited to non-extreme conditions.

Soil food webs

Food webs in the soil are fundamentally based on relationships of invertebrates with microorganisms. These relationships are organized at different levels which depend on the size of the organisms (Fig. 18.1).

Microorganisms directly exploit resources; they comprise the first level. Microfauna mainly act as predators of microflora; this is the only kind of interaction that they can develop since their small size does not allow any significant mutualism.

Mesofauna comprise a mixture of microbe and fungal grazers and invertebrates, which rely on the 'external rumen' feeding strategy. They create suitable conditions for microbial life in their faecal pellets and an intense microbial activity results in the digestion of part of the undigested organic matter. By reingesting their faeces at that stage, invertebrates may make use of assimilable organic matter, and possibly feed, at least partly, on the microbial biomass.

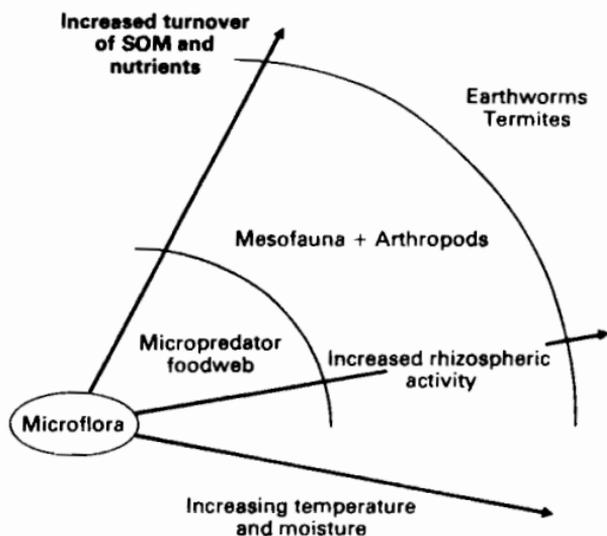


Fig. 18.1. Relationships among soil microflora and soil fauna. a conceptual model. For explanations see text.

Macrofauna rely on mutualistic interactions with microorganisms to extract assimilable compounds from the decomposing materials. They may use the external rumen strategy. Some of them, especially the termites, and earthworms, have developed with microorganisms facultative or obligate internal mutualist systems of digestion. This is the case with earthworms which stimulate the activity of microflora ingested with soil by adding large amounts of water (up to 100%) and mixing significant amounts of readily assimilable organic compounds (Barois and Lavelle, 1986). These additions and the intense mixing in the gut trigger intense microbial activity. In the posterior part of the gut, organic matter has been digested and the worm may absorb part of the assimilable compounds. Termites have even more sophisticated inhabitational (*sensu* Lewis, 1985) mutualist relationships with microflora; in the lower termites obligate associations with protozoa have been described.

In soils where climatic constraints do not allow large invertebrates to live, microbial activity is mainly regulated by micro foodwebs (e.g. Sestedt and James, 1987). When these constraints are released, large invertebrates become dominant regulators of the microorganisms that they influence directly, as explained above, or via predation on micro and mesofauna. The behaviour of earthworms feeding partly on protozoa (Pearce and Phillips, 1980; Rouelle *et al.*, 1985) and nematodes (Dash *et al.*, 1980; Yeates, 1981) is an example of this type of interaction. In these conditions, micro foodwebs are still an essential component of the soil system, but they tend to restrict their activities to specific microsites (e.g. root tips in the rhizosphere). Macrofauna operate at much larger scales of time and space, and behave as ecosystem engineers (Stork and Eggleton, 1992). When present, effects of microorganisms and smaller invertebrates are largely dependent on their physical activities (mixing litter and soil, building structures and galleries and aggregating the soil) as well as metabolic activities (utilization of the available organic resources, development of mutualist or antagonist relationships).

In the humid tropics there are seldom strong climatic or edaphic limitations to colonization of the soil by macroinvertebrates. They become predominant regulators of soil biological activities. Voluntary or involuntary modifications of their communities thus affect other soil organisms within biological systems of regulation. These systems link key macroinvertebrates (e.g. termites or earthworms) to roots, to the whole microflora, and to mesofauna living in the part of the soil that they affect by their activities. Four such systems have been identified, i.e. the rhizosphere, the litter system, the drilosphere (earthworms) and the termitosphere (termites).

Soil macro-invertebrate communities and types of land use**General effects**

Types of land use deeply affect the composition and abundance of soil macrofauna communities. Microclimate and food resources together with application of pesticides are major factors that affect the diversity and abundance of communities. The initial disturbance linked to the clearance of the original ecosystem rapidly eliminates a large number of species especially the ones with narrow niches and slow population turnover rates (Fig 18.2).

Annual cropping is the most detrimental practice as regards soil fauna communities. Within a few weeks of initial cultivation, biomass dramatically decreases. Traditional cultivation techniques in general may be more conservative and in some areas, local fauna may better resist the disturbance. None the less, the average biomass recorded in such environments (ca. 10 g fresh weight m^{-2}) is more than two to four times as low as average values measured in original forest and grassland ecosystems.

Pastures often have a much higher overall biomass of macroinvertebrates than the original ecosystems. This is mainly due to the proliferation of populations of one or two indigenous or exotic earthworm species, and

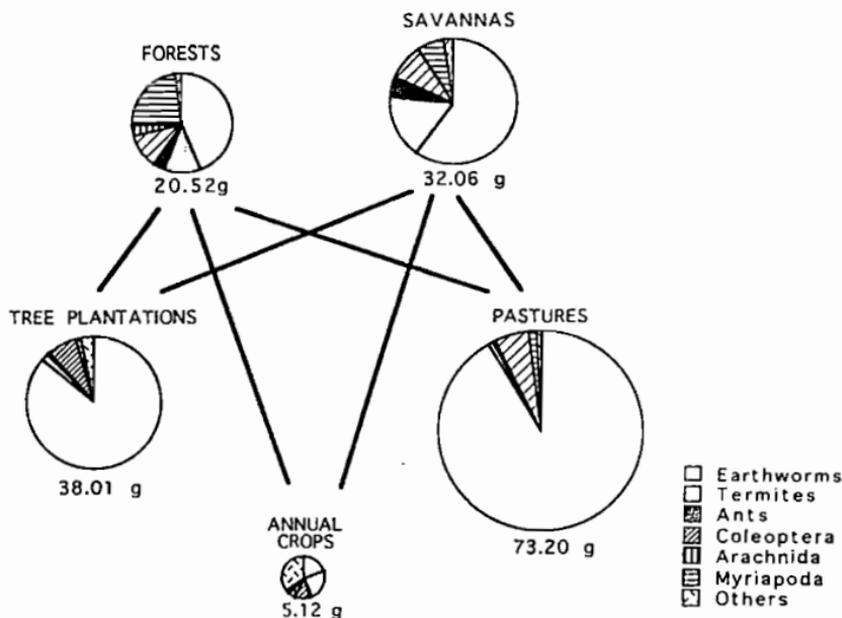


Fig. 18.2. Structure of soil macrofauna communities in major types of land use in the humid tropics.

the local development of Coleoptera larval communities, e.g. in Central American pastures (Villalobos and Lavelle, 1990). In pastures of tropical America, Australia and Asia two species of earthworm, *Pontoscolex corethrurus* and *Polyphretima elongata*, may build a large biomass of 1–4 t ha⁻¹ fresh weight. In regions of natural savannah in Africa, local species adapt naturally to pastures and their biomass may be enhanced by grazing (Kouassi, 1987). However, overgrazing may result in the decline and disappearance of earthworm communities (Castilla and Sanchez, unpublished).

Finally, perennial crops and agroforestry systems generally have large macrofauna biomasses which may be higher than in the original ecosystem. Tree plantations with legume covers may be suitable environments for both indigenous forest species and exotic colonizers, as they offer abundant and diverse resources for decomposers. As a result, these ecosystems often have diverse and high biomass of macroinvertebrates and represent types of land use which sustain both acceptable levels of biodiversity and overall activity.

The energetic bottle neck

These systems, however, may not be able to sustain active macroinvertebrate communities for indefinite periods of time. Sampling conducted

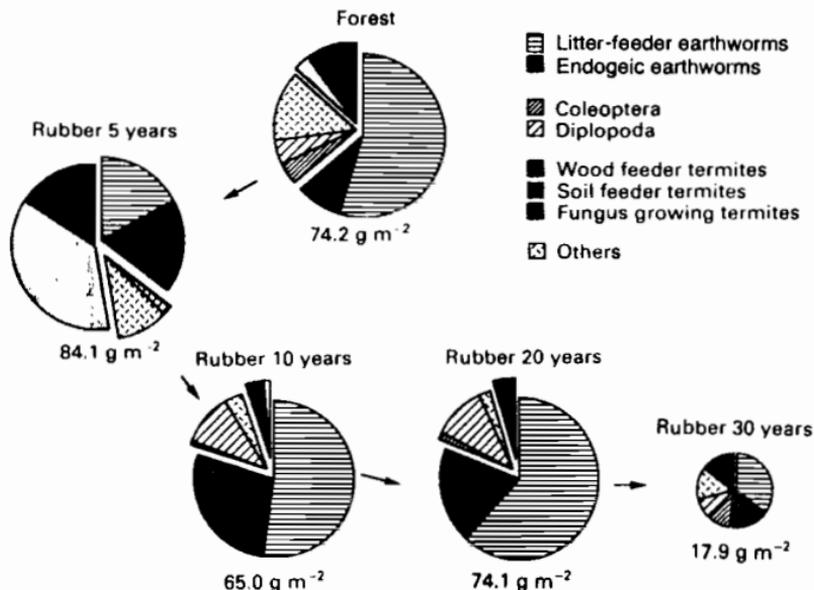


Fig. 18.3. Soil macrofauna communities in *Hevea* plantations of different ages and in the original forest (Gilot et al., in press).

in Hevea plantations of different ages showed that communities change with time and tend to be severely depleted after 30 years. At Bimbresso (Côte d'Ivoire), soil macrofauna biomass was large in the original forest (74.2 g m^{-2}); earthworms comprised most of this biomass, but termites and myriapods were significant elements in this community (Fig. 18.3). In the 5-year-old plantation, biomass was still high, but composition was different. Termites, especially xylophagous termites, were overdominant. In 10- and 20-year-old plantations, biomass of macroinvertebrates was sustained at high levels (65.0 and 74.1 g m^{-2} respectively) but xylophagous termites had nearly disappeared. They had been replaced by large earthworm communities, especially of large endogeic species feeding on soil organic matter. After 30 years the community was highly depleted as was the production of rubber. These results demonstrate the dynamic changes in the community as the Hevea plantation ages. It is likely that this community had been maintained for 20 years by the large energy input from the wood of trunks, branches and large roots in the early years of the plantation. Xylophagous termites first exploited these resources. Earthworms came later in the succession to feed on organic material transformed by the termites. After 20 years, the initial flux of energy faded and organic resources sustained a lower biomass. Changes in the herbaceous cover may also explain part of the observed variations. During the first few months, a legume cover (*Pueraria phaseoloides*) had been maintained. This cover was rapidly replaced by a poor herbaceous stratum which was reduced to a minimum as the canopy closed.

These results clearly emphasize the need for significant amounts of energy sources to maintain active soil macrofauna communities.

The colonization issue

Energetic deficiencies may not be the only process whereby communities are depleted. In some circumstances species which might adapt to the newly created conditions may not be able to colonize because they are not present and/or do not have the ability to invade the site rapidly. This is especially true for earthworms and termites as not all the existing functional groups are present in a given biogeographical area. Such a situation gives scope for a wide range of manipulative experiments. In temperate soils, inoculation of well-adapted earthworm species has been implemented in a number of situations, e.g. for the improvement of pastures in New Zealand, and Australia (Syers and Springett, 1984), reclamation of degraded sites (Curry and Boyle, 1987) or improvement of polder soils (Hoogerkamp *et al.*, 1983). In soils of the humid tropics critical targets might be to introduce species with expected favourable effects on the soil function in low input agricultural systems (termites).

Manipulative Experiments: Introduction of Endogeic Earthworms in Low Input Agricultural Systems

In Peru, Mexico and Côte d'Ivoire, situations have been identified where the introduction of earthworms was feasible. They comprise traditional systems based on slash-and-burn agriculture. Research has been conducted which demonstrates that carefully chosen adapted species may build up sizeable populations. These populations affect plant production and soil fertility as assessed in terms of soil organic matter (SOM) and nutrient conservation, and conservation of soil physical properties. Most of the results presented here have been obtained at Yurimaguas (Peru) in acid Ultisols under a traditional rotation with no fertilizers, or continuous maize cropping fertilized after the third cropping cycle.

Experimental design and general methodology

Soil monoliths 60 cm in diameter and 50 cm deep were isolated from the soil of a 20-year-old secondary forest and a nylon mesh was used to prevent any movement of earthworms. After clearing and burning the forest, these units were cleared of native earthworms by an application of carbofuran to create 'no earthworm' situations. After six weeks, earthworm populations were introduced. The species chosen, *Pontoscolex corethrurus* is very widespread in all disturbed soils of the humid tropics; it has a large tolerance for a wide range of edaphic factors, except for drought. It has also the ability to build numerous populations rapidly when placed in favourable conditions (Lavelle *et al.*, 1987). At Yurimaguas, 120 such experimental units were installed. 108 of them were cropped to a traditional rotation system with no fertilizers; 12 were cropped to maize with fertilizers from the fourth cropping cycle onwards. Six different treatments were applied, i.e. three levels of organic treatments (no organic residues) (C); organic residues produced on the experimental unit (CR), and CRV i.e. CR + legume green manure of *Centrosema macrocarpum* (2.5 t ha⁻¹ dry weight), with or without earthworms.

In 'with earthworm' treatments, a relatively low initial (36 g m⁻²) biomass was introduced. It was believed that biomass would rapidly reach an equilibrium representing the actual carrying capacity of the system for the species. The experiment was designed to have six successive cropping cycles. At each harvest, aboveground production was measured in all units. 'Internal' parameters, i.e. characterization of SOM, earthworm and root biomass, bulk density, infiltration and aggregation were measured on three experimental units which were destroyed for sampling. During the growth period, soil water content and the decomposition rates of organic residues were monitored. Methods are basically the ones proposed in the Tropical

Soil Biology and Fertility programme (TSBF).

In a nearby plot, 20 units were allocated to continuous maize cropping to monitor dynamics of SOM using natural ^{13}C labelling, by shifting from a pure C3 vegetation (forest) to a pure C4 maize culture to sustain significant production in the system. Fertilizers (100 N, 20 P, 20 K) were applied from the fourth cropping cycle onwards to sustain production.

At Lamto, similar experiments were installed with a native species (*Millsonia anomala*) under continuous maize cropping in a forest soil, and continuous yam cultivation in a savannah soil.

Establishment of earthworm populations

The establishment of introduced populations was not equally successful at all sites. At Lamto (Côte d'Ivoire), populations were sustained at very low biomass ($3\text{--}4\text{ g m}^{-2}$ after four crops). There was clear indication from a specific experiment that the limitation to earthworm settlement was the lack of food (Gilot *et al.*, 1992).

At Yurimaguas, populations actively reproduced in all treatments. They responded significantly to organic inputs, with the lowest biomass in treatments without residues and highest biomass in treatments receiving either crop residues alone or crop residues + legume green manure (Fig. 18.4).

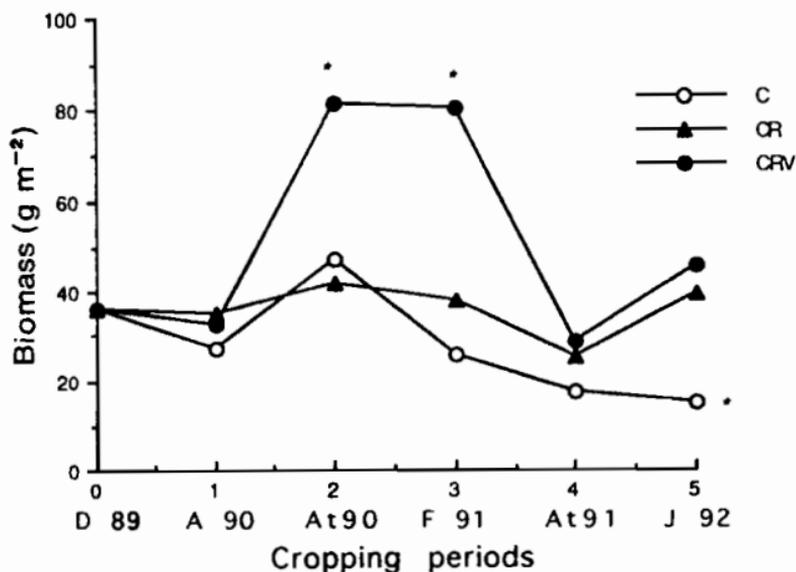


Fig. 18.4. Changes in biomass of *Pontoscolex corethrus* in a traditional cropping rotation submitted to three different organic treatments at Yurimaguas (* indicate significant differences with other treatments at the same date): (C: no organic inputs; CR: application of crop residues produced at the site; CRV: crop residues + 2.5 t ha^{-1} legume green manure).

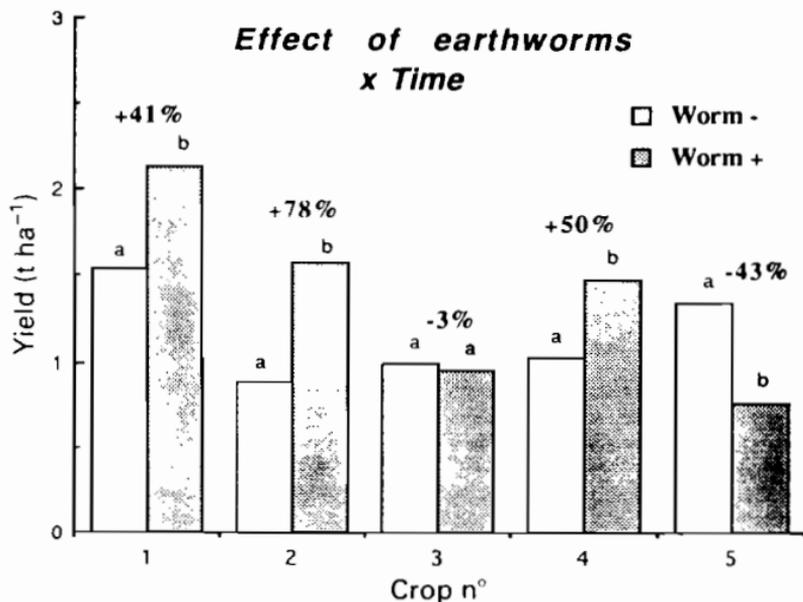


Fig. 18.5. Effect of earthworm activities on grain production at five successive harvests irrespective of organic treatments.

Crop production was sustained at acceptable levels according to local standards with grain production in the range 0.8–2.4 t ha⁻¹. There were significant effects of earthworms on crop production.

Grain production was increased on the average by 27% during the first five cropping cycles (Fig. 18.5). A maximum increase of 78% was obtained at the second harvest, whereas a significant decrease of 43% was observed at the fifth harvest. The next crop will show whether this decrease indicated a significant inversion of the trend, or simply was the consequence of accidental effects of earthworms, e.g. on water availability at a critical stage of plant growth. The response was higher in treatments without residues (+ 36%) or receiving crop residues + legume green manure (+ 36%) than in treatments with crop residues only (+ 8%).

In the plot with continuous maize, the average increase of production due to the introduction of earthworms amounted to 130%. This effect was especially spectacular at the second harvest with production of 0.8 t and 3.2 t ha⁻¹ in treatments 'without' or 'with' earthworms. After three successive cropping cycles, production had dramatically decreased in both systems. Therefore, to maintain the crop, fertilizers were applied. At the fifth crop, production was twice as high in the earthworm treatments as in the no-earthworm treatments (Fig. 18.6).

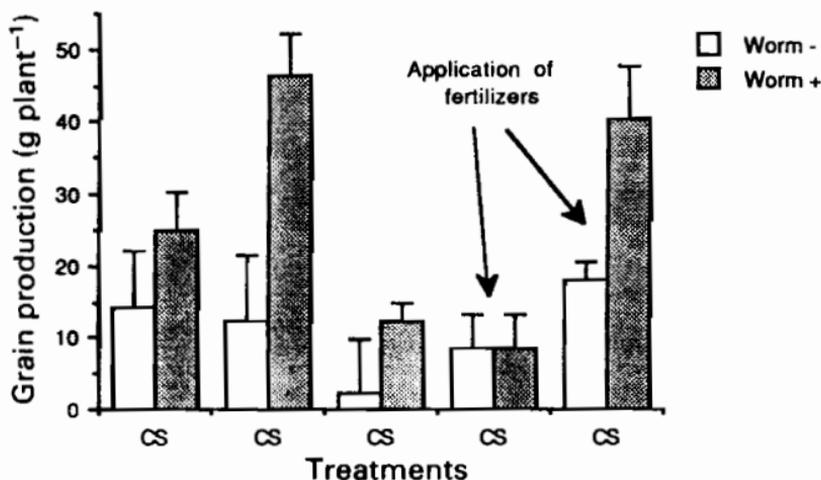


Fig. 18.6. Effect of earthworm inoculation on grain production in a continuous maize crop at Yurimaguas. CS, surface application of stubble.

These results indicate that: (i) earthworms can prolong and increase production; and (ii) their positive effects may not be explained simply in terms of the improvement of the nutrient supply to plants, since their effect remains significant when fertilizers are used to correct nutrient deficiencies.

Effects of earthworms on SOM and nutrient dynamics

After five cropping cycles, earthworm activities had not prevented losses of soil organic matter (Fig. 18.7). Nevertheless, the quality of organic matter as assessed by particle size fractionation had significantly changed (Feller, 1979). At Lamto, the proportion of SOM in the coarse fraction ($> 50 \mu\text{m}$) decreased less in the earthworm than in the no-earthworm treatment. On the other hand, more organic matter from the fine fractions seemed to have been mineralized (Fig. 18.8). Earthworm activities did not help maintain microbial biomass as this was significantly lower (by 23%) in treatments with earthworms.

Neither did earthworm activities impede the depletion of nutrients. A progressive return towards acid pH and high levels of A1 saturation occurred in all treatments. None the less, ^{15}N from labelled legume green manure applied at the soil surface was better recovered by plants in the presence than in the absence of earthworms. This demonstrated significant qualitative differences in nutrient cycling, oriented towards a more efficient use of available nutrients.

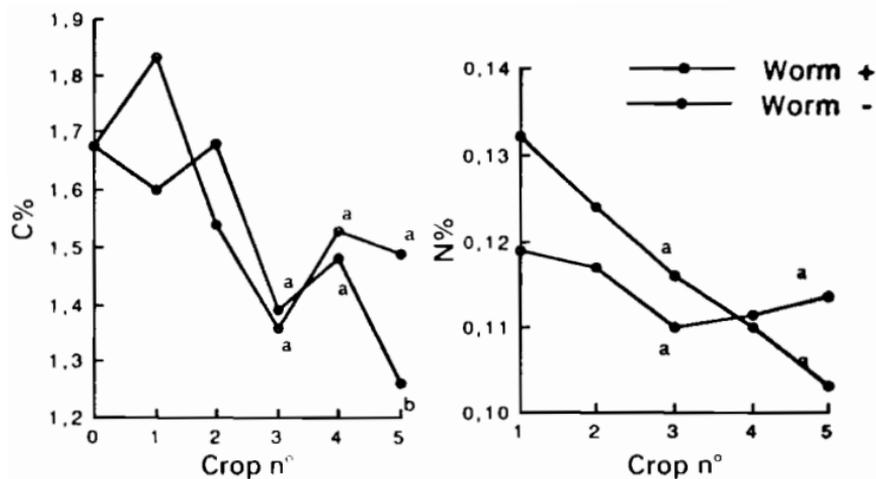


Fig. 18.7. Variation of C and N contents of the 0–10 cm strata with time and treatments.

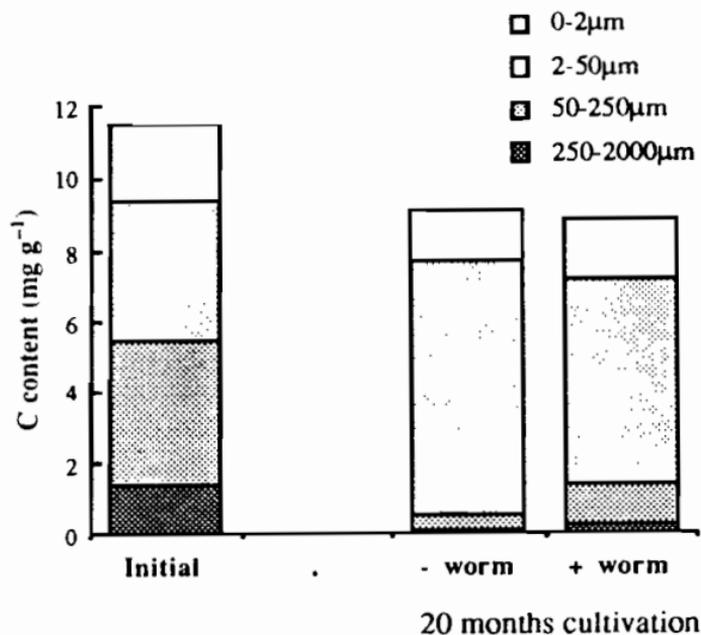


Fig. 18.8. Partition of the soil organic matter between granulometric fractions in the maize plot at the initial time and after the fourth crop.

Changes in soil physical properties

All soil physical properties measured were significantly affected by earthworm activities. Rough calculations based on assessments of earthworm biomass and on the results of past laboratory experiments gave an estimate of $150 \text{ t ha}^{-1} \text{ year}^{-1}$ dry soil ingested, equivalent to 10–15% of the upper 10 cm of soil. *P. corethrurus* ingests small aggregates and organic debris of a size smaller than the size of the mouth (i.e. up to 2 mm). The effects on soil aggregation were highly significant after five crops at Yurimaguas. In 'with earthworm' treatments, the relative proportion of large (> 10 mm) and intermediate (2–5 mm) aggregates was significantly increased, whereas the reverse effect was observed in the absence of earthworms. Earthworms clearly increased soil macroaggregation and they counteracted the trend for soil disaggregation observed in the conventional system.

These changes of macroaggregation had effects on other global physical parameters. In the presence of earthworms, bulk density was significantly increased; infiltration rate was first decreased, and then returned to values

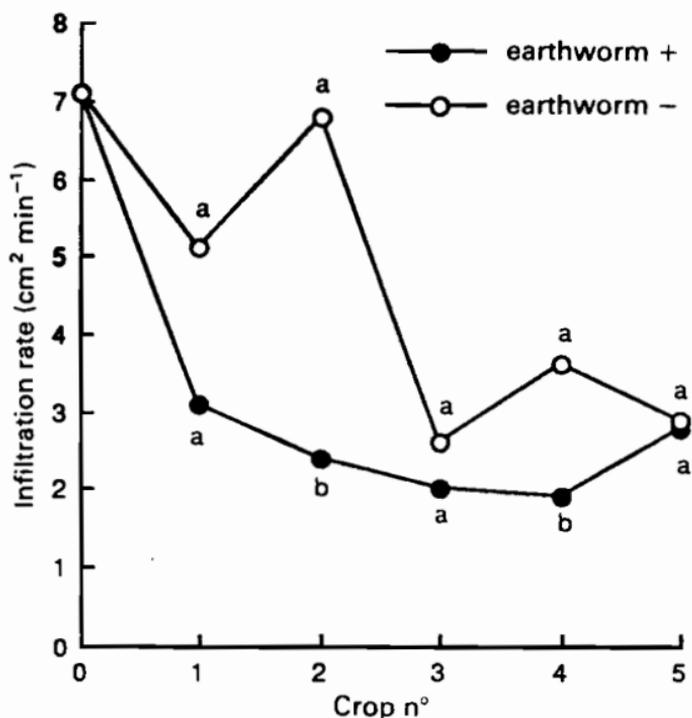


Fig. 18.9. Changes of infiltration with time. Data with different letters indicate significant differences at a given time. Bulk density was significantly higher than the initial value at time 3 in the earthworm treatment. Organic treatments had no effect.

similar to those of control treatments, after the earthworms had increased their production of surface casts and created a macropore system at the soil surface (Fig. 18.9).

Discussion

Invertebrates are major determinants of soil processes in tropical ecosystems. Whereas insect pests have been actively fought, the potential for beneficial use of insect activities has not been taken fully into consideration in the design of management practices. Current research demonstrates that practices which annihilate the activities of soil fauna are unlikely to be sustainable in the long term.

Soil fauna communities have contrasting reactions to changes induced by human land management. Their abundance and diversity are indicators of the quality of soils expressed in terms of soil organic matter, nutrient content, and physical properties such as bulk density, porosity and water regime. Annual crops generally support depleted communities, with especially low earthworm populations, whereas termites are usually less affected. Perennial cultures (e.g. sugar cane), pastures, and plantations (e.g. oil palm with a legume cover) generally have less diverse communities than the original ecosystem, but biomass is often higher due to colonization by peregrine earthworm species, and persistence of key native species. However, as the system degrades a depletion of the soil macrofauna occurs.

The abundance of soil fauna communities is significantly affected by the availability of suitable food resources and by their diversity. This is the reason why communities are much depleted in annual crops which have non-permanent and little-developed root systems, and limited inputs of organic residues. In some cases, the activity of soil fauna may be sustained for some time at the expense of energetic sources which had been accumulated in the original ecosystem. Examples of such sources are the dead woody material in recently deforested areas or coarse particle size fractions in SOM reserves. Our observations suggest that some termites or earthworms may live on resources with high lignin contents and/or high C:nutrient ratio. Therefore, there is scope for the use in carefully designed conditions of wastes like sawdust or coir (e.g. Pashanasi *et al.*, 1992). Before using such practices, the timing and placement of these residues will need to be addressed to prevent asynchrony between nutrient availability and plant requirements.

Preliminary experiments conducted for two years on five successive cropping cycles have given some insight on the effect of monospecific populations of endogeic earthworm communities on traditional agricultural systems. During that period there was no evidence that the depletion of SOM and the nutrient reserves of the soil were decreased by introduced

earthworms. Nevertheless, qualitative differences in SOM, as assessed in terms of particle size fractions, were different and indications of better use of nutrients by plants were obtained. Soil fauna activities in general might result in the long term in the appearance of a new state of equilibrium which might be characterized by lower amounts of SOM, but with a much faster turnover rate, as a result of both increased mineralization of the organic matter in the supposedly more recalcitrant fine soil fraction, and the relative protection of coarse fractions. The duration of our experiments was too short to reach a new state of equilibrium of the system.

Earthworms had major effects on soil physical properties. The species chosen significantly increased macroaggregation in the upper 10 cm. Bulk density was significantly higher in the presence of earthworms (+ 15%). Infiltration was first decreased up to the stage when earthworms started to deposit surface casts and open macropores at the soil surface. Significant changes were observed in water regime, with increased flooding or drought at very moist or dry periods. Not all earthworms will have such effects (Casenave and Valentin, 1988). In wet savannahs of Côte d'Ivoire, Blanchart (1990) has described complementary effects of large earthworm species, which can transform a significant proportion of the soil microaggregates into larger macroaggregates, and smaller-size species splitting up these large aggregates into smaller ones which are mixed with root litter. Earthworm casts and other faunal structures often have high structural stabilities and the overaccumulation of these structures may alter physical properties in the soil. Complementary biotic or abiotic processes which regulate the dynamics of aggregation are thus necessary. These may include assemblages of species from different zoological groups acting simultaneously or in temporal successions (David, 1988; Blanchart, 1990).

References

- Anderson, J.M. and Flanagan, P. (1989) Biological processes regulating organic matter dynamics in tropical soils. In Coleman, D.C., Oades, T. and Uehara, G. (eds.) *Dynamics of Soil Organic Matter in Tropical Ecosystems*, NifTAL project, University of Hawaii, Honolulu, pp. 97-125.
- Andrén, O., Paustian, K. and Rosswall, T. (1988) Soil biotic interactions in the functioning of agroecosystems. *Agriculture, Ecosystems and Environment* 24, 57-65.
- Barois, J. and Lavelle, P. (1986) Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biology and Biochemistry* 18(5), 539-541.
- Blanchart, E. (1990) Rôle des vers de terre dans la formation et la conservation de la structure des sols de la savane de Lamto (Côte d'Ivoire). Thèse Université Rennes I., 278 pp.

- Blanchart, E. and Spain, A. (1989) Rôle des vers de terre dans l'élaboration et la conservation de la structure des sols de savane. In: Lavelle, P. (ed.) *Processus Biologiques et Fertilité du Sol dans les Savanes Humides de Côte d'Ivoire. Recherches Fondamentales et Appliquées sur le Rôle des Vers de Terre*, Ministère de l'Environnement (SRETIE), Paris, pp. 26-43.
- Casenave, A. and Valentin, C. (1988) *Les États de Surface de la Zone Sahélienne. Leur Influence sur l'Infiltration*. Rapport CEE-ORSTOM, 202 pp. ORSTOM, Bondy, France.
- Curry, J.P. and Boyle, K.E. (1987) Growth rates, establishment and effect on herbage yield of introduced earthworms in grassland on reclaimed cutover peat. *Biology and Fertility of Soils* 3, 95-98.
- Darwin, C. (1881) *The Formation of Vegetable Mould Through the Action of Worms with Observations on their Habits*. Murray, London.
- Dash, M.C., Senapati, B.K. and Mishra, C.C. (1980) Nematode feeding by tropical earthworms. *Oikos* 34, 322-328.
- David, J.F. (1988) Les peuplements de Diplopodes d'un massif forestier tempéré sur sols acides. Thèse Université Paris VI, 225 pp.
- Feller, C. (1979) Une méthode de fractionnement granulométrique de la matière organique des sols: application aux sols tropicaux à texture grossière, très pauvres en humus. Cahiers de l'ORSTOM. *Série Pédologie* 17(4), 339-346.
- Gilot, C., Lavelle, P., Kouassi, Ph. and Guillaume, G. (1992) Biological activity of soils in Hevea sands of different ages in Côte d'Ivoire. *Acta Zoologica Fennica* (in press).
- Hoogerkamp, M., Rogaar, H. and Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchell, J.E. (ed.) *Earthworm Ecology: from Darwin to Vermiculture*. Chapman and Hall, London, New York, pp. 85-105.
- Huhta, V., Setälä, H. and Haimi, J. (1988) Leaching of N and C from birch leaf litter and raw humus with special emphasis on the influence of soil fauna. *Soil Biology and Biochemistry* 20, 875-878.
- Kouassi, P.K. (1987) Etude comparative de la macrofaune endogée d'écosystèmes guinéens naturels et transformés de Côte d'Ivoire. Doctorat de 3ème cycle, Université d'Abidjan, 115 pp.
- Lavelle, P. (1988) Earthworm activities and the soil system. *Biology and Fertility of Soils* 6, 237-251.
- Lavelle, P., Barois, I., Cruz, C., Hernandez, A., Pineda, A. and Rangel, P. (1987) Adaptive strategies of *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta), a peregrine geophagous earthworm of the humid tropics. *Biology and Fertility of Soils* 5, 188-194.
- Lavelle, P., Alegre, J., Barois, I., Fragoso, C., Gilot, C., Gonzalez, C., Kanyonyo ka Kajondo, Martin, A., Melendez, G., Moreno, A. and Pashanasi, B. (1992a) *Conservation of Soil Fertility in Low Input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities*. CCE-STD2 programme. Final report project n° TS2 * 0292-F (EDB).
- Lavelle, P., Spain, A.V., Blanchart, E., Martin, A. and Martin, S. (1992b) The impact of soil fauna on the properties of soils in the humid tropics. In: *Myths and Science of Soil of the Tropics*. Soil Science Society of America, special publication, 29, 157-185.

- Lavelle, P., Dangerfield, M., Fragoso, C., Eschenbrenner, V., Lopez-Hernandez, D., Pashanasi, B. and Brussaard, L. (1993) The relationship between soil macrofauna and tropical soil fertility. In Swift, M.J. and Woormer, P. (eds) *Tropical Soil Biology and Fertility*, John Wiley, New York (in press).
- Lee, K.E. (1985) *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press, New York.
- Lewis, D.H. (1985) Symbiosis and mutualism: crisp concepts and soggy semantics. In: Boucher, D.H. (ed.) *The Biology of Mutualism*, Croom Helm, Beckenham, p. 29.
- Pashanasi, B., Melendez, G., Szott, L. and Lavelle, P. (1993) Effect of inoculation with the endogeic earthworm *Pontoscolex corethrus* (Glossoscolecidae) on N availability, soil microbial biomass, and the growth of three tropical fruit tree seedlings in a pot experiment. *Soil Biology and Biochemistry* 24, 1655-1660.
- Persson, T., Baath, E., Clarholm, M., Lundkvist, H., Söderström, B.E. and Sohlenius, B. (1980) Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a scots pine forest. *Ecological Bulletins* 32, 419-459.
- Petersen, H. and Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39, 287-388.
- Pearce, T.C. and Phillips, M.J. (1980) The fate of ciliates in the earthworm gut: an in vitro study. *Microbial Ecology* 5, 313-319.
- Rouelle, J. (1983) Introduction of amoebæ and *Rhizobium japonicum* into the gut of *Eisenia foetida* (Sav.) and *Lumbricus terrestris* L. In: Satchell, J.E. (ed.) *Earthworm Ecology*. Chapman and Hall, London, pp. 375-381.
- Rouelle, J., Pussard, M., Randriamamonjizaka, J.L., Loquet, M. and Vincelas, M. (1985) Interactions microbiennes (Bactéries, Protozoaires), alimentation des vers de terre et minéralisation de la matière organique. *Bulletin of Ecology* 16, 83-88.
- Seastedt, T.R.T.T.C. and James, S.W. (1987) Experimental manipulations of arthropod, nematode and earthworm communities in a north American tallgrass prairie. *Pedobiologia* 30, 9-17.
- Setälä, H. and Huhta, V. (1991) Soil fauna increase *Betula pendula* growth: laboratory experiments with coniferous forest floor. *Ecology* 72, 665-671.
- Setälä, H., Tynismaa, M., Martikainen, E. and Huhta, V. (1991) Mineralization of C, N and P in relation to decomposer community structure in coniferous forest soil. *Pedobiologia* 35, 285-296.
- Stork, N.E. and Eggleton, P. (1992) Invertebrates as determinants and indicators of soil quality. *Agriculture, Ecosystems and Environment* (in press).
- Swift, M.J. (1986) Tropical soil biology and fertility (TSBF): inter-regional research planning workshop. Report of the third Workshop of the decade of the Tropics/TSBF program. *Biology International*, Special Issue 13, 68 pp.
- Swift, M.J. and Boddy, L. (1985) Animal-microbial interactions in wood decomposition. In: Anderson, J.M., Rayner, A.D.M. and Walton, D.W.H. (eds) *Animal-Microbial Interactions*. Cambridge University Press, Cambridge, pp. 89-131.
- Syers, J.K. and Springett, J.A. (1984) Earthworms and soil fertility. *Plant and Soil* 76, 93-104.
- Trofymow, J.A. and Coleman, D.C. (1982) The role of bacterivorous and fungivorous nematodes in cellulose and chitin decomposition in the context of a root (rhizosphere) soil conceptual model. In: Freckman, D.W. (ed.) *Nematodes in Soil Ecosystems*. University of Texas Press, Austin, Texas, pp. 117-137.

- Veeresh, G.K., Rajagopal, D. and Viraktamath, C.A. (1991) *Advances in Management and Conservation of Soil Fauna*. Oxford & IBH Publishing, New Dehli, Bombay, Calcutta.
- Villalobos, F.J. and Lavelle, P. (1990) The soil coleoptera community of a tropical grassland from Laguna Verde, Veracruz (Mexico). *Revue d'Ecologie et de Biologie du Sol* 27, 73–93.
- Yeates, G.W. (1981) Soil nematode populations depressed in the presence of earthworms. *Pedobiologia* 22, 191–196.

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In : Greenland D.J. (ed.), Szabolcs I. (ed.) Soil resilience and sustainable land use. Wallingford : CAB, 1994, p. 291-308.