

Effects of Earthworms on Soil Structure and Physical Properties

Eric Blanchart¹, Alain Albrecht², Julio Alegre³, A. Duboisset⁴, Cécile Gilot⁵, Beto Pashanasi⁷, Patrick Lavelle⁴ and Lijbert Brussaard⁶

¹Laboratoire Biologie et Organisation des Sols Tropicaux, IRD, Fort-de-France, Martinique; ²Laboratoire d'Étude du Comportement des Sols Cultivés, IRD, Montpellier, France; ³ICRAF, La Molina, Peru; ⁴Laboratoire d'Ecologie des Sols Tropicaux, IRD, Bondy, France; ⁵Laboratoire de Pédobiologie, IRD, Dakar, Senegal; ⁶Department of Terrestrial Ecology and Nature Conservation, Agricultural University, Wageningen, the Netherlands; ⁷ICRAF/INIA, Estación Experimental 'San Ramón', Yurimaguas, Peru

Summary

The effects of earthworms on soil structure and the resulting physical properties in natural or cultivated systems were studied in the different sites of the Macrofauna project. Four main results were obtained from these experiments :

1. In kaolinitic soils (Lamto, Manaus, Yurimaguas), irrespective of clay content, endogeic earthworms play a major role in soil structure formation and maintenance, while in smectitic soils (Martinique), the effects of earthworms on soil structure formation and maintenance are not as clear. In the Vertisols of Martinique, the effect of roots and organic materials seem predominant in soil structure development and earthworms play a secondary role.

2. Endogeic earthworm species have different effects on soil properties. Large earthworms such as *Pontoscolex corethrurus* or *Millsonia anomala* egest large and compact casts. They increase the proportion of large aggregates in soil and the bulk density; they are called 'compacting species'. Conversely, small earthworm species such as eudrilid worms feed at least partly on large compact casts

and egest smaller and fragile aggregates. They decrease the proportion of large aggregates in soil and the bulk density; they are called 'decompacting species'. The effect of 'compacting species' on soil structure formation seems to be linked to the presence of organic residues at the soil surface. In agroecosystems of Yurimaguas (Peru), the intense activity of *P. corethrurus* and the coalescence of surface casts lead to the formation of a compact surface crust which impedes water infiltration in the absence of organic residues, but a favourable macroaggregate structure develops in the presence of organic residues and leguminous mulch.

3. The introduction of earthworms in agroecosystems changes soil physical properties and especially water retention and infiltration. The introduction of 'compacting species' in agroecosystems tends to decrease the infiltration rate and to increase water retention capacity, while the introduction of 'decompacting species' increases the infiltration rate and decreases water retention capacity.

4. The stability of structures produced by earthworms in kaolinitic soils is very high and these structures may last for a long time in soils. For instance, at Lamto, the mean life span of casts was estimated to be 26 months in a shrub savanna. Large and compact casts were still observed many months after earthworm eradication. Thus, the effects of earthworms on soil physical properties may last for 2–3 years after earthworms have been removed from the soil.

The joint presence of both 'compacting' and 'decompacting' species and organic residues in tropical agroecosystems appears to be necessary to sustain physical soil fertility.

Introduction

The importance and functional significance of earthworms in the soils of the humid tropics have received much attention in the last few years. Although studies were carried out mainly in natural ecosystems (savannas or forests), a few experiments were done in agroecosystems, especially in the Macrofauna project. In cultivated areas, earthworm communities are strongly modified as compared with natural systems, showing low species diversity and colonization by competitive endogeic species which have specific functions (Chapters 1–3; Fragoso *et al.*, 1997).

Soil structure is an important component of soil fertility as it affects physical processes (erosion, runoff, infiltration, aeration, drainage, water retention, soil evaporation, thermal and mechanical properties of soil), nutrient cycling (mineralization, immobilization, ion exchange), carbon cycling (respiration, organic inputs, root and microorganism turnover, decomposition, humification and physical protection of organic matter, localization of organic matter) and biological activity (movement of soil fauna, microorganism activity) (Dindal, 1985; Elliott and Coleman, 1988; Jastrow and Miller, 1991; Lee and Foster, 1991; Lavelle *et al.*, 1992; Oades, 1993).

In natural tropical and temperate ecosystems, earthworms are usually considered to be responsible for a 'good' soil structure and improved soil physical properties (infiltration, water retention, resistance to erosion), although negative effects have also been reported (Rose and Wood, 1980), e.g. coalescence of excrements forming a sticky and compact soil surface, impeding water infiltration.

The present chapter aims to analyse and synthesize the results obtained in a few sites of the humid tropics by the Macrofauna team on the effects of endogeic earthworm species on soil structure and associated physical properties, in natural and especially in cultivated systems (Table 5.1). The physical properties of casts produced by the animals will be described, and the consequences of their casting and burrowing activities for aggregation, porosity and resulting properties will be analysed.

Materials and Methods

Sites

The relationship between endogeic earthworms and soil structure was studied in a few sites of the humid tropics (Table 5.1): Lamto (Ivory Coast), La Mancha (Mexico), Yurimaguas (Peru), Manaus (Brazil), St Anne (Martinique) and Iyerpadi (India).

Experiments

Pot experiments were conducted at Lamto (Derouard *et al.*, 1997) using three crops (maize, rice and peanut), at La Mancha (Barois *et al.*, 1992) using maize and beans, and in Cameroon with maize (Brussaard *et al.*, unpublished data). Field experiments were set up at Lamto with maize and yam (Gilot, 1994), at La Mancha with maize (six successive crops) (Barois *et al.*, 1992), at Yurimaguas with six successive crops (maize, rice, cowpea, rice, rice and rice) (Pashanasi *et al.*, 1992), at Iyerpadi with tea (Senapati *et al.*, 1994a) and at St Anne with pangola grass (*Digitaria decumbens*; Albrecht, 1993). In these experiments, effects of both earthworm introduction and crop residue application were studied.

Measurements of soil structure and physical properties

Soil structure was assessed through the observations of thin sections, either under plain light or under UV light. Aggregate size distribution for sandy soils

	Lamto (Ivory Coast) 6°13'N, 5°02'W	La Mancha (Mexico) 19°36'N, 96°22'W	Yurimaguas (Peru) 5°45′S, 75°05′W	Manaus (Brazil) 3°60'S, 60°00' W	St Anne (Martinique) 14°36'N, 62°34'W	Iyerpadi (India) 10°40'N, 77°E
Annual mean temperature (°C)	27.8	24.5	26	26.7	26.7	
Rainfall (mm)	1200	1345	2100	2100	1440	
Dry period (months)	2	5	2	2	3	
Natural ecosystems	Savanna	Deciduous forest	Forest	Forest	Forest	Forest
Soil	Ultisol	Regosol	Ultisol	Oxisol	Vertisol	
Sand content	85%	80%				
Clay (type, content)	Kaolinite (4.5%)	Kaolinite (12%)	Kaolinite (20%)	Kaolinite (80%)	Smectite (> 60%)	Kaolinite
Organic matter content (0–10 cm)	2%	3–7%	3%	5%	3–7%	
Manipulated earthworm species	Millsonia anomala	Pontoscolex corethrurus	Pontoscolex corethrurus	Pontoscolex corethrurus	Polypheretima elongata	Pontoscolex corethrurus
	Eudrilid worms					
Experimental crops	Maize (Zea mays)	Maize (<i>Zea mays</i>)	six successive crops:	Brachiaria humidicola	Digitaria decumbens	Tea gardens
	yam (<i>Diascorea</i> alata)	(six successive crops)	Maize, rice, cowpea, rice, rice, rice		Market-gardening crops	

Table 5.1. Characteristics of study sites.

Pot experiment	Maize, rice, peanut, Panicum maximum	Maize, beans				
Cast						
Production	x			×		
Physical properties	x	x	x	x	x	
Soil						
Aggregate size distribution	x		x	x	x	x
Porosity	x	x	x	x	x	
Infiltration rate	x		x		x	
Water holding capacity	x		x		x	
Erodibility					x	
Site description	Blanchart (1990), Gilot (1994)	Barois <i>et al.</i> (1992)	Pashanasi <i>et al.</i> (1992), Alegre <i>et al.</i> (1995), Duboisset (1995)	Fontaine (1994)	Albrecht (1993) IRD-SECI (1994)	Senapati <i>et al.</i> (1994a) Senapati <i>et al.</i> (1994b)

was measured using the dry-sieving method described by Blanchart (1990), which allows the separation of several size classes. Aggregation and aggregate stability of the Vertisol of Martinique were measured using the method described by Albrecht *et al.* (1992) (soil is submitted to increasing shaking time in water). The total porosity in sandy soils was assessed through the measurement of bulk density or shrinkage curves analyses, and pore size distribution in casts was measured using mercury porosimetry. For the swelling soil of Martinique, we measured the air-specific volume (structural porosity which is not influenced by water content). Infiltration rates were measured at Lamto in pot experiments and at Yurimaguas by measuring water percolation with a 110 mm internal diameter cylinder, driven into the soil to a depth of 150 mm. Soil erodibility was also studied at St Anne using a mini-rainfall simulator on a 1 m^2 area.

Physical Properties of Earthworm Casts

Transformations in the earthworm gut

After the soil has been ingested by earthworms, it undergoes many transformations in the earthworm gut (Chapter 3). Soil macrostructure is strongly modified due to intense mixing and water addition which starts in the gizzard. A modification of soil microstructure has also been observed in some cases, after soil particles have been dispersed and reorganized around bacterial colonies or organic particles (Barois *et al.*, 1993; Chapuis *et al.*, 1996). Conversely, in clayey kaolinitic Latosols of Central Amazonia, soil passing through the intestinal tract of *Pontoscolex corethrurus* is not disaggregated completely; microaggregates from 10 to 100 μ m in diameter are neither broken nor dispersed (Fontaine, 1994). The same phenomenon was observed for *Polypheretima elongata* in Vertisols of Martinique (Charles, Blanchart and Bernard, unpublished data).

Water content in casts

When egested, casts are characterized by a high water content (Barois and Lavelle, 1986). Although part of the water is reabsorbed in the posterior part of the gut, casts are wet and pasty when egested. Casts of *Millsonia anomala* have a water content of 29% when egested, i.e. 2.5 times the water content at field capacity (12%) of Lamto savanna soils. In Mexico, casts of *P. corethrurus* had a water content of 99%, while soil water content was 35% at field capacity (Barois and Lavelle, 1986). In Martinique, casts of *P. elongata* have a water content of at least 70%, while vertisol water content at field capacity is approximately 40% (Blanchart, unpublished data).

Particle size distribution in casts

The particle size distribution in casts is generally of smaller size classes as compared with that of soil; this is very clear for sandy soils and for small earthworm species or individuals (Chapter 3). Using image analysis on Yurimaguas soil thin sections, Duboisset (1995) showed that casts of *P. corethrurus* have a significantly higher content of fine particles and a non-significantly lower content of coarse particles than the non-ingested soil (Fig. 5.1).

Density of casts

Cast density has been measured for a few endogeic earthworm species; depending on the species, it may be higher or lower than the bulk density of soil (Lal, 1987). Highest values were reported for *M. anomala* casts (1.8–2.0 Mg m⁻³) as compared with the bulk density of soil (1.45 Mg m⁻³ in the upper 10 cm) (Blanchart *et al.*, 1993). Their total pore volume was 0.13 m⁻³ Mg⁻¹ (total porosity 25%) mainly in the 18–25 µm class. Casts of *M. anomala* probably have a higher water retention capacity than bulk soil due to the abundance of small pores and despite their relatively low total porosity. Lal (1987) also observed different pore size distributions for *Hyperiodrilus africanus* casts and control soil; casts were characterized by a higher proportion of fine pores. The difference in pore size distributions between casts of *P. corethrurus* and kaolinitic clayey soils of Central Amazonia is mainly for pores > 1 µm which are absent in casts and present in control soil (Chauvel *et al.*, 1997). For Ultisols of Yurimaguas, Duboisset (1995) measured a lower porosity in *P. corethrurus*



Fig. 5.1. Coarse and fine particles and pores in non-ingested soil (0–4 cm) and casts of *Pontoscolex corethrurus* (Yurimaguas, Peru), as a percentage of thin section surface (Duboisset, 1995).

Vertisols of Martinique, bulk density varies with water content; it is thus better to use the specific air volume as an indicator of soil porosity. This volume is equal to 0.045 m³ Mg⁻¹ (SE 0.012, n = 27) for casts of *P. elongata* cultured on a pasture soil (soil organic carbon in 0–10 cm = 30 g C kg⁻¹ soil) and 0.026 m³ Mg⁻¹ (SE 0.004, n = 22) for casts of *P. elongata* cultured on a food-cropped soil (soil organic carbon in 0–10 cm = 15 g C kg⁻¹ soil) (Fig. 5.2) (Blanchart, unpublished data). Soil organic matter in Vertisols seems to be a determining factor of cast physical properties.

Water stability and mechanical resistance of casts

Earthworm casts, generally made up of fine particles and wet when egested, have a low water stability; they are very fragile and may be easily dispersed (Shipitalo and Protz, 1988). At Lamto, fresh casts of megascolecid and eudrilid worms disappeared after a precipitation of 18 mm, when they were not protected by vegetation (Blanchart, 1990). With time and drying or drying–rewetting cycles, casts become more stable (Blanchart, 1990; Marinissen and Dexter, 1990; Hindell *et al.*, 1994); this would explain why many authors have noted a better stability for casts than for control soil (De Vleeschauwer and Lal, 1981). In Martinique (Vertisols), water stability tests were done on cultivated soil, fresh and air-dried casts of *P. elongata*. Without any mechanical shaking, the median aggregate diameters, i.e. the particle diameters corresponding to 50% of particle weight on the particle size distribution cumulative curves, were calculated as: $170 \mu m$ for soil, $27 \mu m$ for fresh casts and $210 \mu m$ for air-dried casts (Blanchart, unpublished data). At Lamto, large air-dried aggregates (> 10 mm) collected in treatments with earthworms



Fig. 5.2. Specific air volume of casts of *Polypheretima elongata* cultured in a low organic carbon (15 g C kg⁻¹ soil) and a high organic carbon (30 g C kg⁻¹ soil) Vertisol (Martinique) (mean and SE) (Blanchart, unpublished data).

(*M. anomala*) only or with plants (*Panicum maximum*) only had different mechanical resistance: a crushing pressure higher than 0.6 kg cm^{-2} was needed to break air-dried aggregates created in earthworm treatments, whereas 0.2 kg cm^{-2} was enough to break air-dried aggregates created in the presence of plants only (Blanchart, 1990).

Ageing and stabilization of casts

Mechanisms of cast stabilization have been investigated often (reviewed in Lee, 1985; Shipitalo and Protz, 1989; Marinissen and Dexter, 1990; Zhang and Schrader, 1993). Duboisset (1995), using image analysis of thin sections of soil and casts, noted a different evolution of structure between internal and external parts of casts during cast drying. Porosity was less important in the external part of casts than in the internal part, irrespective of the age of the cast, and this difference increased with time (Fig 5.3). The proportion of large pores increased in the internal part of casts. This author also noted an increase of elongated pores with cast ageing.

The cortex of casts

Under daylight, thin sections of Lamto soils showed a dark peripheral layer (i.e. cortex) made of fine particles around earthworm casts (Blanchart, 1992). This cortex was investigated further by scanning electron microscopy; it is



Fig. 5.3. Evolution with time of porosity (large and small pores) in the outer and inner parts of casts of *Pontoscolex corethrurus*, during air-drying (Yurimaguas, Peru) (Duboisset, 1995).

approximately 25 μ m thick and gives the surface of the casts a smooth and closed aspect (Blanchart *et al.*, 1993). This cortex was also observed in casts of other species and in more fine textured soils: *P. corethrurus* in Mexico (Barois *et al.*, 1993) and *P. corethrurus* in Amazonia (Grimaldi, Blanchart and Sarrazin, unpublished data). Gilot (1994) observed that destruction of *M. anomala* casts in soil begins with the disappearance of the cortex before casts break down completely or are ingested by smaller worms (Blanchart *et al.*, 1997). When the porosity of these casts was measured by mercury intrusion, this cortex impeded mercury penetration at low pressures.

The large size, compaction, stability and presence of a cortex which characterize large earthworm casts such as those of *M. anomala* involve: (i) a low diffusion of oxygen; in the middle of > 10 mm casts, conditions may be anoxic and favour denitrification (Elliott *et al.*, 1990); and (ii) the physical protection of organic matter (Martin, 1991; Ladd *et al.*, 1993). Martin and Marinissen (1993) emphasized the importance of physical processes as regulators of biological processes.

Effects of Earthworm Manipulation on Soil Aggregation and Porosity

The production of casts by endogeic earthworms leads to strong modifications of soil structure and associated soil properties.

At Lamto, where the endogeic earthworm community egests more than 1000 Mg ha⁻¹ year⁻¹ (Lavelle, 1978), a macroaggregate structure is present in the upper 20 cm of soil (50% of soil as aggregates > 2 mm, and 20% of soil as aggregates < 400 μ m) (Blanchart, 1992). Various pot or field experiments showed that this structure was due to earthworm activity. Field studies manipulating *M. anomala* showed that earthworm treatments rapidly built a macroaggregate structure from a destructured (sieved through 2 mm) soil (Blanchart, 1992). These studies showed that after 14 months of experimentation, soils in a treatment without earthworms had a smaller percentage of aggregates > 2 mm (5%) than soils in a treatment with earthworms (45%). These results were confirmed by a pot experiment, with or without plants (Blanchart *et al.*, 1990; Derouard *et al.*, 1997) showing the importance of *M. anomala* for soil aggregation.

Gilot (1994) studying maize growth on a 2 mm sieved soil, in the presence or absence of *M. anomala*, found that after 10 months of experimentation, the original structure was found in the treatments with earthworms, i.e. 50% of soil as aggregates > 2 mm compared to 30% in the treatment without earthworms. From 20 months onwards, bulk density was higher in inoculated than in non-inoculated treatments at 0–10 cm depth, with values of 1.47 and 1.37 Mg m⁻³, respectively. This was particularly obvious if mulch was not

applied at the soil surface. At 10–20 cm depth, bulk density was also significantly higher in the inoculated than in the non-inoculated treatment.

The effects of eudrilid worms (small-sized *Chuniodrilus zielae* and *Stuhlmannia porifera*, and medium-sized *H. africanus*) on aggregation have also been demonstrated (Blanchart *et al.*, 1989; Derouard *et al.*, 1997). These studies showed that these worms were able to form aggregates of 2-5 mm in diameter when introduced in a 2 mm sieved soil, but most of their casts had diameters in the range of 0.5-2 mm. Thus *M. anomala* is largely responsible for the formation of aggregates > 2 mm and small eudrilid earthworms for the formation of aggregates of 0.5 to 2 mm (Figs 5.4 and 5.5). Derouard *et al.* (1997),



Fig. 5.4. Aggregation and bulk density in pot experiments at Lamto (Ivory Coast) for different earthworm populations and three crops (adapted from Derouard *et al.*, 1997).



Fig. 5.5. Evolution of bulk density and macro-aggregates in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast) (adapted from Blanchart *et al.*, 1997).

in pot experiments, showed a decrease of total porosity in the *M. anomala* treatment; there were no differences between porosity in control treatments without earthworms and porosity in Eudrilidae treatments.

Additional experiments allowed a precise measurement of the role of endogeic earthworms and especially large (*M. anomala*) and small (Eudrilidae) earthworms in the conservation of Lamto's soil structure (Blanchart *et al.*, 1997). Soil monoliths collected in the field were defaunated by a short immersion in warm water (without noticeable modification of soil structure and plants), and earthworms were introduced or not in these monoliths, which were replaced in the field. Four treatments were applied: (i) control soil without earthworms; (ii) original soil fauna; (iii) *M. anomala*; and (iv) small eudrilid earthworms.

After 28 months of experimentation, soil in the treatment with *M. anomala* was characterized by 60% of aggregates > 2 mm, versus 45% in the original fauna treatment, 20% in control soil, and 18% in the treatment with small eudrilid worms. Small and large earthworms also had different effects on soil porosity (Blanchart, 1990; Blanchart *et al.*, 1997). *M. anomala* formed large sized and compact aggregates; the consequence was an increase in macroporosity (~1mm) and microporosity (~10 μ m) and a decrease of mesoporosity (~100 μ m). As a consequence, bulk density increased, structural porosity increased with time (especially mesoporosity), and water retention capacity was raised. When earthworms were excluded from the soil, total porosity increased with time (especially mesoporosity), bulk density decreased, structural porosity tended to be higher than textural porosity. When only small eudrilid earthworms were present, bulk density decreased, structural porosity was much higher than textural porosity, and water retention capacity was much higher than textural porosity, and water retention capacity decreased (Figs 5.6 and 5.9).

The conclusion from these experiments is that eudrilid worms ('decompacting species') promote the destruction of large aggregates formed by large 'compacting' earthworms like *M. anomala*. It can be inferred that the macroaggegate structure of the upper 20 cm of Lamto's soils resulted from the antagonistic activities of 'compacting' and 'decompacting' earthworms (Blanchart *et al.*, 1997).

Aggregate size distribution and bulk density were also studied at Yurimaguas (Peru), in treatments where *P. corethrurus* were introduced or not (Alegre *et al.*, 1995). Without earthworms, aggregates < 0.5 mm increased, aggregates 2–10 mm decreased (from 41 to 33% of soil) and porosity increased with time. With earthworms, aggregates < 0.5 mm decreased, aggregates > 10 mm increased (from 25 to 31% of soil) and porosity decreased (especially in the upper 10 cm of soil).

On a smaller scale, Duboisset (1995), using thin section descriptions and image analysis, described the effect of introduction of *P. corethrurus* and/or residues and/or leguminous mulch on aggregation and porosity after 3 years of experimentation (six crops). He showed two different effects in the presence of earthworms and in the absence of leguminous mulch: in the upper 1.5 cm,



Fig. 5.6. Evolution of porosity (structural and textural) in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast). MA = *Millsonia anomala*, Co = control, NE = no earthworms, EU = eudrilid earthworms (adapted from Blanchart *et al.*, 1997).

earthworm activity induced a compaction of the soil surface through coalescence of unstable casts and thus formation of a surface crust; below 1.5 cm depth, the structure was macro-aggregated. The simultaneous presence of worms, residues and mulch led to a macro-aggregated structure from 0 to 4 cm depth (Fig. 5.7). The compact surface due to the coalescence of earthworm casts in the absence of leguminous mulch was characterized by a reduced porosity (absence of macroporosity and reduced microporosity). The structural effect of P. corethrurus in the absence of organic inputs resulted in the formation of burrows, while in the presence of residues and mulch, the pore size distribution was highly modified. The proportion of macropores between aggregates increased at the expense of aged burrows, whereas microporosity decreased due to the increase of macroporosity and to the compaction in casts. Organic inputs modified earthworm effects on soil porosity by retaining structures such as macroporosity close to the soil surface and vertical burrows opening at the soil surface. Connectivity between macroporosity and microporosity was increased by earthworm activity mainly in the presence of crop residues and leguminous mulch (Fig. 5.7).

The effects on soil structure of earthworm introduction or eradication in agroecosystems were also studied in other sites of the Macrofauna project. In the tea gardens (India), the introduction of *P. corethrurus* in nursery bags filled with 2 mm sieved soil induced a higher formation of macroaggregates > 2 mm than in treatments without earthworms, irrespective of the applied organic matter (Senapati, unpublished data).

In Central Amazonia, transformation of forests into pastures led to a strong modification of soil macrofauna and a dominance of earthworms such as *P. corethrurus*. As a consequence, the proportion of large aggregates and soil



+ Pontoscolex corethrurus

Fig. 5.7. Effects of earthworm introduction and crop residue application on aggregation (macro- and micro-aggregates), porosity (macro- and microporosity) and plant debris in the soil (0–4 cm) of Yurimaguas (Peru) as proportions of surface of soil thin sections. A = surface strata (0–1.5 cm), B = deeper strata (1.5–4 cm) (adapted from Duboisset, 1995).

bulk density increased (5–25 cm depth) (Barros *et al.*, 1996). In a degraded soil under old pasture, the intense activity of *P. corethrurus* produced a compact structure in the upper 10 cm of soil with severe adverse consequences on water infiltration and soil aeration (Fontaine, 1994). In this horizon, interaggregate porosity was only made of cracks, but porosity of $10-100 \mu m$ was well developed. In less degraded soils covered with pastures and a few shrubs, total fauna were much more diverse and soil structure was different, i.e. aggregation and porosity were much better developed. Conversely, *P. corethrurus* was able to decompact soils compacted by deforestation

machines through an increase of stable porosity of pores in the range $10-100 \mu m$ which led to a higher water retention capacity and a better drainage of gravity water (Fontaine, 1994).

In Martinique, aggregate size distribution was measured in a large field experiment with four experimental treatments: recently established pasture (PW), control with earthworms excluded by chemicals (P), control with inoculation of a high density of earthworms (PW+) and control with plants and worms excluded (C). Results showed no significant differences among treatments with plants (PW, PW+, P). Median aggregate diameters were almost identical among these treatments at all soil depths (460-520 µm between 0 and 5 cm, 170-210 µm between 35 and 40 cm). Treatments with no plants and no earthworms (C) produced smaller mean weight diameters, especially close to the soil surface (300 μ m at 0–5 cm) (Blanchart, unpublished data). After 2 h of shaking, median aggregate diameters were higher for the (C) treatment than for treatments with plants (75 and 12-23 µm, respectively, at 0-5 cm). These results indicate that in these clayey soils, contrary to sandy soils at Lamto, plants are more important than worms in promoting soil aggregation. The presence of grass roots and earthworms also resulted in a twofold increase of the specific air volume, as compared with treatments with neither roots nor earthworms. This porosity was not significantly different between treatments with plants and without earthworms, and treatments with plants and with earthworms (Fig. 5.8) (Blanchart et al., unpublished data).

At La Mancha (Mexico), Barois et al. (1992) measured equal porosity in different treatments of earthworms and residues. In pot experiments in



Fig. 5.8. Evolution with depth of specific air volume of 5 cm³ aggregates in a Vertisol for three different treatments, after 1 year of experimentation (Martinique) (means and confidence interval P < 0.05, n = 12) (Blanchart, unpublished data 1994).

Cameroon with maize, with or without residues, with or without earthworms (probably polyhumic earthworms, measuring 7–40 cm), Brussaard *et al.* (1997) showed a significant, negative effect of earthworms on bulk density after 2 months of experimentation, while mulch had no significant effect.

Consequences for Soil Physical Properties

Water infiltration and retention capacity

At Lamto, *M. anomala* decreased infiltration (3.29 mm h^{-1}) compared with a treatment without earthworms (4.18 mm h⁻¹) (Gilot, 1994). In a field experiment, Blanchart *et al.* (1997) showed the effects of 'compacting' and 'decompacting' species on water retention capacity (Fig. 5.9). Pot experiments also showed that the introduction of *M. anomala* and small Eudrilidae (to a lesser extent) decreased the infiltration rate (22.3 ml min⁻¹ with *M. anomala* and 53 ml min⁻¹ without earthworms). Conversely, *H. africanus* tended to increase the infiltration rate in a soil cropped to maize (Fig. 5.10) (Derouard *et al.*, 1997). In fact, these authors pointed out the importance of plant species on infiltration rates with different earthworm populations was inversely proportional to the modification of the percentage of macroaggregates ($R^2 = 0.663$, P < 0.01) and bulk density ($R^2 = 0.520$, P < 0.02). In this soil, macropores created by *M. anomala* allowed gravity water to infiltrate, and micropores (0.01–50 µm) of casts retained available water.



Fig. 5.9. Evolution of water retention capacity and easily accessible water in undisturbed soil (0–10 cm) submitted to different earthworm populations in a field experiment (Lamto, Ivory Coast). MA = *Millsonia anomala*, Co = control, NE = no earthworms, EU = eudrilid earthworms (adapted from Blanchart *et al.*, 1997).



Fig. 5.10. Infiltration rate in a 2 mm sieved soil (pot experiments) with different earthworm populations and two crops after 80 days of experimentation. C = control, HA = Hyperiodrilus africanus, EU = eudrilid earthworms, MA = Millsonia anomala, EU + MA = association of eudrilid earthworms and Millsonia anomala (Derouard et al., 1997).

At Yurimaguas, infiltration rates decreased with all treatments with time, but more rapidly when earthworms were present despite the absence of a surface crust and a better connectivity between macro- and microporosity when both earthworms and organic inputs were present (Duboisset, 1995). Sorptivity (initial infiltration) also decreased in the presence of earthworms (Alegre *et al.*, 1995). These authors also observed different water regimes depending on earthworm activity. In the dry season, soil was drier in treatments with earthworms and, in the rainy season, soil was wetter in treatments with earthworms. They hypothesized that the increase in porosity measured in the absence of earthworms induced a better water retention capacity.

In a pot experiment in Cameroon, with pots that were free drained, Brussaard *et al.* (unpublished data) showed a significantly positive effect of earthworms on hydraulic conductivity, whereas mulch had no significant effect. Hydraulic conductivity was higher in treatments with earthworms and mulch (0.53 cm min⁻¹) than with mulch only (0.09 cm min⁻¹). In West Africa, Casenave and Valentin (1988), using rainfall simulation, measured a fivefold higher infiltration if casts were present at the soil surface (10–15 mm h⁻¹) than if they were absent (2 mm h⁻¹). In Australia, infiltration was three times higher in a no-till Vertisol with *P. elongata* than in a conventionally tilled soil with much lower earthworm populations. Macropores created by these animals were continuous from surface to depth and seven times more numerous in the no-till system (cited in Robertson *et al.*, 1994). This was not studied in Martinique.

Soil erodibility

Fresh earthworm casts are rather sensitive to erosion when deposited at the soil surface. They may be washed away and thus strongly contribute to soil loss, especially in places where rainfall may be intense. Darwin (1881) noted in India the importance of earthworm casts in erosion and in formation of alluviated soils during the monsoon period. More recently, Nooren et al. (1995) showed in the Ivory Coast the importance of earthworms in the formation of sandy surface horizons due to a downslope runoff of clay particles contained in earthworm casts. Blanchart (1990) observed at Lamto that fresh casts of Megascolecidae (mainly M. anomala) disappeared under a rain of 18 mm only if they were not protected by vegetation cover; those protected by vegetation could persist for many months. In contrast, casts of Eudrilidae are dispersed easily and can even be dispersed by runoff water. Thus they strongly contribute to the formation of a surface crust which may impede water infiltration and increase erosion. Introduction of M. anomala earthworms in destructured (2 mm sieved) soil never presented a crust at the soil surface, whereas a 2-3 mm thick crust was observed in the treatment without worms (Blanchart, 1992). Conversely, Duboisset (1995) observed a surface crust in earthworm treatments in the absence of crop residues and leguminous mulch in the Yurimaguas experiment (Fig. 5.7). Thus, it seems that earthworm activity leads to two contradictory phenomena: fresh cast egestion at the soil surface either (i) increases soil loss and crust formation or (ii) increases surface roughness and improves infiltration. The role of organic matter (mulch or residues) that stabilizes casts is very important in preventing crust formation when earthworms are active. Le Bissonnais (1989) emphasized that small aggregates dry more rapidly than large ones and thus are more subject to disaggregation (slaking), especially when water input is limited. It is thus likely that in the soil, eudrilid casts disappear more rapidly than those of M. anomala. In Martinique, rainfall simulation on Vertisols showed differences in the erodibility, measured as turbidity (concentration of soil in runoff water), in different treatments. Turbidity was greater in treatments without plants and without earthworms than in treatments with plants only. The effect of earthworms alone was a high turbidity until 18 months of experimentation and then a reduced turbidity at month 24. On average, their activity tended to increase erodibility compared with treatments with plants alone (Blanchart et al., unpublished data). Faivre and Chammaro (1995), studying erosion and particle leaching in soils of Colombia, showed two positive effects of soil macrofauna: (i) homogenization of the soil profile which at least partially stopped particle leaching and (ii) continuous regeneration of a macroaggregate structure which maintains particles likely to be leached.

Medium-term Effects of Earthworm Activity on Soil Physical Properties

The effects of endogeic earthworms may last for many months in soil, even after the disappearance of earthworms. The stability of structures produced by earthworms in kaolinitic soils is very high, and these structures may last for a long time in soils. For instance, at Lamto, the mean life span of large endogeic earthworm casts was estimated to be 26 months in a shrub savanna and 11 months in a grass savanna submitted to waterlogging during the rainy season (Blanchart, 1990). After eradication of earthworms, large and compact casts were still observed after 28 months (Blanchart et al., 1997). Observations of thin sections helped to determine the evolution of soil structure for different earthworm populations. Gilot (1994) observed that in soils without earthworms, aged casts lose their peripheral cortex before a complete disaggregation. Field experiments also showed that small eudrilid earthworms have the ability to accelerate the disaggregation of large casts. Derouard et al. (1997) observed that these small worms are able to perforate M. anomala casts and thus to promote their destruction. Thus the effects of earthworms on soil properties (especially soil physical properties and soil organic matter dynamics) and plant growth may last 2-3 years after earthworms have been removed from the soil. In smectitic soils, the life span of earthworm structures may be shorter than in kaolinitic soils, as shrinkage-swelling processes limit their preservation.

Conclusions

Earthworms play a major role in modifying soil processes. They modify soil profiles by burrowing, moving particles within and between horizons, forming and disintegrating aggregates, and changing porosity, aeration and water infiltration and retention capacity.

Studies in the tropics on endogeic earthworms showed important but contradictory effects (depending on soil type, clay type and earthworm species) on the soil structure and consequent physical properties.

We can classify earthworms into two main groups based on their effects on physical properties.

1. Medium or large sized species such *M. anomala, P. corethrurus* and *P. elongata* egest very large casts. These large aggregates are relatively compact, dispersible when fresh, and have a cortex which affects air and water movement between the inner and the outer parts of casts. These aggregates are never reingested by these species as long as they keep their macro-aggregate structure. These worms tend to decrease total soil porosity and strongly modify pore size distribution; they decrease the infiltration rate and improve water retention capacity. They counteract erosion through the formation

of aggregates which stabilize with time and thus limit particle runoff and leaching; they also limit the formation of surface crust in the presence of surface-applied organic matter. When these worms only are present in soils, with high biomass or density or without surface mulch, soil becomes compact, infiltration is impeded and earthworms die (Blanchart, 1990). Crusted soil surface strata impeding infiltration and root development have been observed with *P. corethrurus* (cited in Rose and Wood, 1980; Fontaine, 1994; Duboisset, 1995). Under these conditions, intense production of labile casts may lead, due to abiotic factors, to the formation of a microhorizon (some centimetres thick) which is very compact with a micro-aggregated substructure. This formation depends on the coalescence of surface casts in humid conditions (Duboisset, 1995).

These effects were clearly demonstrated in kaolinitic soils but are not so clear in smectitic soils. Actually, whatever the particle size distribution, the importance of organic matter in determining the effects of large sized earthworms on soil physical properties is very important (Duboisset, 1995). Organic matter inputs enhance the effects of earthworm activity on physical properties. For smectitic soils such as Vertisols, most of the physical properties (aggregation, aggregate stability, erodibility) are linked to the organic matter content, while porosity is linked mainly to grass root activity. In these soils, earthworm activity is not as important as in kaolinitic soils.

2. Small sized earthworms (Eudrilidae at Lamto) generally have an opposite effect. Their casts are smaller aggregates (0.5–2 mm). Their activity tends to increase the total porosity of soil, to strongly modify pore size distribution, to increase infiltration and to decrease water retention capacity. They promote erosion as their casts are very fragile and already disappear under low rainfall. Soil loss is thus increased. These worms can increase large sized aggregate turnover; they can destroy casts created by large worms and limit the development of a crusted and impermeable surface horizon.

These two types of worms have opposite impacts on soil physical properties. Their simultaneous presence permits the conservation of a dynamic structure. At Lamto, when both types of earthworms are excluded from soil, the macro-aggregated structure tends to disappear (Blanchart *et al.*, 1997). Shaw and Pawluk (1986) similarly showed the importance of earthworm species associations (anecic and endogeic worms) in building a good structure in temperate soils.

Cultivation of tropical soils may lead to significant degradation. Soil physical degradation is characterized mainly by a collapse of structure: decrease of aggregate size and aggregate water stability, decrease of macroporosity and total porosity, compaction of surface horizons and formation of surface crust (Lal, 1988; Leprun, 1994). This degradation is the cause and the consequence of increased erosion, which is a major problem with severe economic and environmental consequences (Lal, 1991). All studied earthworms showed both enhancing and weakening effects on soil structure and/or soil physical properties, irrespective of soil type (clayey or sandy). Large sized earthworms appear to enhance most of the physical properties, but they cannot be used alone due to the development of sticky, compact and asphyxiating horizons. The effects of these 'compacting' earthworms must be corrected through the use of: (i) small 'decompacting' species; the earthworm community at Lamto is a good example of these antagonistic actions (Blanchart *et al.*, 1997). Apparently, the simultaneous presence of earthworms with antagonistic properties is a prerequisite for a dynamic soil structure. This underscores the claim of Lal (1991) that the best technological options for a sustainable management of water and soil resources are those which maintain or improve numerous populations and a taxonomic diversity of biota in soils. (ii) Crop residues and legume green manure which seem favourable to earthworms–soil properties relationships (Duboisset, 1995).

Acknowledgements

We gratefully acknowledge the contribution of Dr Christian Hartmann, Dr Michel Brossard and Professor Paul Hendrix during the preparation of this manuscript for their generous advice and stimulating discussions concerning soil physical properties.

References

- Albrecht, A. (1993) Restoration of degraded vertisols (Martinique) by root and earthworm activities in a large field experiment. In: Lavelle, P. (ed.) Conservation of Soil Fertility in Low-input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities (Macrofauna Project). Report of the CCE Project No. TS2*0292-F(EDB), IRD, Bondy.
- Albrecht, A., Rangon, L. and Barret, P. (1992) Effets de la matière organique sur la stabilité structurale et la détachabilité d'un vertisol et d'un ferrisol (Martinique). *Cahiers IRD, Série Pédologie* 27, 121–133.
- Alegre, J., Pashanasi, B. and Lavelle, P. (1995) Dynamics of soil physical properties in Amazonian agroecosystems inoculated with earthworms. Soil Science Society of America Journal 60, 1522–1529.
- Barois I. 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, 539-541.
- Barois, I., Patrón, C., Fragoso, C. and Gonzalez, C. (1992) Field experiments at La Mancha (Veracruz, Mexico). In: Lavelle, P. (ed.) Conservation of Soil Fertility in Low-input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities (Macrofauna Project). Report of the CCE Project No. TS2*0292-F(EDB), IRD, Bondy.

- Barois, I., Villemin, G., Lavelle, P. and Toutain, F. (1993) Transformation of the soil structure through *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. *Geoderma* 56, 57–66.
- Barros, M.E., Blanchart, E., Desjardins, T., Fernandez, E., Matos, J., Neves, A., Sarrazin, M., Chauvel, A. and Lavelle, P. (1996) Relação entre a macrofauna e a agregação do solo em três sistemas na Amazônia Central. XIII Latino-American Congress of Soil Science 'Solo-Suelo 96', 4–8 August 1996, Aguas de Lindoia, São Paulo.
- 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). PhD Thesis, The University of Rennes I. 263 pp.
- Blanchart, E. (1992) Role of earthworms in the restoration of the macroaggregate structure of a de-structured soil under field conditions. Soil Biology and Biochemistry 24, 1587–1594.
- Blanchart, E., Lavelle, P. and Spain, A.V. (1989) Effects of two tropical earthworms (Oligochaeta: Eudrilidae) on the size distributions of aggregates in an African soil. *Revue d'Ecologie et de Biologie du Sol* 26, 417–425.
- Blanchart, E., Lavelle, P. and Spain, A.V. (1990) Effects of the biomass and size of Millsonia anomala (Oligochaeta: Acanthodrilidae) on particle aggregation in a tropical soil in the presence of Panicum maximum (Gramineae). Biology and Fertility of Soils 10, 113–120.
- Blanchart, E., Bruand, A. and Lavelle, P. (1993) Casts of Millsonia anomala (Oligochaeta: Megascolecidae) in shrub savanna soils (Côte d'Ivoire). Geoderma 56, 119–132.
- Blanchart, E., Lavelle, P., Braudeau, E., Le Bissonnais, Y. and Valentin, C. (1997) Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. Soil Biology and Biochemistry 29, 431–439.
- Casenave, A. and Valentin, C. (1988) Les états de surface: une des clefs de l'hydrologie sahélienne. Proceedings of the Sahel Forum on the State-of-the-art of Hydrology and Hydrogeology in the Arid and Semi-arid areas of Africa. UNESCO/IWRA, Urbana, Illinois, pp. 61–72.
- Chapuis, L., Brossard, M., Lavelle, P. and Schouller, E. (1996) Organic and inorganic phosphorus transformations in a ferralsol ingested by a geophagous earthworm. *IV International Symposium on Plant-Soil Interactions at Low pH*, March 17–24 1996, Belo-Horizonte, Brazil.
- Chauvel, A., Barbosa, E.M., Blanchart, E., Grimaldi, M., Ferraz, J., Martins, P.D., Topall, O., Barros, E., Desjardins, T., Filho, N.F., Miranda, I.P.A., Sarrasin, M. and Mitja, D. (1997) Mise en valeur de la forêt et modifications écologiques. In: Théry H. (ed.) Environnement et Développement en Amazonie Brésilienne. Editions Belin, pp. 42-75.
- Darwin, C.R. (1881) The Formation of Vegetal Mould Through the Action of Worms, with Observations of Their Habits. Murray, London, 326 pp.
- Derouard, L., Tondoh, J., Vilcosqui, L. and Lavelle, P. (1997) Effects of earthworm introduction on soil processes and plant growth. Soil Biology and Biochemistry 29, 541–545.
- De Vleeschauwer, D. and Lal, R. (1981) Properties of worm casts under secondary tropical forest regrowth. *Soil Science* 132, 175–181.
- Dindal, D.L. (1985) Soil animals and soil fabric production: facts and perceptions. Quaestiones Entomologicae 21, 587–594.
- Duboisset, A. (1995) Caractérisation et Quantification par Analyse d'Image des Modifications Structurales Engendrées par Pontoscolex corethrurus (Glossoscolecidae,

Oligochaeta) sur un Sol Ferrallitique Cultivé (Pérou). DEA Thesis, The University of Nancy I.

- Elliott, E.T. and Coleman, D.C. (1988) Let the soil work for us. *Ecology Bulletin* 39, 23–32.
- Elliott, P.W., Knight, D. and Anderson, J.M. (1990) Denitrification in earthworm casts and soil from pasture under different fertilizer and drainage regimes. *Soil Biology* and Biochemistry 22, 601–605.
- Faivre, P. and Chamarro, C. (1995) Facteurs biotiques et mécanismes de lessivage particulaire dans les sols. L'exemple des toposéquences caractéristiques des Andes de Colombie. Etude et Gestion des Sols 2, 25–41.
- Fontaine, V. (1994) Rôle des Macro-invertébrés dans la Structuration de Sols Dégradés d'Amazonie. DEA Thesis, University of Paris XII, 44 pp.
- Fragoso, C., Brown, G.G., Patrón, J.C., Blanchart, E., Lavelle, P., Pashanasi, B. and Senapati B.K. (1997) Agricultural intensification, soil biodiversity and agroecosystem function: the role of earthworms. *Applied Soil Ecology* 6, 17–35.
- Gilot, C. (1994) Effets de l'Introduction du Ver Géophage Tropical Millsonia anomala Omodeo en Systèmes Cultivés sur les Caractéristiques des Sols et la Production Végétale en Moyenne Côte d'Ivoire. PhD Thesis, University of Paris XI, 178 pp.
- Hindell, R.P., McKenzie, B.M. and Tisdall, J.M. (1994) Relationships between casts of geophagous earthworms (Lumbricidae, Oligochaeta) and matric potential. II. Clay dispersion from casts. *Biology and Fertility of Soils* 18, 127–131.
- Jastrow, J.D. and Miller, R.M. (1991) Methods for assessing the effects of biota on soil structure. Agriculture, Ecosystems and Environment 34, 279–303.
- Ladd, J.N., Foster, R.C. and Skjemstad, J.O. (1993) Soil structure: carbon and nitrogen metabolism. *Geoderma* 56, 401–434.
- Lal, R. (1987) Tropical Ecology and Physical Edaphology. John Wiley & Sons, Chichester, 732 pp.
- Lal, R. (1988) Effects of macrofauna on soil properties in tropical ecosystems. Agriculture, Ecosystems and Environment 24, 101–116.
- Lal, R. (1991) Soil conservation and biodiversity. In: Hawksworth, D.L. (ed.) The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture. CAB International, Wallingford, pp. 89–1()4.
- Lavelle, P. (1978) Les vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème. Publication Laboratoire Zoologie Paris, E.N.S., Vol. 12, 310 pp.
- Lavelle, P., Blanchart, E., Martin, A., Spain, A.V. and Martin, S. (1992) Impact of soil fauna on the properties of soils in the humid tropics. In: Lal, R. and Sanchez, P.A. (eds) *Myths and Science of Soils of the Tropics. SSSA Special Publication* No. 29, Soil Science Society of America, Madison, Wisconsin, 157–185.
- Le Bissonnais, Y. (1989) Analyse des processus de microfissuration des agrégats à l'humectation. *Science du Sol* 27, 187–199.
- Lee, K.E. (1985) Earthworms. Their Ecology and Relationships with Soils and Land Use. Academic Press, Sydney, 411 pp.
- Lee, K.E. and Foster, R.C. (1991) Soil fauna and soil structure. *Australian Journal of Soil Research* 29, 745–775.
- Leprun, J.C. (1994) Effets de la mise en valeur sur la dégradation physique des sols. Bilan du ruissellement et de l'érosion de quelques grands écosystèmes brésiliens. *Etude et Gestion des Sols* 1, 45–65.

- Marinissen, J.C.Y. and Dexter, A.R. (1990) Mechanisms of stabilization of earthworm casts and artificial casts. *Biology and Fertility of Soils* 9, 163–167.
- Martin, A. (1991) Short- and long-term effect of the endogeic earthworm Millsonia anomala (Omodeo) (Megascolecidae, Oligochaeta) of a tropical savanna, on soil organic matter. Biology and Fertility of Soils 11, 234–238.
- Martin, A. and Marinissen, J.C.Y. (1993) Biological and physico-chemical processes in excrements of soil animals. *Geoderma* 56, 331–347.
- Nooren, C.A.M., Van Breemen, N., Stoorvogel, J.J. and Jongmans, A.G. (1995) The role of earthworms in the formation of sandy surface soils in a tropical forest in Ivory Coast. Geoderma 65, 135–148.
- Oades, J.M. (1993) The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56, 377–400.
- IRD-SECI (1994) Restoration of degraded vertisols (Martinique) by root and earthworm activities in a large field experiment. In: Lavelle, P. (ed.) Conservation of Soil Fertility in Low-input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities (Macrofauna Project). Report of the CCE Project No. TS2*0292-F(EDB), IRD, Bondy.
- Pashanasi, B., Alegre, J., Lavelle, P. and Schaefer, R. (1992) Large-scale field experimentation. Field experiments at Yurimaguas. In: Lavelle, P. (ed.) Conservation of Soil Fertility in Low-input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities (Macrofauna Project). Report of the CCE Project No. TS2*0292-F(EDB), IRD, Bondy.
- Robertson, L.N., Radford, B.J., Bridge, B., McGarry, D., Blakemore, R.J. and Sabag, M. (1994) Tropical earthworms under cropping in Queensland. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. and Grace, P.R. (eds) Soil Biota, Management in Sustainable Farming Systems. CSIRO, Australia, pp. 33–34.
- Rose, C.J. and Wood, A.W. (1980) Some environmental factors affecting earthworm populations and sweet potato production in the Tari Basin, Papua New Guinea. *Papua New Guinea Agriculture Journal* 31, 1–13.
- Senapati, B.K., Panigrahi, P.K., Giri, S., Patnaik, A. and Lavelle, P. (1994a) Restoration of degraded soil in intensive tea plantation (India). In: Lavelle, P. (ed.) Conservation of Soil Fertility in Low-input Agricultural Systems of the Humid Tropics by Manipulating Earthworm Communities (Macrofauna Project). Report of the CCE Project No. TS2*0292-F(EDB), IRD, Bondy.
- Senapati, B.K., Panigrahi, P.K. and Lavelle, P. (1994b) Macrofaunal status and restoration strategy in degraded soil under intensive tea cultivation in India. In: *Transactions of the 15th World Congress of Soil Science*, Vol. 4a. ISSS, Acapulco, Mexico, pp. 64–75.
- Shaw, C. and Pawluk, S. (1986) The development of soil structure by Octalosion tyrtaeum, Apporectodea turgida and Lumbricus terrestris in parent materials belonging to different textural classes. Pedobiologia 29, 327–339.
- Shipitalo, M.J. and Protz, R. (1988) Factors influencing the dispersibility of clay in worm casts. Soil Science Society of America Journal 52, 764–769.
- Shipitalo, M.J. and Protz, R. (1989) Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* 45, 357–374.
- Zhang H. and Schrader S. (1993) Earthworm effects on selected physical and chemical properties of soil aggregates. *Biology and Fertility of Soils* 15, 229–234.

Earthworm Management in Tropical Agroecosystems

Edited by P. Lavelle, L. Brussaard and P. Hendrix



CABI Publishing is a division of CAB International

CABI Publishing CAB International Wallingford Oxon OX10 8DE UK

Tel: +44 (0)1491 832111 Fax: +44 (0)1491 833508 Email: cabi@cabi.org CABI Publishing 10E 40th Street Suite 3203 New York, NY 10016 USA

Tel: +1 212 481 7018 Fax: +1 212 686 7993 Email: cabi-nao@cabi.org

CIP

© CAB *International* 1999. All rights reserved. No part of this publication may be reproduced in any form or by any means, electronically, mechanically, by photocopying, recording or otherwise, without the prior permission of the copyright owners.

A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Earthworm management in tropical agroecosystems / edited by P. Lavelle, L. Brussaard and P. Hendrix.

p. cm.
Includes bibliographical references and index.
ISBN 0-85199-270-6 (alk. paper)
1. Earthworm culture -- Tropics. 2. Earthworms -- Ecology -- Tropics. 1.
Lavelle, P. (Patrick) II. Brussaard, L. (Lijbert) III. Hendrix, Paul F.
SF597.E3E27 1999
639'.75--dc21 99-12081

ISBN 0 85199 270 6

Typeset by AMA DataSet Ltd, UK Printed and bound in the UK by Biddles Ltd, Guildford and King's Lynn