



6

Effects of Earthworms on Soil Organic Matter and Nutrient Dynamics Following Earthworm Inoculation in Field Experimental Situations

Cécile Villenave¹, Fabienne Charpentier², Patrick Lavelle², Christian Feller³, Lijbert Brussaard⁴, Beto Pashanasi⁵, Isabelle Barois⁶, Alain Albrecht³ and José C. Patrón⁶

¹Laboratoire de Biopédologie, IRD, Dakar, Sénégal;

²Laboratoire d'Ecologie des sols Tropicaux IRD, Bondy, France;

³Laboratoire d'Etude du Comportement des Sols Cultivés, IRD, Montpellier, France; ⁴Department of Terrestrial Ecology and Nature Conservation, Agricultural University, Wageningen, the Netherlands; ⁵INIA, Estación Experimental 'San Ramón', Yurimaguas, Peru; ⁶Benemérita Universidad Autónoma de Puebla, Centro de Investigaciones en Ciencias Microbiológicas, Puebla, Mexico

Summary

In agrosystem field experiments, earthworm inoculation did not impede depletion of soil organic stocks in most cases, in spite of increased carbon inputs through enhanced primary production. Slight evidence of soil organic matter (SOM) protection was found in poorly structured soil, such as a yam plot in Ivory Coast (soil sieved before experimentation), and a pasture plot on Martinique. Aggregation inherited from past earthworm activities probably maintains SOM protection after earthworms have disappeared; longer term experiments are necessary to observe C dynamics after the disappearance of inherited earthworm structures.

In two experiments with maize in Ivory Coast and Peru, the activity of earthworms led to a small increase in the incorporation of organic matter from

surface mulch in the SOM. Most of the C incorporated into the SOM originated from root material, and earthworm activities only slightly modified this pattern. Earthworm activity had significant effects on the distribution of C among particle size fractions. The general trend was a depletion of large ($> 50 \mu\text{m}$) particles and an accumulation of small ($< 2 \mu\text{m}$) particles.

Nutrient depletion in low-input cropping systems was not impeded by earthworm activities; at Yurimaguas, however, some signs of a better conservation of K were noted after 3 years in the traditional rotation.

Introduction

In the humid tropics, earthworms participating in soil processes are principally endogeic. These earthworms generally are geophagous and interact directly with SOM (Bouché, 1977; Lavelle, 1981; reviewed by Lee, 1985). They affect soil by their feeding and mechanical activities. Earthworm activity creates structures (casts and galleries) which modify soil aggregation, porosity and the connectance among pores (Aina, 1984; Lee and Ladd, 1984; Blanchart *et al.*, 1990). However, high variability has been demonstrated in the effects of different earthworm species on soil aggregation, a major process whereby earthworms affect the dynamics of SOM. In contrast with many anecic earthworms, geophagous earthworms do not always improve aeration of soil and infiltration of water; rather the activities of some species result in soil compaction and increases in soil bulk density (Blanchart *et al.*, 1997; see Chapter 4).

The effects of earthworms on SOM dynamics vary with the scales of time and space over which they are considered. Chemical characteristics of fresh and older casts differ from the non-ingested soil (Blanchart *et al.*, Chapter 5). Laboratory studies show that endogeic earthworms stimulate the mineralization of SOM during digestion (Syers *et al.*, 1979; Lavelle *et al.*, 1992). In fresh casts, larger amounts of mineral nutrients (e.g. nitrogen and phosphorus) occur than in non-ingested soil (Barois *et al.*, Chapter 3). On the scale of months, mineralization of carbon was found to have ceased in the ageing casts of *Millsonia anomala* (Martin, 1991). However, most of these results were observed under laboratory conditions; therefore, medium- or large-scale experiments are necessary to understand the effect of earthworm inoculation on the time scale of years and the spatial scale of landscapes.

Six field experiments were conducted over 3–6 years in the tropics, including sites in Africa, the Caribbean, Central and South America, in order to test the hypothesis that introduction of adapted endogeic earthworms into low external input agricultural systems reduces loss of SOM and plant nutrients generally observed in such systems (Siband, 1972; Feller and Milleville, 1977; Aweto *et al.*, 1992) and stimulates plant growth. These effects result from the modification of the dynamics of the SOM being ingested by earthworm. First, more mineral nitrogen and phosphorus become available in greater synchrony with plant demand due to greater mineralization of SOM during

digestion. Later, the SOM defecated would be protected in the compact structure of casts on the scale of months to years.

Research Approach

The data set collected as part of the Macrofauna programme comprises experimental field plots inoculated with earthworms compared with non-inoculated controls. The effect of the introduction of earthworms on the dynamics of soil organic matter was tested mainly in low-input cropping systems of the humid tropics: Lamto (Ivory Coast), Yurimaguas (Peru), La Mancha (Mexico) and in an intensive pasture: St Anne (Martinique, French West Indies). The main characteristics of the sites, rainfall, soil type, soil texture and natural vegetation are presented in Table 6.1. Medium-term experiments were conducted at four sites for 2–6 years.

Low-input cropping systems

Natural ecosystems were cleared to establish 0.28–1.28 m² experimental areas enclosed in nylon mesh net or PVC sheets to a depth of 40 cm. Native earthworms were eliminated either by application of a pesticide (Carbofuran) with a short residence time in soil (Yurimaguas, Lamto), hand sorting of the soil (Lamto) or soil tillage and hand sorting (La Mancha). Then, a population of the selected species (*M. anomala* at Lamto and *Pontoscolex corethrurus* at Yurimaguas and La Mancha) was introduced in selected treatments and cultivation started. The biomasses of earthworms introduced into the microplots were similar to those found in the nearby natural ecosystems. The earthworm populations were recovered after every cropping period, except for the continuous maize plot at Yurimaguas (Table 6.1). In all plots (except yam in Ivory Coast), above-ground crop residues were either applied as surface litter or removed, resulting in a 2 × 2 factorial arrangement of treatments (± earthworms × ± litter inputs). No chemical inputs were added (except in the 6-year continuous maize crop at Yurimaguas where NPK fertilization was added after the second year).

Pasture plot

The role of earthworms was also investigated in the restoration of a degraded soil converted to pasture. At St Anne (Martinique, French West Indies), an experimental plot (140 × 60 m) of pangola grass pasture (*Digitaria decumbens*) was established on a soil following 15 years of continuous market gardening cultivation. One year after the sowing of *D. decumbens*, two subplots 5 × 10 m

Table 6.1. Characteristics of the experimental stations and the experimental plots; analyses done in the different places are indicated with an x.

	Mexico	Peru		Martinique (West Indies)	Ivory Coast	
	Continuous maize (<i>Zea mays</i>)	Crop rotation maize + rice + cowpea + rice (3)	Continuous maize (<i>Zea mays</i>)	Pasture (<i>Digitaria decumbens</i>)	Continuous yam (<i>Dioscorea alata</i>)	Continuous maize (<i>Zea mays</i>)
Rainfall (mm)	1345	2100	2100	1300	1200	1200
Soil taxa ^a	Psamment	Typic paleudult	Typic paleudult	Vertisol	Ultisol	Ultisol
Sand (%)	74.4	55	55	10	78.1	87.6
Silt (%)	8.6	22	22	30–40	17.0	8.5
Clay (%)	16.0	23	23	50–60	6.0	4.7
Vegetation before experiment	Weed fallow	Secondary forest	Secondary forest	Market gardening	Guinean savanna	Secondary forest
Experiment duration (years)	3	3	6	2.5	3	3
Cropping cycles (numbers)	6	6	6	—	3	6
Introduced earthworm species	<i>P. corethrurus</i>	<i>P. corethrurus</i>	<i>P. corethrurus</i>	<i>P. elongata</i>	<i>M. anomala</i>	<i>M. anomala</i>
Chemical inputs	0	0	NPK fertilization	0	0	0
Crop residues	Exported or left	Exported or left	Left	—	Left	Exported or left
Final earthworm populations	Contamination of control	Maintenance	Not sampled	Maintenance	Still present but lower abundance than introduced	Still present but lower abundance than introduced

C content	x	x		x	x	x
C physical fractionation			x	x	x	x
¹³ C labelling			x			x
N content	x	x		x	x	x
Potential of N mineralization					x	
Other nutrients		x			x	x
References	Patron <i>et al.</i> (unpublished data)	Pashanasi <i>et al.</i> (1996)	Charpentier (1996)	Blanchart <i>et al.</i> (unpublished data)	Gilot (1997)	Gilot (1994)

^a By USDA classification system.

were separated and two treatments initiated, one which reduced earthworm colonization by applying carbofuran, and another was reinoculated with *Polypheretima elongata* at a rate of 90 ind m⁻². Changes in SOM were observed during 3 years after the inoculation.

Analyses

The different analyses for each plot are summarized in Table 6.1. The effects of earthworms on soil organic carbon were studied at three levels: changes in the stocks of soil organic carbon (or changes in the C content) with time; rates of incorporation of fresh organic matter in the SOM using ¹³C labelling (Mariotti, 1991); and changes in the distribution of the organic carbon associated with particle size fractions (Gavinelli *et al.*, 1995). Nitrogen was the most studied nutrient; changes in the nitrogen stocks (or nitrogen content) of the soil were analysed focusing on the earthworm effects.

In the discussion, conditions in which earthworms had affected the SOM and nutrient contents are analysed, and the management required to optimize the positive effect of the earthworm activities are discussed.

Changes in Soil Organic Matter, Nitrogen and Other Nutrient Contents

Changes of carbon stocks during the cultivation period

Changes in carbon stocks were investigated in the maize plot at Lamto in the 0–10 and 10–20 cm strata (Fig. 6.1a). Soil bulk density and C contents were measured at each date for the two treatments.

After 3 years of maize cultivation (six cropping cycles) at Lamto, the stock of C in the upper 10 cm of soil had decreased significantly from 1.64 kg m⁻² to 1.14 and 1.23 kg m⁻² in the control and inoculated treatments, respectively (Fig. 6.1a). The soil C lost after 3 years of cropping represented, on average, 28% of the initial C. The difference between the two treatments was not significant at any date. In the 10–20 cm depth strata, the decrease of the C stock during the experiment was not significant and no difference between inoculated treatment and control was measured.

At Yurimaguas, after 3 years of crop rotation, C stock in the upper 10 cm of the soil had decreased by 7 and 10%, respectively, in control and in systems inoculated with earthworms (significant decrease in C contents) (Fig. 6.1b). Although systems with earthworms tended to have more C from the second cropping cycle, no difference between treatments was observed at the end of the experiment.

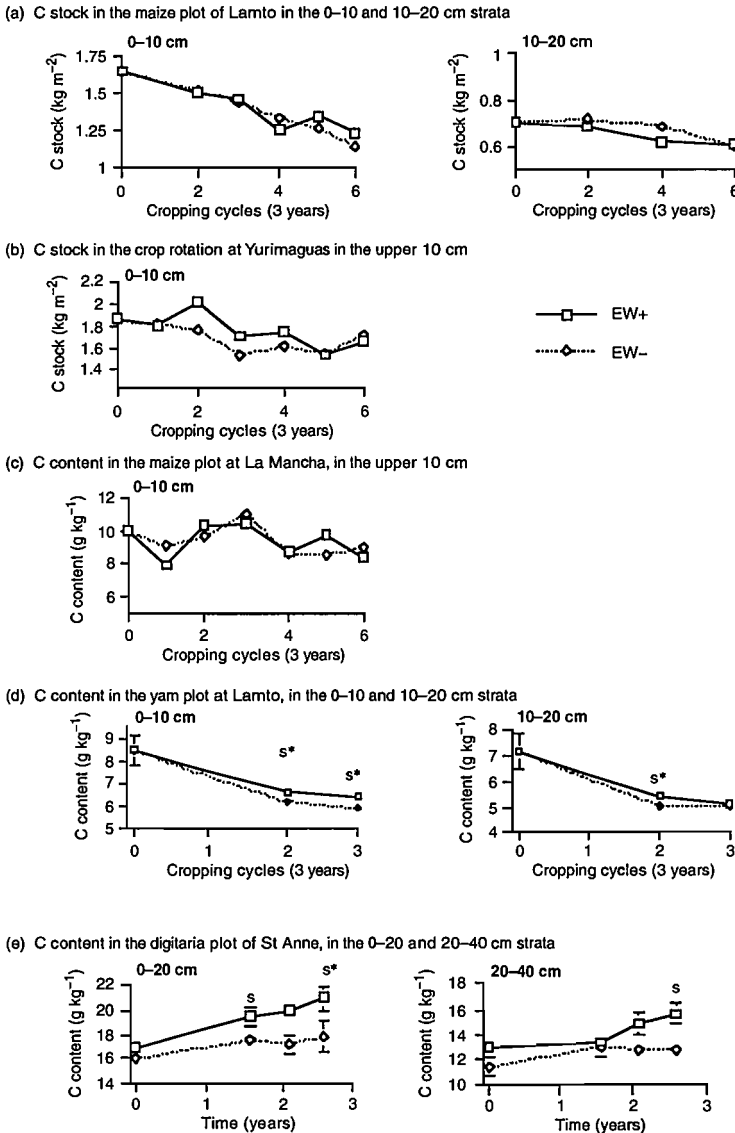


Fig. 6.1. Changes in the soil organic carbon (stocks or contents) in the different plots during 3 years of the experiment. Inoculated treatments are compared with control: significant differences are indicated on the graphs (bars = standard errors; s*, significant differences between treatments, $P < 0.10$; s, $P < 0.05$). EW–: without earthworms, EW+: with earthworm inoculation. (Adapted from Gilot, 1994; Pashanasi *et al.*, 1997; Blanchart, unpublished data; Patron *et al.*, unpublished data.)

One of the effects of earthworm activity in the rotation plot at Yurimaguas and in the maize plot at Lamto was a significant average increase in soil bulk density of 8 and 5%, respectively, in average from the first cropping period to the last one. In the other four plots, the soil bulk density was not measured in the different treatments for each date, so C stocks were not calculated.

At La Mancha, the total C content fluctuated during the 3 years of cropping. The C loss after 3 years (0–10 cm) was not significant but represented 12% of the initial C; no differences were observed between inoculated treatment and control in the C contents (Fig. 6.1c). It was not possible to distinguish treatment effects at La Mancha after the first year because the control plots were colonized by *P. elongata* from adjacent treatments.

In the yam plot at Lamto, the carbon content in the soil (0–10 cm) decreased significantly by 25% after 3 years of yam cultivation (Fig. 6.1d). The activity of earthworms reduced this loss by 6% in 3 years, but the difference was not highly significant ($0.05 < P < 0.10$). In the deeper strata, C content had decreased by 29% after 3 years in the non-inoculated control; no significant difference between treatments remained at the end of the experiment. At the second harvest, a higher C content (6.5%) was observed in the inoculated treatment ($0.05 < P < 0.10$).

At St Anne, pasture establishment on a degraded soil resulted in a SOM increase, after 30 months, C content of soil increased significantly by 12% in the control in the 0–20 cm strata but not in the 20–40 cm strata. After 2.5 years from the inoculation of earthworms, C content increased to 21.0 g kg⁻¹ in the upper 20 cm in inoculated treatments, whereas it reached 17.8 g kg⁻¹ in the control (Fig. 6.1e); *P. elongata* activities induced a significant increase of over 15% compared with the control. The increase in C content in the presence of earthworms was also significant in the 20–40 strata 30 months after inoculation.

Incorporation of fresh organic matter into the soil organic matter

At Lamto and Yurimaguas, the medium-term dynamics of SOM have been investigated through changes in the ¹³C/¹²C ratio induced by vegetation changes from C₃ to C₄ photosynthetic pathways, particularly maize cultivation (C₄) after forest (C₃) clearing (Balesdent *et al.*, 1987; Mariotti, 1991). This natural labelling of SOM by the ¹³C/¹²C ratio enabled the calculation of the final soil C that derived from the maize (roots and crop residues). The effect of earthworm activity on the incorporation of fresh organic matter into the SOM was measured. Isotopic analyses were done on composite samples with no replicates.

After 3 years of continuous maize cultivation at Lamto, the C derived from maize incorporated into the 0–10 cm stratum represented from 0.10 to 0.15 kg C m⁻² (6.4–10.3% of the total soil C in the 0–10 cm stratum), depending on the treatment (Fig. 6.2) (Gilot *et al.*, 1995). The quantity of fresh organic

		C stock at year 3 (0–10 cm)	% of C-C ₄ incorporated in SOM	Surface-applied crop residues	
NO CROP RESIDUES	EW–	C-C ₃	C-C ₄	7.7%	0 kg C m ⁻²
		1.24	0.10		
	1.34 kg C m ⁻²				
	EW+	C-C ₃	C-C ₄	6.4%	0 kg C m ⁻²
1.38		0.095			
1.48 kg C m ⁻²					
MULCHING OF CROP RESIDUES	EW–	C-C ₃	C-C ₄	8.4%	0.024 kg C m ⁻² → 2.9%
		1.36	0.124		
	1.48 kg C m ⁻²		C-C ₄	0.830 kg C m ⁻²	
	EW+	C-C ₃	C-C ₄	10.3%	0.053 kg C m ⁻² → 6.2%
1.29		0.148			
1.44 kg C m ⁻²		C-C ₄	0.850 kg C m ⁻²		

Crop residues
incorporated to
SOM

Fig. 6.2. Soil carbon budget (0–10 cm) in the continuous maize plot at Lamto after 3 years of cultivation (EW–: without earthworms, EW+: with earthworm inoculation). C-C₃: C of the original forest soil; C-C₄: C of fresh maize input. (Adapted from Gilot *et al*, 1995.)

matter incorporated into the soil when the crop residues were returned as surface mulch were higher than when they were removed. The increase of 24 g C m⁻² of C-C₄ incorporated into the SOM between EW-M+¹ and EW-M– represented 20% of the C-C₄ incorporated into EW-M+, while the increase of 53 g C m⁻² between EW+M– and EW+M+ represented 36% of the C-C₄ incorporated into EW+M+. Even when crop residues were left on the soil surface, the main part of the C from the maize that was incorporated into the SOM originated from the root system. Most of the C from the mulch was mineralized; only 2.9–6.2% of the C from the mulch became incorporated into the SOM. The contribution of plant roots to SOM is comparable with other data from the

¹ EW-M– (without earthworms, without mulch); EW-M+ (without earthworms, with mulch); EW+M– (with earthworms, without mulch); EW+M+ (with earthworms, with mulch).

literature, indicating that 5–20% of the photosynthesized C was found as a residue in the soil (Hetier *et al.*, 1980; Merckx *et al.*, 1986). The use of maize stover as an organic input resulted in a soil carbon sequestration efficiency of 3%. *Millsonia anomala* activities had no consequent effect on the incorporation of the C from maize in the SOM in the absence of a mulch. However, there was a higher incorporation of the C-C₄ from mulch into the SOM in the presence of earthworms; a supplement of 24 g C m⁻² (i.e. an increase of 20% compared with the control) was incorporated into the SOM in the inoculated treatments. It had already been observed that *M. anomala* is unable to utilize crop residues on the soil surface in an efficient manner (Gilot, 1994).

When maize was cultivated continuously at Yurimaguas, the C stock decreased by 15% (mean of the two earthworm treatments) over 6 years to a depth of 30 cm. The measured quantity of C-C₄ incorporated into SOM was greater at Yurimaguas than at Lamto due to the longer duration of experiment and deeper sampling of the soil. After 6 years of continuous maize cropping, C₄-C incorporated into the SOM represented 8.3% of the soil organic C stock from 0–30 cm depth in the inoculated treatment (Fig. 6.3). This retention of maize litter resulted in addition of 0.25 kg C m⁻² into the SOM, representing 11.1% of the measured maize input (root biomass at harvest + mulch) (Charpentier, 1996). In the non-inoculated control, only 0.18 kg C-C₄ m⁻² from the maize was incorporated into the SOM in the upper 30 cm, representing 6.2% of total soil C. Total C-C₄ incorporated into the soil represented 8.9% of measured C input (i.e. roots at harvest + stover, but not exudates or roots decomposed before harvest).

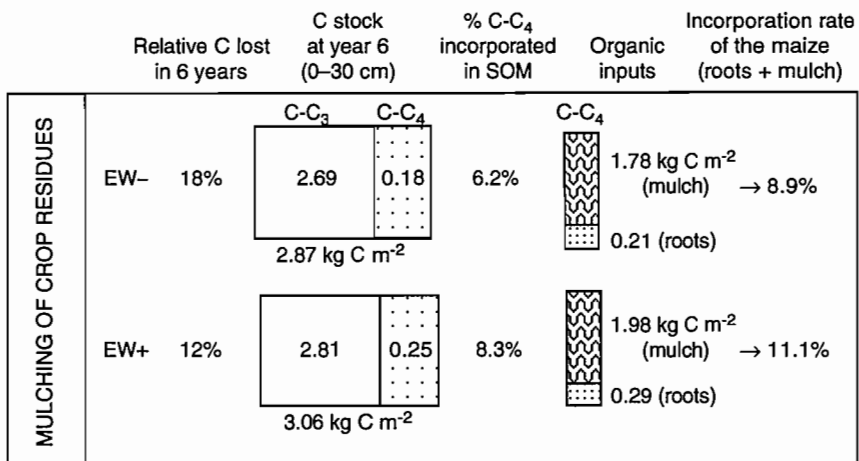


Fig. 6.3. Soil carbon budget (0–30 cm) in the continuous maize plot at Yurimaguas after 6 years of cultivation (EW–: without earthworms, EW+: with earthworm inoculation). C-C₃: C of the original forest soil, C-C₄: C of fresh maize input. (Adapted from Charpentier, 1996.)

In both sites, the activity of earthworms led to a small increase in the incorporation of fresh organic matter into the SOM when crop residues were left on the soil. Most of the C incorporated into SOM originated from root material, and earthworm activities only slightly modified this pattern.

Changes in carbon distribution among particle size fractions

Physical fractionation of organic matter allowed the separation of different pools of soil organic matter (Feller, 1994) into plant debris ($> 20 \mu\text{m}$), the organo-silt complex ($2\text{--}20 \mu\text{m}$) and the organo-clay compartment ($< 2 \mu\text{m}$). This method was used to characterize the SOM at Lamto, Yurimaguas (continuous maize plot) and St Anne, and to identify the effects of earthworms on the distribution of C between fractions.

The recovery of total C using this method varied from 96 to 101%, with a mean value of 99.5% for the 13 treatments. The cumulative carbon content of the fractions ranged from 93 to 103% (except for Yurimaguas, treatment EW-: 88%). Dispersion of silt and clay fractions was satisfactory in most treatments, except at Yurimaguas.

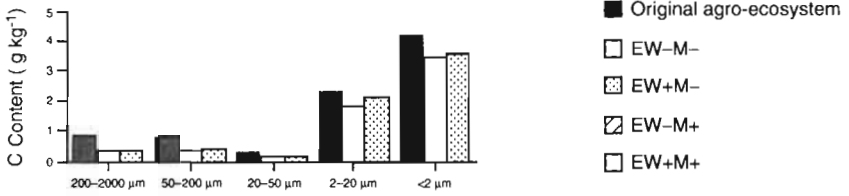
In the yam plot at Lamto, the slightly higher amount of C in inoculated treatments did not appear to be closely linked to a specific fraction of SOM (Gilot, 1997). However, the C remaining in the $2\text{--}20 \mu\text{m}$ fraction at the end of the experiment tended to be higher in the inoculated treatment than in the control (Fig. 6.4a). Before cropping, the savanna soil at Lamto had a high proportion ($> 75\%$) of C contained in the finer fractions ($< 20 \mu\text{m}$); the absolute value of the C of these fractions decreased with cropping but the proportion increased up to 81% in the non-inoculated soil and 87% in treatment with earthworms. Due to land cultivation, the highest relative decrease (percentage initial C) was measured in the fractions $> 50 \mu\text{m}$.

In the maize plot of Lamto (after forest clearing), reduction of the C stock following land clearing resulted from the disappearance of the coarse fractions ($50\text{--}200 \mu\text{m}$ and $200\text{--}2000 \mu\text{m}$), which represented 53% of the carbon at the onset of cropping but only 31% after 3 years of cropping (Fig. 6.4b). The decrease of C present in coarse fractions was higher in the presence of earthworms (60% of the coarse fractions disappeared after 3 years) than in their absence (50%). These losses of C due to the earthworm activity in the coarse fractions were slightly lower when fresh crop residues were left in the field than when they were removed following harvest (Gilot *et al.*, 1995).

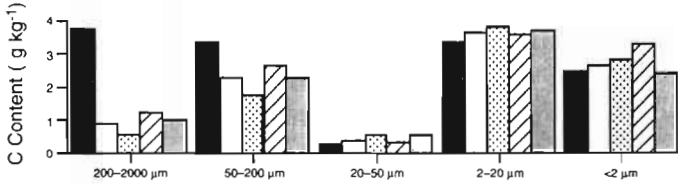
After 6 years of continuous maize cultivation at Yurimaguas, reduction of the C stock following land clearing was due to a decrease of the C contained in all fractions $> 20 \mu\text{m}$. As in the maize plot after forest clearing at Lamto, earthworm activity induced a decrease of the C contained in the coarse fractions ($> 50 \mu\text{m}$) (Fig. 6.4c).

At St Anne, the distribution of the total C was not measured at the onset of the experiment; rather the effect of the earthworm inoculation after

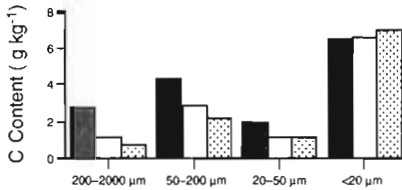
(a) Lamto, yam (3 years after earthworm introduction)



(b) Lamto, maize (3 years after earthworm introduction)



(c) Yurimaguas, continuous maize (6 years after earthworm introduction)



(d) St Anne, pasture (2 years after earthworm introduction)

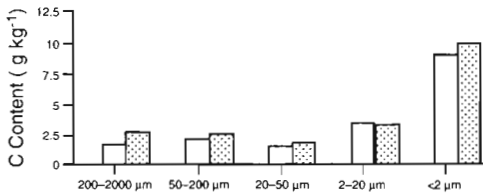


Fig. 6.4. Distribution of the total C of the soil among particle size fractions: comparison of the initial and final dates in the four plots (EW-: without earthworms, EW+: with earthworm inoculation; M-: exportation of the crop residues, M+: crop residues left on the soil surface). (Adapted from Gilot *et al.*, 1995; Charpentier, 1996; Blanchart *et al.*, unpublished data.)

2 years was compared (Fig. 6.4d). The increase of total C content of the soil in inoculated treatment was not linked to the increase in C in a particular fraction: the C content increased in both coarse fractions ($> 20 \mu\text{m}$) and in the finer ones ($< 2 \mu\text{m}$).

Soil nitrogen

In the continuous maize crop at Lamto, nitrogen stocks in the upper 10 cm decreased significantly from 167 g m^{-2} to 116 and 132 g m^{-2} in the control and in the inoculated treatments, respectively. The difference between treatments at each date was not significant (Fig. 6.5a). In the 10–20 cm strata, the decrease in nitrogen in 3 years was not significant across or between treatments.

At Yurimaguas, no significant decrease of the total nitrogen content was measured during the 3 years of cultivation in the crop rotation plot, the final stocks of nitrogen were 117 and 126 g m^{-2} , with and without earthworms respectively (Fig. 6.5b). The increase of N content after land clearing at Yurimaguas probably resulted from nitrogen inputs following burning and the incorporation of ashes into the soil even if most of the N may volatilize. Nitrogen tended to be higher in the inoculated treatments during the first 2 years of the experimentation, but it was significantly higher only when measured after the first cropping period.

At La Mancha, nitrogen content decreased by 40% in the 0–10 cm depth during 3 years and was less variable than carbon content between dates; however, no difference between treatments was observed (Fig. 6.5c).

Nitrogen contents in the yam plot at Lamto did not decrease in either treatments in the 0–10 and 10–20 cm strata. Final nitrogen content was 5% higher when earthworms were introduced ($0.05 < P < 0.1$) in the 0–10 cm layer but no differences were measured at deeper depths (10–20 cm) (Fig. 6.5d).

Following pasture establishment at St Anne, the nitrogen content increased significantly during 30 months in the non-inoculated control. A slight, but non-significant difference existed between the nitrogen content in the two treatments at the beginning of the experiment (Fig. 6.5e). Thirty months after earthworm inoculation, the soil nitrogen content (0–40 cm) was significantly higher than in the control ($P < 0.05$).

In most of the low external input cropping experiments, soil nitrogen contents decreased with time and earthworms had no effect on the soil nitrogen changes, except in the yam plot at Lamto and the crop rotation at Yurimaguas. Lower fluctuations were generally observed for nitrogen than for carbon, indicating a smaller heterogeneity in the spatial distribution of nitrogen, and temporal availability following the burning of the primary vegetation and establishment of crops.

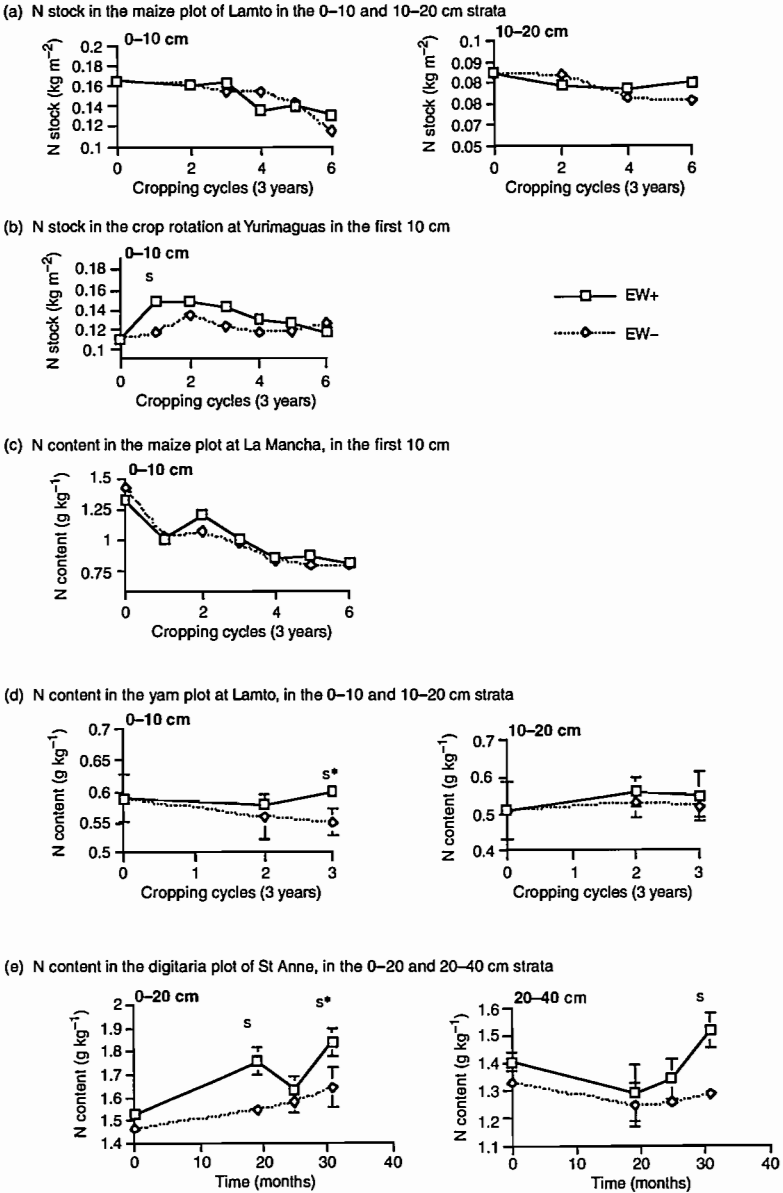


Fig. 6.5. Changes in the soil organic nitrogen (stocks or contents) in the different plots during 2 or 3 years of experimentation. Inoculated treatments are compared with control: significant differences are indicated on the graphs (bars = standard errors; s*, significant differences between treatments, $P < 0.10$; s, $P < 0.05$). (Adapted from Gilot, 1994; Pashanas *et al.*, 1997; Blanchart *et al.*, unpublished data; Patron *et al.*, unpublished data.)

In the yam plot of Lamto, the potential anaerobic nitrogen mineralization was increased by 36% in the inoculated plots (Tsakala, 1994) after the second cropping period in April 1992 (Fig. 6.6), whereas the total nitrogen content of the soil was not different between treatments. This increase was not related to total soil nitrogen, suggesting that earthworm activities increase N availability but not total N supply.

Phosphorus and exchangeable cation contents

At Lamto, analyses of phosphorus and cation contents were done with no replicates. Available P (Olsen–Dabin method; Dabin, 1967) decreased mainly in the yam plot of Lamto (–53% in 3 years, mean between the two treatments). Final P contents (Table 6.2) were slightly higher in inoculated treatment, at Lamto (+19 and +21%, respectively, in the yam and the maize plot) and Yurimaguas (+11%) (Gilot, 1994; Pashanasi *et al.*, 1997).

At Lamto, except for Ca in the maize plot, treatment EW+, contents of exchangeable K, Ca and Mg decreased during the 3 years of cropping by, respectively, 15, 22 and 25% in the yam plot and 50, 0 and 30% in the maize plot (mean between the two treatments) (Table 6.2). No great differences between treatments were observed in the yam plot; in the maize plot, the final Ca and Mg were 12 and 15% higher, respectively, in the inoculated treatment than in the non-inoculated control.

At Yurimaguas, exchangeable cation contents increased after the land clearing (Pashanasi *et al.*, 1997). After six cropping cycles, K content was significantly higher in inoculated treatments (+114%), but Ca and Mg were not.

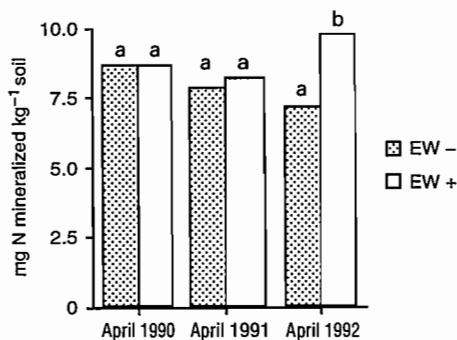


Fig. 6.6. Soil N mineralization in incubation experiments under laboratory conditions from a yam plot (Lamto 0–10 cm) in mg of total mineral nitrogen/100 g soil [before cultivation (1990); before the second (1991) and the third cropping period (1992)]. Significant differences are indicated on the graph (t-test, $P < 0.05$). EW–: without earthworms, EW+: with earthworm inoculation. (Adapted from Tsakala, 1996.)

Table 6.2. Available phosphorus and exchangeable K, Ca, Mg contents in the two plots of Lamto and in the crop rotation at Yurimaguas.

		Initial date	Final date (3 years of cropping)	
			EW–	EW+
Olsen P (mg kg ⁻¹)	Cropping sequence (Yurimaguas) ^a	13.3	9.0	10.0
	Yam (Lamto) ^b	10.30	4.42	5.29
	Maize (Lamto)	8.32	8.21	9.95
K (mEq 100 g ⁻¹)	Cropping sequence (Yurimaguas)	0.70	0.70	1.50*
	Yam (Lamto)	0.21	0.17	0.18
	Maize (Lamto)	0.23	0.13	0.10
Ca (mEq 100 g ⁻¹)	Cropping sequence (Yurimaguas)	2.50	8.00	10.00
	Yam (Lamto)	2.25	1.75	1.78
	Maize (Lamto)	4.46	4.24	4.73
Mg (mEq 100 g ⁻¹)	Cropping sequence (Yurimaguas)	1.20	2.70	2.90
	Yam (Lamto)	1.30	0.95	1.00
	Maize (Lamto)	0.85	0.54	0.62

^aYurimaguas: six replicates per treatment; ^bLamto: no replicates (composite samples).

*Significant difference between EW– and EW+ at the final date ($P < 0.05$).

Discussion

The experiments were conducted in the humid tropics on different soils with different plants and earthworm species. The main effects of the earthworm activities on the SOM and nutrient dynamics on the investigated time scale will be discussed considering the convergence of results between the different plots (Table 6.3).

Carbon protection by earthworms activities

In laboratory experiments, Martin (1991) demonstrated that soil carbon was protected from mineralization within the compact structure of casts of

Table 6.3. Recapitulative table on the effects of earthworms on the SOM and nutrient dynamics (0–10 cm).

Earthworm effect on	Lamto		Yurimaguas		La Mancha	St Anne
	Yam (0–10 cm)	Maize (0–10 cm)	Rotation ^a (0–10 cm)	Maize	Maize (0–10 cm)	Pasture (0–20 cm)
C stock or C content under cultivation or pasture in the superficial strata	(+)	0	+/0		0	(0–20 cm) +
C stock or C content in deeper strata	(10–20 cm) 0	(10–20 cm) 0				(20–40 cm) +
Incorporation of C from the crop to the C-soil		0 if CR ^b exported + if CR left		(+) (CR left)		
C content in fractions > 50 µm (plant debris)	0	– if CR exported (–) if CR left		—		(+)
C content in the fractions < 50 µm (silt and clay-sized fractions)	(+)	0		0		(+)
N stocks	(+)	0	0		0	+
N availability	+					
Exchangeable cations	(+)	(+)	+ K			
P available	(+)	(+)	(+)			

+, the presence of earthworms induces an increase in the considered characteristic; (+), trend towards a positive effect; –, the presence of earthworms induces a decrease in the considered characteristic; +/-, effect in the first period of the experiment; 0, no effect of the presence of earthworms.

M. anomala produced under laboratory conditions. The carbon mineralized from incubated casts was almost 3.7 times less in the casts (3% year⁻¹) than that from non-ingested soil (11% year⁻¹). This experiment, which suggested a positive effect of earthworm activities on the sequestration of soil carbon, was not confirmed completely in subsequent field experiments. In most experiments (maize, Lamto; maize, La Mancha; crop rotation and continuous maize, Yurimaguas), earthworm activities did not reduce the decrease of SOM stocks during cultivation after land clearing. Evidence for SOM protection by

earthworms was only shown in the yam plot in the top layer (0–10 cm). In St Anne pasture, a more rapid reconstitution of the carbon stock to a depth of 40 cm was associated with earthworm activities (Table 6.3).

Soil physical properties, particularly soil structure, largely determine the degree to which earthworm activities impact upon soil characteristics. Those soils which were in the greatest stage of degradation benefited from earthworm activities. This was the case in Martinique, where continuous cultivation had resulted in poor soil structure (Albrecht *et al.*, 1992), and in the yam cultivation treatments at Lamto. In this last plot, the soil was modified prior to the plot installation by the breakdown of the soil aggregation (sieving prior to the introduction of earthworms).

Other experiments were established in non-degraded ecosystems where earthworms were naturally abundant (Lavelle, 1978; Lavelle and Pashanasi, 1989). Native earthworms were killed by chemical or physical methods, before the beginning of the experiments, but the physical conditioning of soils resulting from former macrofauna activities was still effective.

In degraded soils with a poor physical structure, earthworm activity may enhance the protection of carbon that would have been mineralized if it was not protected in macro-aggregates produced by earthworms. From the results obtained, we hypothesize that the positive effect of earthworms on SOM conservation via soil aggregation does not require the constant presence of active earthworm populations. Rotations that include every 3 or 4 years of cultivation, at least, 2 years of a grass fallow to stimulate earthworm activities may be sufficient to maintain macro-aggregation in the long term. Furthermore, earthworms (*P. elongata*, for example) serve to better incorporate surface litter into the soil, as was the case in the pasture at St Anne.

Currently, complementary information on the effect of earthworms on carbon dynamics for longer periods can only be derived from modelling. In the absence of long-term experiments, the effects of earthworms over 10–100 years on SOM were simulated in the natural savanna of Lamto using the CENTURY model (Parton *et al.*, 1987). When suppression of physical protection of C in earthworm casts was simulated, the model indicated that SOM decreased by 10% in 30 years, the largest proportion being lost in the slow pool. This suggests that the slow pool of soil carbon may be considerably affected by the activity of earthworms. The slow pool of CENTURY is recoverable through particle size separation, and correlates with the particulate organic matter described by Carbardella and Elliott (1993) and Gavinelli *et al.* (1995) which is often embedded within stable soil aggregates,

In another modelling exercise simulation with CENTURY, earthworm activities were simulated through incorporation of litter below surface casts and gentle tillage due to bioturbation (Lierman, 1996). The simulation of earthworm presence resulted in a decrease in soil organic C during the first 3 years of cultivation after deforestation at Yurimaguas (Fig. 6.7). In the longer term (30 years), the trend was reversed since C accumulated in the slow and passive

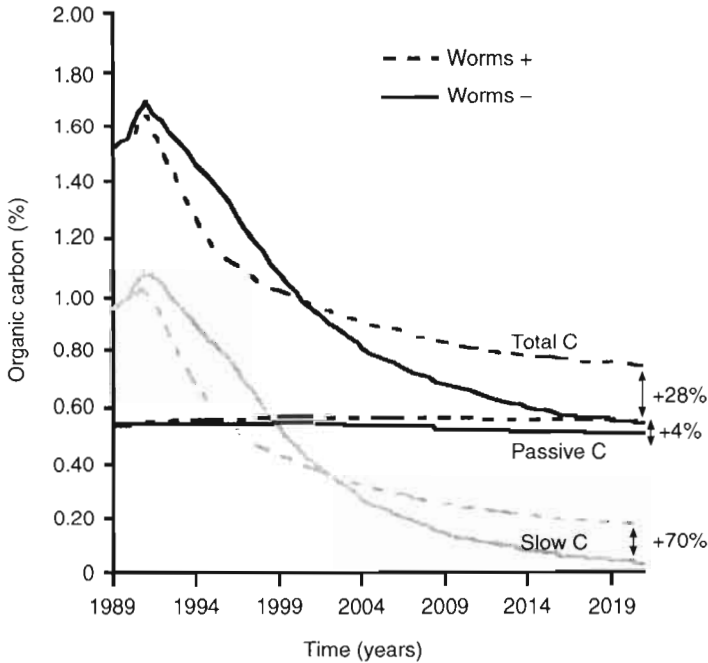


Fig. 6.7. Simulation of soil organic carbon dynamics using CENTURY after deforestation and 30 years of continuous cropping at Yurimaguas. (Adapted from Lierman, 1996.)

pools. After 40 years, C content was 28% higher in treatments where the presence of earthworms is simulated.

The effect of earthworm activity on the total nitrogen content of the soil was limited. A higher final nitrogen content in an inoculated treatment compared with a non-inoculated control was measured in the continuous yam cultivation plot, but differences were small (5%). At St Anne, earthworm activity led to a more rapid increase in the nitrogen content of soil (12%). In the yam plot, the potential of nitrogen mineralization was also higher in inoculated treatments before the last cropping period. Earthworm casts have high contents of mineral N, when compared with non-ingested soil, which persist for several days after deposition (Lavelle *et al.*, 1992; Parkin and Berry, 1994; Chapter 3). Therefore, soils with active earthworm populations may have higher rates of nitrogen mineralization, as in the yam plot. In another experiment, Gilot-Villeneuve *et al.* (1996) observed that, in the presence of *M. anomala*, a higher quantity of nitrogen derived from fresh organic input mixed into the soil was incorporated into the growing maize. Moreover, lower quantities of nitrogen from these inputs were recovered in the soil in forms easily available for plants.

Data available for the other nutrients are too scarce to discriminate the effect of earthworms, but trends suggested increased availability of several cations and P in earthworm-inoculated soils after 3 years.

How do earthworms affect SOM?

In plots in which the C content of the sand fractions was high (continuous maize at Lamto and Yurimaguas), the main effect of the presence of earthworms was on the changes in the distribution of C among particle size fractions, with a greater decrease of the C contained in these fractions ($> 50 \mu\text{m}$ and especially $> 200 \mu\text{m}$). Moreover, the C content of the silt and clay fractions was greater in treatments with earthworms than without earthworms. In the yam plot, the carbon in the sand fractions was not abundant and did not decrease more with earthworms than without earthworms; however, a slight increase in the carbon content of the fraction $< 20 \mu\text{m}$ was observed. In the pasture plots of St Anne, the carbon content of all the fractions (except 2–20 μm) was slightly increased in inoculated treatments.

In annual cropping systems, carbon of the sand fractions ($> 50 \mu\text{m}$) seems to be ingested preferentially by earthworms and partly comminuted, the non-digested part being accumulated in fractions of finer ($< 20 \mu\text{m}$) size. Parmelee *et al.* (1990) showed in the field that lumbricids were responsible for the breakdown of coarse OM in temperate agrosystems.

These trends observed at the field level are consistent with laboratory studies: the proportion of organic matter associated with coarse fractions sharply decreased in casts of *M. anomala* while that of the finest fractions tended to increase (Martin, 1991). Endogeic earthworms are able to assimilate SOM from all the particle size fractions (Martin *et al.*, 1992), but the yield efficiency differs depending on the quality of the organic matter ingested. In fact, fresh plant materials are the most energetic resources for *M. anomala* and *P. corethrurus* (Zaidi, 1985; Spain, *et al.*, 1990; Martin and Lavelle, 1992) which prefer fresh rather than humified organic matter.

Fresh organic materials on the soil surface were not utilized efficiently by earthworms because only 10% of the measured carbon input was incorporated into the soil organic matter. However, in the Lamto experiment, the proportion of the carbon originating from the crop (roots + aerial parts) in the total soil carbon was slightly higher in inoculated treatments when the crop residues were left in the field (Table 6.3). The 20% increase of incorporated crop C to soil C at first suggests that earthworms forage for these materials and that the digestibility of crop residues is relatively low, or that plant debris enters the soil independently of earthworm foraging. It did not result from a higher carbon input in the soil in this plot. At Yurimaguas, simultaneous higher carbon input into the soil (higher root production), better incorporation and lower mineralization in inoculated treatments accounts for the 40%

increase in incorporation of fresh organic matter into SOM in the presence of earthworms.

The endogeic earthworms examined during these experiments (*M. anomala* and *P. corethrurus*) are not able to forage efficiently for surface litter. The incorporation of crop residues in the soil, whether indirectly by the effects of gravity and rainfall or through the activity of soil organisms, is of major importance for an efficient recycling of these resources by geophagous earthworms.

Carbon costs of earthworm activities

The activity of earthworms is highly dependent on the presence of a source of carbon. When earthworms are introduced into an agroecosystem, they rely upon soil carbon and subsequent organic inputs for their activities. When carbon resources are not sufficiently abundant, earthworm activity is reduced. This has been observed in the continuous maize cultivation at Lamto (Gilot, 1994). But what level of carbon input is necessary to maintain an earthworm population above a critical threshold of about 40 g fresh wt m⁻², beyond which plant growth may be significantly increased (see Chapter 6)?

The discrete steps of substrate ingestion, assimilation and productivity are presented in Fig. 6.8 allowing for a C budget to be calculated. The data used to estimate the different parameters have been measured by Lavelle (1977, 1978) for populations of *M. anomala* at Lamto. No budget was established for other tropical earthworm species; however, *M. anomala* is thought to be a low efficiency species.

Figure 6.9 estimates the amount of assimilable carbon needed to feed a certain biomass of earthworms. Earthworm fresh weights are converted to grams of carbon using the factor 0.032 (Lavelle, 1978). For a biomass of 40 g fresh wt m⁻² of earthworms (~1.28 g C), 58.9 g C m⁻² (i.e. 1300 kg dry matter ha⁻¹ year⁻¹ organic matter with 45% C) are used by the earthworm population. This represents, for example, 4% of the soil carbon in the Lamto maize experiment after 3 years of cropping (or ~20% of the coarse fractions: > 200 μm). In the Lamto continuous maize experiment and in the Yurimaguas crop rotation plot, the mulch left on the soil surface plus the root biomass represented 55–340 g C m⁻² and 113–320 g C m⁻², respectively, depending on the cropping period. This quantity of carbon added to the

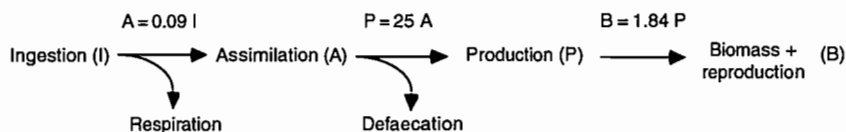


Fig. 6.8. Energy budget of an earthworm population [calculated for *Millsonia anomala* at Lamto (Ivory Coast). Lavelle, 1978].

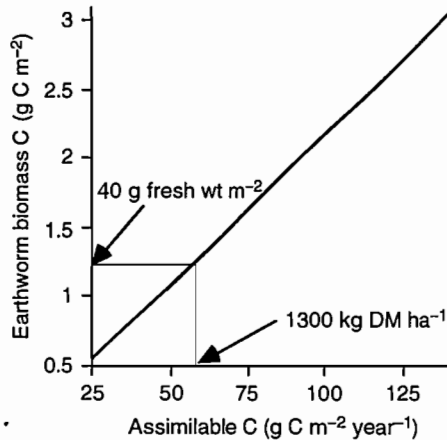


Fig. 6.9. Relationship between the biomass of an earthworm population of *Millsonia anomala* and the assimilable carbon needed for its nutrition.

agroecosystem was sufficient to feed the earthworms when it was incorporated into the soil.

However, carbon sources other than crop residues must be considered. The effect of different organic materials (sawdust, coffee pulp, etc.) on earthworm activities has been tested (Senapati *et al.*, Chapter 7). They found that organic materials with very high C/N ratio and high lignin content could be consumed by geophagous earthworms resulting in sustained population size. These materials, usually considered as waste, may be used in agroecosystems to feed the earthworms which will digest these resources, using some of the carbon for their production, and incorporate the main part of this carbon and its nutrients into the SOM.

Conclusions

The inoculation of earthworms in degraded soils at St Anne accelerated the process of restoration of soil organic matter stocks by a pasture. In annual cropping systems, planted in cleared natural forest soil, earthworms did not efficiently prevent SOM stocks from being depleted during cultivation. It is hypothesized that the initial macro-aggregate soil structure (forest soil with high biological activity) was conserved during the course of the experiment and no positive effects of the earthworm activity due to changes in aggregation could be observed.

Moreover, annual cropping systems were not favourable for the establishment of earthworm populations. Management of earthworms may only be possible when sufficient carbon (quantity and quality) is available to feed them. This is the case, for example, when grass is cultivated, since pastures

have a high root production during a large part of the year, and a significant part of above-ground production is returned to the soil as dung. However, annual cropping systems may also be appropriate when crop residues are left in the agroecosystem and incorporated into the soil (mechanically or by other soil organisms). When fresh or little decomposed organic matter is present in the soil, earthworms feed preferentially on this resource and accelerate its decomposition. As they ingest these residues, nutrients are released and made available to the plants (Gilot-Villeneuve *et al.*, 1996).

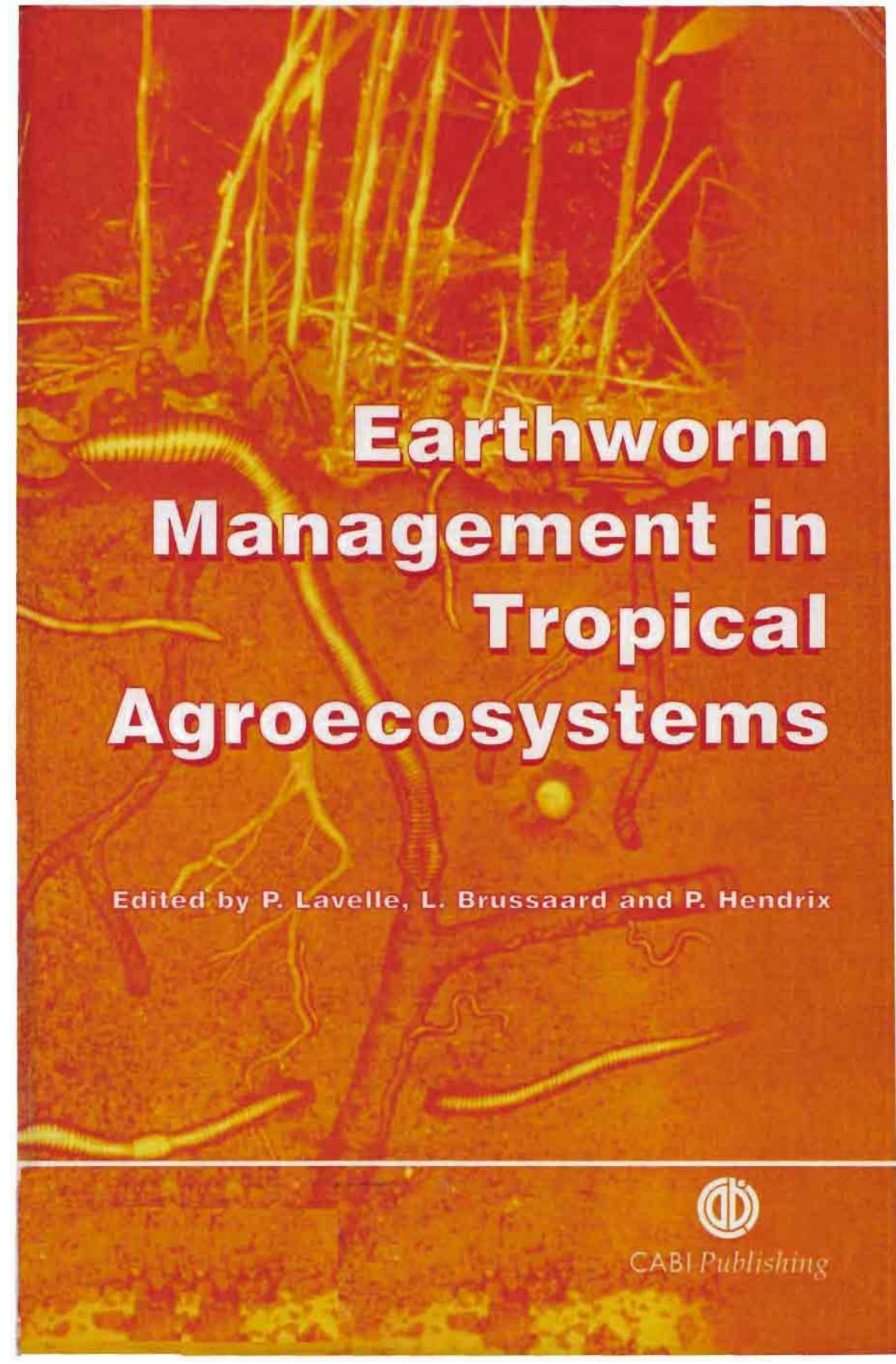
Efficient earthworm activity in low external input cropping systems of annual plants may only be obtained with simultaneous management of crop residues or other carbon sources. However, the use of earthworms seems more promising for the restoration of degraded soil: the inoculation by earthworms of short grass fallow (3–4 years) may allow a more rapid reconstitution of the SOM stock and ameliorate the soil structure thanks to a high earthworm activity due to the huge carbon input to the soil via the roots.

References

- Aina, P.O. (1984) Contribution of earthworms to porosity and water infiltration in a tropical soil under forest and long-term cultivation. *Pedobiology* 26, 131–136.
- Albrecht, A., Rangon, L. and Barret, P. (1992) Effet de la matière organique sur la stabilité structurale et la détachabilité d'un vertisol et d'un ferrisol (Martinique). *Cahier IRD, série Pédologie* 27, 121–133.
- Aweto, A.O., Obe, O. and Ayanniyi, O.O. (1992) Effects of shifting and continuous cultivation of cassava (*Manihot esculenta*) intercropped with maize (*Zea mays*) on a forest alfisol in south-western Nigeria. *Journal of Agricultural Science, Cambridge* 118, 195–198.
- Balesdent, J., Mariotti, A. and Guillet, B. (1987) Natural ^{13}C abundance as a tracer for soil organic matter dynamics studies. *Soil Biology and Biochemistry* 19, 25–30.
- Blanchart, E., Lavelle, P. and Spain, A. (1990) Effects of biomass and size of *Millsonia anomala* (Oligochaeta: Acanthodrilidae) on particle aggregation in a tropical soil in the presence of *Panicum maximum*. *Biology and Fertility of Soils* 10, 113–120.
- Blanchart, E., Lavelle, P., Braudeau, E., Le Buissonais, Y. and Valentin, C. (1997) Regulation of the soil structure by geophageous earthworm activities in humid savannah of Côte d'Ivoire. *Soil Biology and Biochemistry* 29, 431–439.
- Bouché, M.B. (1977) Stratégies lombriciennes. *Ecology Bulletin (Stockholm)* 25, 122–132.
- Cambardella, C.A. and Elliott, T.E. (1993) Methods for physical separation and characterization of soil organic matter fractions. *Geoderma* 56, 449–457.
- Charpentier, F. (1996) Effets de l'inoculation d'un Ver de Terre Endogé sur la Dynamique de la Matière Organique d'un Sol Ferrallitique Cultivé de l'Amazonie Péruvienne. Thèse de Doctorat, Mémoires des Sciences de la Terre, Université de Paris VI.
- Dabin, B. (1967) Application des dosages automatiques à l'analyse des sols. 3ème partie. *Cahier IRD, Série Pédologie* 5, 257–286.

- Feller, C. (1994) La Matière Organique Dans les Sols Tropicaux à Argiles 1:1. Recherche de Compartiments Organiques Fonctionnels. Une Approche Granulométrique. Thèse de Docteurs Sciences, Université Strasbourg. 393p + annexes 236 p.
- Feller, C. and Milleville, P. (1977) Evolution des sols de défriche récente dans la région des Terres neuves (Sénégal oriental). I. Présentation de l'étude et évolution des principales caractéristiques morphologiques et physico-chimiques. *Cahier IRD, Série Biologie* 12, 199–211.
- Gavinelli, E., Feller, C., Larré-Larrouy, M.C., Bacye, B., Djegui, N. and de D. Nzila, J. (1995) A routine method to study soil organic matter by particule-size fractionation: examples for tropical soils. *Communications in Soil Sciences and Plant Analysis* 26, 1749–1760.
- Gilot, C. (1994) Effets de l'Introduction du Vers Géophage Tropical *Millsonia anomala* Omodeo en Systèmes Cultivés sur les Caractéristiques des Sols et la Productivité Végétale en Moyenne Côte d'Ivoire. Thèse de Doctorat, Institut National Agronomique de Paris-Grignon.
- Gilot, C. (1997) Effects of a tropical geophageous earthworm, *M. anomala* (Megascolecidae), on soil characteristics and production of a yam crop in Ivory Coast. *Soil Biology and Biochemistry* 29, 353–359.
- Gilot, C., Mariotti, A., Charpentier, F., Lavelle, P. and Feller, C. (1995) Variations des Stocks de Carbone d'un Sol Ferrugineux Tropical (Lamto, Côte d'Ivoire) avec la Mise en Culture et en Pâturage. Rôle des Vers de Terre. Etude avec ¹³C. Programme SOFT, Subvention DRAEI/93078.
- Gilot-Villenave, C., Lavelle, P. and Ganry, F. (1996) Effects of a tropical geophageous earthworm, *Millsonia anomala*, on some soil characteristics, on maize residue evolution and on maize production in Ivory Coast. *Applied Soil Ecology* 4, 201–211.
- Hetier, J., Guiraud, G., Moutonnet, P., Bossy, A., Marol, C., Chone, T., Schouller, E., Fardeau, J.-C. and Andreux, F. (1980) Culture de maïs en milieu contrôlé: analyse des bilans d'azote et de carbone par ¹⁵N et ¹⁴C. *Science du Sol—Bulletin de l'A.F.E.S.* 2, 127–140.
- Lavelle, P. (1977) Bilan énergétique des populations naturelles du ver de terre géophage *Millsonia anomala* (Oligochète, Acanthodrilidae) dans la savane de Lamto (Côte d'Ivoire). *Géo-Eco-Trop* 2, 149–157.
- Lavelle, P. (1978) Les vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème. VI. *Publication Laboratoire Zoologie E.N.S.*, Paris, Vol.12.
- Lavelle, P. (1981) Stratégies de reproduction chez les vers de terre. *Acta Ecologica* 2, 117–133.
- Lavelle, P. and Pashanasi, B. (1989) Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiology* 33, 283–291.
- Lavelle, P., Melendez, G., Pashanasi, B. and Schaefer, R. (1992) Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex corethurus* (glossoscolecidae). *Biology and Fertility of Soils* 14, 49–53.
- Lee, K.E. (1985) *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press, New York.
- Lee, K.E. and Ladd, J.N. (1984) Some recent advances in soil biology and biochemistry. *Australian Society of Soil Science—National Soils Conference*, Brisbane.

- Lierman, C. (1996) Simulation de l'Effet de Vers de Terre Tropicaux sur la Dynamique de la Matière Organique et la Production Végétale. Diplôme d'Etudes Approfondies, Universités de Paris XI, VI et Institut National Agronomique de Paris-Grignon.
- Mariotti, C. (1991) Le carbone 13 en abondance naturelle, traceur de la dynamique de la matière organique des sols et de l'évolution des aléoenvironnements continentaux. *Cahiers de l'IRD, Serie Pédologie* 299–314.
- Martin, A. (1991) Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biology and Fertility of Soils* 11, 234–238.
- Martin, A. and Lavelle, P. (1992) Effect of soil organic matter quality on its assimilation by *Millsonia Anomala*, a tropical geophagous earthworm. *Soil Biology and Biochemistry* 24, 1535–1538.
- Martin, A., Mariotti, A., Balesdent, J. and Lavelle, P. (1992) Estimates of soil organic matter assimilation of a geophageous tropical earthworm based on ¹³C natural abundance. *Ecology* 73, 118–128.
- Merckx, R., van Ginkel, J.H., Sinnaeve, J. and Cremers, A. (1986) Plant-induced changes in the rhizosphere of maize and wheat. *Plant and Soil* 96, 85–93.
- Parkin, T.B. and Berry, E.C. (1994) Nitrogen transformation associated with earthworm casts. *Soil Biology and Biochemistry* 26, 1233–1238.
- Parmelee, R.W., Beare, M.H., Cheng, W., Hendrix, P.F., Rider, S.J., Crossley, D.A. and Coleman, D.C. (1990) Earthworms and enchytraeids in conventional and no-tillage agroecosystems: a biocide approach to assess their role in organic matter breakdown. *Biology and Fertility of Soils* 10, 1–10.
- Parton, W.J., Schimel, D.S., Cole, C.V. and Ojima, D.S. (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of American Journal* 51, 1173–1179.
- Pashanasi, B., Lavelle, P., Alegre, J. and Charpentier, F. (1997) Effect of inoculation with the endogeic earthworm *Pontoscolex corethrus* on soil chemical characteristics and plant growth in a low-input agricultural system of Peruvian Amazonia. *Soil Biology and Biochemistry* (in press).
- Siband P (1972) Etude de l'évolution des sols sous culture traditionnelle en Haute-Casamance. Principaux résultats. *L'Agronomie Tropicale* 27, 574–591.
- Spain, A.V., Safigna, P.G. and Wood, A.W. (1990) Tissue carbon sources for *Pontoscolex corethrus* (Oligochaeta, Glossoscolecidae) in a sugarcane ecosystem. *Soil Biology and Biochemistry* 22, 703–706.
- Syers, J.K., Springett, J.A. and Sharpley, A.N. (1979) The role of earthworms in the cycling of phosphorus in pasture ecosystems. In: Crosby, T.K. and Pottinger, R.P. (eds) *Second Australian Conference on Grassland Invertebrate Ecology*. Wellington, New Zealand.
- Tsakala, R. (1994) Evolution Spatio-temporelle de la Minéralisation du Carbone et de l'Azote Dans les sols de Deux Parcelles à Lamto (Côte d'Ivoire). Mémoire DESS, Université Paris XII.
- Zaidi, Z. (1985) Recherches sur les Modalités de l'Interdépendance Nutritionnelle entre Vers de Terre et Microflore Dans la Savane Guinéenne de Lamto (Côte d'Ivoire); Esquisse d'un Système Interactif. Thèse 3ème cycle, Paris XI.



Earthworm Management in Tropical Agroecosystems

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



CABI Publishing

CABI Publishing is a division of CAB International

CABI Publishing
CAB International
Wallingford
Oxon OX10 8DE
UK

CABI Publishing
10E 40th Street
Suite 3203
New York, NY 10016
USA

Tel: +44 (0)1491 832111
Fax: +44 (0)1491 833508
Email: cabi@cabi.org

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

© 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. I.

Lavelle, P. (Patrick) II. Brussaard, L. (Lijbert) III. Hendrix, Paul F.

SF597.E3E27 1999

639'.75--dc21

99-12081

CIP

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